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GROUPING AMBIGUOUS NEURAL REPRESENTATIONS: STIMULUS VS. PERCEPT-LEVEL CUES

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ABSTRACT

To create a coherent view of any scene, the visual system must determine how inputs from the scene relate to one another and link them together to ultimately produce percepts of coherent objects separate from other objects and the background. This dissertation aimed to determine how the visual system links spatially separate and neurally ambiguous regions of the visual field. To this end, experiments here used multiple stimuli that create neural ambiguity presented in spatially separated locations within the visual field. Observers reported when the multiple stimuli resulted in "grouped" percepts. Grouped percepts occurred when all of the multiple ambiguous stimuli in view appeared the same or similar in certain features above chance levels. The experiments here made use of multiple methods to create neural ambiguity and used color perception as a model system to measure grouping under different conditions. This allowed testing of different neural theories about how the visual system segments the world. The overarching hypothesis here was that a grouping process acts on low-level representations of visual input and the competition between these low-level representations determines if two or more regions are grouped. Experiment 1 examined whether grouping is driven by competition between percept-level representations (i.e., representations of the possible percepts, regardless of what neural processes gave rise to these representations) or if grouping is limited by different neural levels of competition in the multiple locations. Experiment 2 measured grouping of a novel percept, the superposition of two orthogonal gratings creating a plaid, in order to determine if grouping can act on neural representations of binocularly-integrated components. Experiments 3a and 3b eliminated the possibility that an inhibition of interocular suppression drives the perception of plaids. Experiment 4 used specific physical chromaticities within chromatic surrounds to determine if grouping is driven by a shared color percept or a shared physical chromaticity. Experiment 5 followed up the results from Exp. 4 and tested if grouping persists when there is no shared chromatic information and if grouping can be driven by one chromatic signal (L/(L+M), for

instance) in the presence of a conflicting chromatic signal (S/(L+M), for instance). Experiment 6 tested if both of the two competing neural representations must match exactly, or if grouping can be driven by a single shared competitive neural representation paired with unshared neural representations.

CHAPTER 1

INTRODUCTION

How does the visual system create a coherent interpretation of the world such that components that belong together are seen as single objects separate from components that belong to other objects and the background? This is the central question that the experiments in this dissertation aimed to answer. The processes leading to conscious visual perception take place without notice, thus producing coherent percepts without the observer's awareness of the inherent ambiguities present. These inherent ambiguities arise, in part, from the translation of the three-dimensional world onto the two-dimensional retina, information consolidation, and separate representations of different features of the same object (Barlow, 1981; Barlow, 1986). Also implicit in visual perception is the many neural representations that build up our perception of the physical world. The information represented neurally must combine in precise ways in order to produce a percept that allows for appropriate action. This may mean color information combining with form information to create a percept of a colored object (all features intrinsically linked together; Treisman, 1985; Van Essen, Anderson, & Felleman, 1992), but also may mean linking neural representations across the visual field such that the visual system perceives a continuous region in space as one coherent object rather than a collection of discrete segments (Barlow, 1986; Kovacs et al., 1996; Ngo et al., 2000). Grouping is the term given here for this process of creating coherent percepts. Identifying the cues that lead to grouping is fundamental to understanding how humans perceive the visual world.

1.1 Ambiguity in visual scenes and grouping

The visual system has limitations driven by information consolidation, specific sensitivities of neurons, the three-dimensional world being translated onto the two-dimensional retina,

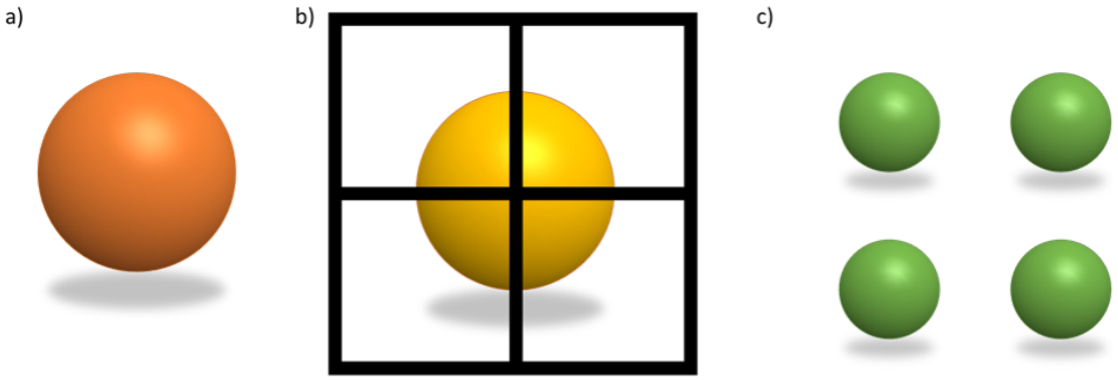

Figure 1.1: a) An orange ball appearing all orange, b) a yellow ball appearing all yellow, and c) four green balls all appearing green.

and more (Barlow, 1981). Due to these limitations, all visual scenes induce neural ambiguity and the processes involved in resolving this ambiguity typically complete their task before conscious perception, meaning that observers usually do not perceive the world as ambiguous. Instead, they experience a coherent view of the scene that can manifest in several ways. One type of coherence is all features of a single object appearing the same – one ball appearing orange across its entire surface, for instance (Fig. 1.1b; see Ngo et al., 2000 as an experimental example). Another is all fragments of a single object appearing the same – one partially occluded ball appearing yellow, for instance (Fig. 1.1a). This type of coherence is difficult to disentangle experimentally from grouping together all fragments of similar, but not single, objects such that they all appear identical – multiple similar fragments not from the same object all appearing green, for instance (Fig. 1.1c; see Kovacs et al., 1996 as an experimental example). These types of coherence are all measured in the laboratory as "grouping" – a process that may include one or more mechanisms. Grouping must be at work in tandem with other processes, such as those that differentiate objects from their backgrounds (like edge detection; Marr & Hildreth, 1980) or those that use spectral information to give evidence as to the illuminant (Lee, 1986; Lee & Smithson, 2016), to name a few. The neural processes for resolving ambiguity that are associated with grouping are the primary focus of this dissertation.

Grouping objects has long been studied by Gestalt psychologists who describe objects with one or more features in common as being "perceptually grouped" (Wertheimer, 1923/1938). For instance, two red objects will be considered one group and two green objects as a separate group. This process is distinct from, but analogous to, grouping ambiguous neural representations. Ambiguous neural representations can be created in the lab by presenting dichoptic stimuli (Levelt, 1965; Wheatstone, 1838). Dichoptic stimuli are two different stimuli shown to corresponding retinotopic locations. This creates neural ambiguity because two or more neural representations are encoding different information for the same area – a physical impossibility (Rubin, 2003). These dichoptic stimuli can differ in any visual feature. When two or more objects have ambiguous features that are in common, they can be grouped such that their resolution occurs non-independently, leading to a shared appearance between the objects (Kovács et al., 1996; Papathomas, Kovács, & Conway, 2005; Slezak & Shevell, 2018; Slezak, Coia, & Shevell, 2019).

Grouping from ambiguous representations has been shown in the chromatic domain with multiple discs of ambiguous colors that could appear either red or green; all discs appeared as red together or as green together more often than chance (Kovács, Papathomas, Yang,& Fehér, 1996; Fig. 1.2a). In the pattern domain, a single disc containing two rivalrous half fields will appear as the same pattern (concentric rings vs. horizontal lines) more often than chance. This occurs despite the Gestalt principle of good-continuation not favoring the complete pattern percepts over the half-image percepts (Ngo, Miller, Liu, & Pettigrew, 2000; Fig. 1.2b). These distinct examples of grouping ambiguous neural representations introduce key questions that have yet to be answered.

The kinds of neural representations that grouping can act on is an area of ongoing study. Answering this question can help elucidate the larger question of what exactly the process is accomplishing for perception. When measuring grouping in ambiguity, is that measuring the ability of the visual system to link together fragments of single objects? This is the way

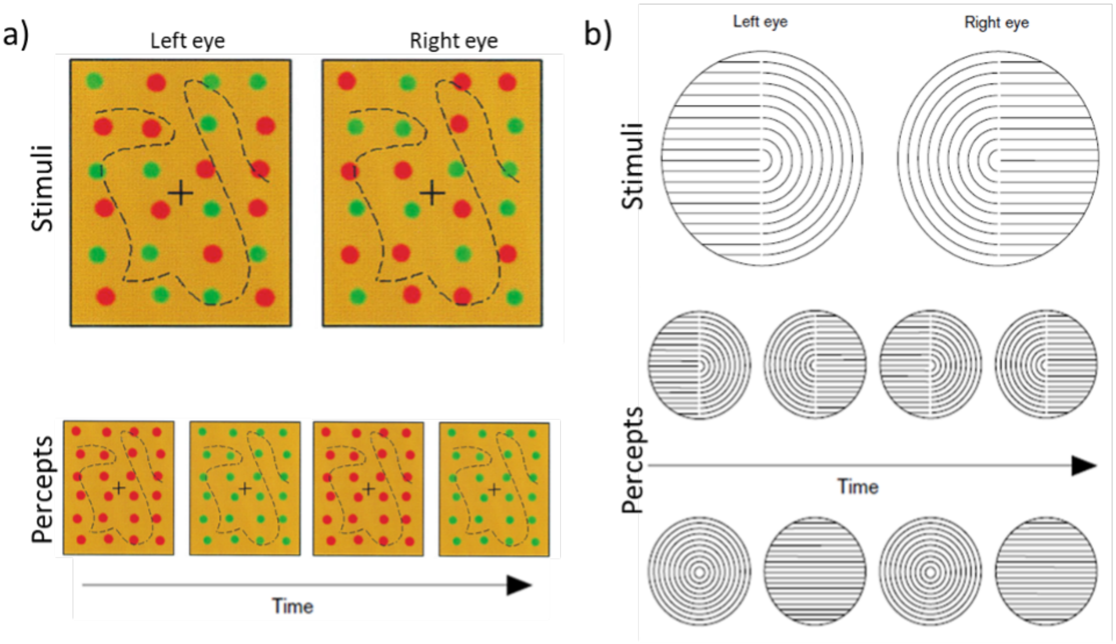

Figure 1.2: Dichoptic images appearing grouped by common color or form. a) adapted from Kovacs et al., 1996, the chromatically rivalrous stimuli (top) sometimes appear grouped by color (bottom). b) adapted from Ngo et al., 2000, the rivalrous patterns (top) often appear as coherent images (bottom) rather than half-fields(middle).

that Kovács and colleagues illustrated "interocular grouping" with the monkey face and the jungle scene – spatially separate components of each coherent image could be re-assembled and perceived as the two separate complete wholes (Kovács et al., 1996). Or is it linking together fragments from separate but similar objects? Evidence shows that two separate but identical objects are perceived over visual noise more often than two separate, non-identical objects (Alais & Blake, 1999). Or is it much lower-level than that – for instance, fragments linked together just by the fact that there are several ambiguous stimulus features in common? Research has shown that features such as orientation, color, spatial frequency, and motion can all contribute to grouping (Papathomas, Kovács, & Conway, 2005). Is grouping percept-driven, or stimulus-driven? It could be that "grouping" as studied in vision today is an amalgamation of multiple processes, each completing a separate task of those listed above, and more. These possibilities are addressed in this dissertation by carefully controlling ambiguity using specific stimuli.

1.2 Perceptual Multistability its Neural Concomitants

1.2.1 Bistability

Visual input with associated neural ambiguity can lead to percepts that alternate between multiple valid interpretations. Classic examples such as the Necker Cube (Necker, 1832) and Rubin's Vase (Rubin, 1921) lead to bistable percepts, during which observers have percepts that alternate between two possibilities (i.e., two faces or one vase, or a front-up cube or front-down cube; Fig. 1.3). These examples, along with other common ambiguous figures, are specifically created to induce bistable percepts from single images that do not require special viewing devices, such as those discussed below. In this regard, these images are easy examples to use to show perceptual bistability, a phenomenon not often experienced or noticed in everyday vision. These images do not, however, allow for careful manipulation of the visual input such that mechanisms by which ambiguity is resolved can be studied. This requires methods presenting incompatible stimuli to the two eyes separately (dichoptic images). Dichoptic images are used in both standard binocular rivalry (SBR), which presents two dissimilar stimuli steadily to the two eyes in matched retinal locations (Levelt, 1965; Wheatstone, 1838), and interocular-switch rivalry (ISR), which also presents two dissimilar stimuli to the two eyes in matched retinal locations and then swaps them between the eyes at 1.5-6 Hz (Logothetis, Leopold, & Sheinberg, 1996; Christiansen, D'Antona, & Shevell, 2017). With these two methods, incompatible stimuli can be carefully controlled in all visual features, such as chromaticity, spatial frequency, and temporal frequency. This allows specific neural hypotheses regarding the process of ambiguity resolution to be tested.

One such neural theory is that ambiguity is resolved through a process that involves binocularly-driven neurons tuned to specific stimulus properties in the dichoptic images

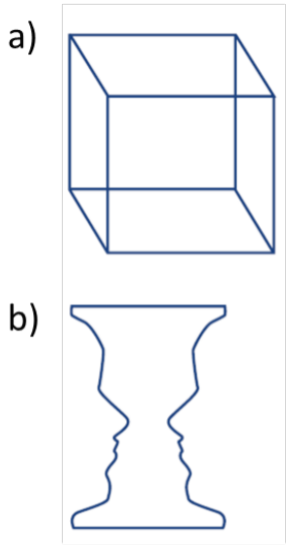

Figure 1.3: Image adapted from Blake & Logothetis, 2002. a) Necker cube that can be seen as front up or front down. b) Rubin's vase that can be seen as one central vase or two faces in profile looking towards the center of the image.

(Kovács et al, 1996; Logothetis, Leopold, & Sheinberg, 1996; Ngo et al., 2000; Slezak & Shevell, 2018). This theory, called "stimulus-rivalry" in the literature, relies on the fact that binocularly-driven neurons will respond to their preferred stimulus irrespective of which eye the stimulus is shown to. Therefore, there is a constant binocularly-driven representation of each stimulus. For instance, if during dichoptic viewing an observer receives a leftward tilted grating to the left eye and a rightward tilted grating to the right eye, a binocularly-driven neuron tuned to the leftward orientation will fire at the same rate if the stimuli to the two eyes are exchanged (the leftward grating in the right eye and the rightward grating in the left). In this example, if the observer were to perceive a leftward tilted grating, then it could be inferred that the binocularly-driven neurons tuned to the leftward orientation are dominant over those tuned to the rightward orientation. Over time, usually a matter of seconds, dominance can shift from one of the active neural representations to the other as the neural populations become adapted and responses fluctuate. This shift in dominance leads also to a shift in perceptual experience from the originally dominant orientation to the previously suppressed orientation (Wilson, 2003; Tong, Meng, & Blake, 2006; Wilson, 2007).

Perceptual alternation will continue as the binocularly-driven neural representations from the dichoptic stimuli compete for dominance.

Conversely, some researchers propose the resolution of ambiguity to be monocularly-mediated (Lee & Blake, 1999; Blake, 2001; Brascamp, Sohn, Lee & Blake, 2013). Responses in monocularly-driven neurons are entirely dependent on the eye to which the stimulus is shown. Monocularly-driven neurons will be active only when their preferred stimulus is shown to the then-dominant eye. A monocularly-driven neuron will always have stimulus properties the neuron is tuned to (for instance, a leftward orientated grating) and an eye that it is tuned to (for instance, the left eye). A specific population of monocularly-driven neurons will fire only if both requirements are met (i.e., a leftward oriented grating is shown to the left eye). In this "eye-rivalry" view, observers perceive alternating percepts due to competition between monocularly-driven neurons such that representations from the left eye compete with representations from the right eye, and observers perceive whatever is shown to the dominant eye. Again, dominance shifts over time so responses fluctuate, leading observers to experience perceptual alternation.

Both theories have evidence in support of them in the literature, but arguably stronger evidence exists for binocularly-mediated resolution of ambiguity. When dichoptic images are swapped between the eyes quickly, as in ISR, observers will still experience steady percepts that alternate slowly between the possibilities from the competing stimuli. Here, if resolution were monocularly mediated, observers would perceive quick alternations in time with the stimulus swaps. In the binocular case, however, there are constant binocularly-driven representations of the two stimuli no matter if the stimuli are steadily presented dichoptically or if they are swapped quickly between the two eyes. Therefore, slow alternations in percept during viewing both steady dichoptic images (SBR) and swapped dichoptic images (ISR) is expected for binocularly-mediated perceptual resolution (Logothetis, Leopold, & Sheinberg, 1996; Denison & Silver, 2012; Christiansen, D'Antona, & Shevell, 2017; Slezak & Shevell, 2018).

1.2.2 Multistability

The discussion above is fairly simplistic, limiting the perceptual outcome to only two possible percepts – one from one stimulus/eye and one from the other stimulus/eye. Rather than being limited to bistability, dichoptic images can often produce perceptual multistability (that is, more than two possible percepts). This multistability can manifest in several ways that can help disentangle different theories about the neural processes that resolve ambiguity. Two such ways are superimposition and feature-misbinding. As previously described, two orthogonal gratings can be displayed dichoptically. Along with the percepts of each individual grating (what would classically be considered the two possible "bistable" percepts) comes a percept of plaid (Liu, Tyler, & Schor, 1992; Burke, Alais, & Wenderoth, 1999). Plaid is the combination of both gratings and can be perceived in alternation with its individual component gratings. This can occur when the component gratings only have one feature in rivalry (orientation) or multiple features in rivalry (orientation and chromaticity, for instance; Slezak, Coia, & Shevell, 2019). Once multiple features are present in a single stimulus, this brings up a second manifestation of multistability: feature-misbinding. Feature-misbinding occurs when observers perceive a combination of features that was never present together in a single stimulus alone. For instance, if two gratings of different orientations and chromaticities were presented dichoptically (e.g., rightward tilted red grating and a leftward tilted green grating), then feature-misbinding could result in the percept of a green rightward tilted grating or a red leftward tilted grating (Hong & Shevell, 2006; Hong & Shevell, 2009). These feature-misbound percepts can alternate perceptually with the correctly-bound component gratings, as well.

Multistability becomes particularly important for learning about grouping mechanisms once there is more than one stimulus with an ambiguous neural representation. If there are

X number of ambiguous neural representations in a visual scene, then there are at least 2^X stable percepts possible since every ambiguous neural representation could be resolved in at least two distinct ways (at least two due to each X number of ambiguous neural representations also having the possibility of multistable percepts, as described in the paragraph above, or in other ways not described here). One important multistable percept is all ambiguous neural representations being resolved in the same way: all components look completely identical or identical in key features. Here, "grouping" is supported if this percept is experienced more often than chance. Chance can be defined simply mathematically by 0.5^X (where X is still the number of ambiguous neural representations), but there are assumptions associated with using p=0.5 (e.g., that there are only two equally likely possible percepts from each competing representation or that a stable percept will be perceived all the time). Chance can also be defined more precisely for each individual observer by showing them each component separately and then calculating the joint probability that they appear the same by chance.

Acknowledging that ambiguous neural representations can lead to multistability rather than just bistability allows more specific questions to be answered, especially those about grouping. Measuring bistable percepts only gives information about how neural representations that faithfully maintain the stimulus properties are perceived. To measure grouping, however, a minimum of two separate ambiguous fragments must be present. In the simplest case, assuming both fragments are only bistable themselves, that gives four total multistable percepts (2 stable local percepts x 2 locations = 4 stable global percepts). Further, multistable percepts like feature-misbound percepts and plaids (from superimposition) provide insight about integration of features, independent features, what kinds of neural representations rival with each other (perhaps after binocular-integration, for instance), and how these factors influence grouping.

Presenting two or more regions with neural ambiguity together allows for testing of theories about the neural representations that can be grouped. This, in turn, can illuminate what cues the visual system uses to link regions of the visual field together as parts of single objects or similar objects. On the experimental level, this can be accomplished by carefully manipulating [1] the kind of ambiguity in each region, [2] the visual features of each region, and [3] what visual cues exist to indicate they are a group irrespective of their ambiguity. By altering these key stimulus properties, neural theories can be experimentally tested. Each stimulus manipulation can contribute to grouping cues on their own, but there may also be interactions between different properties that help disentangle similar theories. These factors will be investigated in this dissertation.

1.3 Color

Color is a useful tool in that it is dissociable from the physical light that creates it. Chromaticity is an aspect of the physical light that hits the retina and that leads to the percept of color, but the relationship between the two is more complex than a one to one relation (i.e. one chromaticity always will be perceived as one color). Color is not a physical property of objects but instead is a perceptual experience that is different from person to person and can depend on the luminance, contrast and other context. For example, a wavelength of light in the middle of the visible spectrum can be perceived as an orange-yellow when on a black background and brown when on a white background (Buck & DeLawyer, 2014). Here, the physical light remains identical while the color perceived changes based on context (the background). Typically in experiments that use color as a tool rather than aim to understand its intricacies, color and chromaticity are confounded. For instance, when multiple chromatically ambiguous fragments in the visual field are presented together, they all appear the same color more often than chance (Kovács et al., 1996; Slezak & Shevell, 2018). Here, observers can perceive multiple fragments of the same colors due to the dichoptic chromaticities being identical in each different area in the visual field. It is unclear, however, if the *color perceived* or the *physical chromaticity* is what drives the grouping process as both have

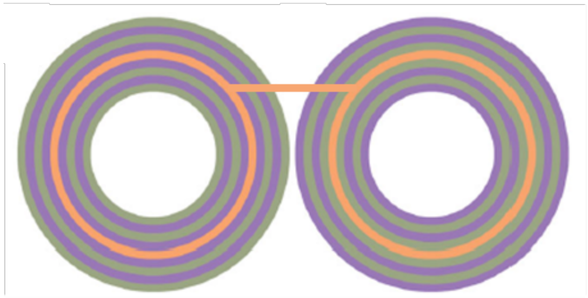

Figure 1.4: Adapted from Monnier & Shevell, 2003. “Red” rings appear pink or orange depending on their surround. Colored bar across top demonstrates the two rings are identical in chromaticity.

ambiguous neural representations and both are present in all fragments. This question of whether grouping acts on representations of physical chromaticity from the stimulus or on representations of the color perceived is addressed in this dissertation.

This introduces, broadly, the concept of dissociating the percept from the stimulus in order to determine what kinds of neural representations can be grouped, and thus illuminate how grouping is initiated in early or late visual processing. Again, typical experiments require participants to respond when they experience percepts that match the stimuli themselves. A few require participants to respond when they perceive very specific combinations of each stimulus alone, usually when the combinations are built from mutually exclusive fragments of each eye’s stimulus that combine to build one coherent percept (e.g. Kovács et al., 1996; Ngo et al., 2000; see Fig. 1.1). Here, expanding from these more limited percepts measured before, different methods will be used to create and measure percepts that do not match exactly what is physically presented. One method used for this purpose is chromatic induction.

Chromatic induction has been defined as color appearance shifts due to simultaneous contrast or chromatic assimilation (Monnier, 2008). This can occur with solid backgrounds, such as described above in the yellow/brown example. Chromatic induction happens most strongly, however, with patterned surrounds of specific spatial frequencies due to S-cone opponent cells (Monnier & Shevell, 2003). Here, a test ring or region is surrounded by two other chromatic areas at the same moderate spatial frequency. The chromatic surround differs only in S-cone activation and causes the test region to appear to shift in color both towards the most directly adjacent chromaticity and away from the more distant chromaticity. For example, a test ring appears "pink" when directly surrounded by purple rings and distantly surrounded by lime rings but appears "orange" when directly surrounded by lime rings and distantly surrounded by purple rings (Fig. 1.4). This induction allows the observer to experience identical retinal input (the test ring) that can appears as different color percepts (the "pink" and "orange" percepts). Induction can also be used in the opposite way: two different chromaticities of test ring can be presented with induction so they produce the same color percept.

1.4 Specific Aims

This dissertation explores the relation between visual input and the percept experienced from neural representations of that input. Two fragments with dichoptic conflicting visual information will be presented together in order to determine what kinds of neural representations can be linked together for their joint resolution. Percepts measured will reflect those associated by their physical stimulus properties as well as conjunctions that lend evidence for specific theories about what neural representations can be grouped. Specifically, stimuli will be presented using interocular-switch rivalry (ISR), a method that uses dichoptic stimuli that are swapped between the eyes at 3.75 Hz. There is evidence that ISR minimizes or eliminates influences from monocularly-driven representations (Kovács et al., 1996; Slezak & Shevell, 2018), meaning that ambiguity resolution is binocularly-driven. Some experiments here also make use of standard binocular rivalry (SBR), a method that presents dichoptic stimuli steadily to the eyes. Here, SBR is used in conjunction with stimuli presented in ISR to determine if low-level monocularly represented differences influence grouping that could be initiated by higher-level binocular representations.

Grouping is a process that involves linking together the resolution of ambiguous neural representations for the purpose of perceiving a coherent view of the whole visual scene. In this vein, it makes sense that there can be several kinds of neural representations that grouping can act on depending on the context. Cues exist in visual information to indicate that components in a scene should appear the same as one another. One such cue is chromaticity. Take for instance two sets of conflicting chromatic signals, of both red and green. Here, grouping would resolve both to be red together or both to be green. If the chromatic signals were conflicting in additional ways, however, then perhaps they should not be resolved identically because there is a cue that their resolution should not be linked. For instance, if one fragment was ambiguously red/green but another was ambiguously red/blue, then their ambiguity may not be resolved identically to both red because they are not ambiguous in the same way. Alternatively, the fact that one of the competing representations does match between the two areas may be enough to overcome this inconsistent grouping cue.

Beyond the complexities surrounding how fragments are ambiguous, all fragments across the visual field produce many different neural representations, such as eye-specific monocular representations, binocular representations, individual feature representations, feature conjunction representations, and so on. When a fragment has neural ambiguity, that means that there are multiples of the same kind of representations, just representing different possible characteristics of the fragment. For instance, a fragment that is 'red' in the left eye and 'green' in the right eye will have [1] competing monocular representations of red/left eye and of green/right eye and [2] competing binocular representations of red and of green. If the fragments were instead a red/gray grating at 45° and a green/grey grating at 135°, then the additional features (orientation and spatial frequency) would increase the number of the other kinds of representations from the fragments. Further, these describe representations that are explicitly from only one stimulus and follow from what is displayed physically to the observer, yet representations that combine input from the two distinct stimuli are active as well (as evidenced by Treisman, 1962; Wu, Kanai, & Shimojo, 2004; Hong & Shevell, 2006; Hong & Shevell, 2009; Wang & Shevell, 2014; Shevell & Wang, 2016). For instance, in the example above involving orthogonal gratings, there could be also active representations of [1] plaids created from both gratings or [2] misbound joint representations of ‘red’ and 135° and of ‘green’ and 45° (if the ambiguity is resolved for each individual feature separately before binding).

Grouping could be acting on low-level neural representations, more faithfully representing the stimuli than percepts. This includes representations that are monocularly-driven so representations inextricably linked to the eye in which the input originated. It also includes binocularly-driven representations, such as those representing chromaticity rather than representations of color that exist after integration of signals across S-cone opponent cells (Monnier & Shevell, 2003). This also encompasses representations of individual gratings, as well as the representations of their superposition (though these representations of plaids must be at a level higher than the component gratings that build them up). Grouping could alternatively be acting on those neural representations that reflect the percepts associated with these low-level representations. This includes representations of perceived color, separable from physical chromaticity. It also includes representations of whole objects rather than their low-level disjointed fragments. This distinction between physical stimuli and the percepts obtained from them is a central subject of this dissertation. Separating these two intertwined characteristics can inform about the nature of the human visual system’s grouping mechanisms.

CHAPTER 2

GENERAL METHODS

2.1 Apparatus

All experiments were conducted using a haploscope positioned in front of a cathode ray tube (CRT) monitor to display the stimuli. The haploscope (Fig. 2.1) was composed of eight mirrors spatially arranged such that, when it is positioned in front of a monitor, an observer can view different stimuli shown to the same retinal location of the two eyes. This works by having the left half of the screen only being displayed to the left eye and the right half of the screen only displayed to the right eye. Six of the eight mirrors are stationary and always remain in the same position. The last two mirrors are connected to each other and mounted on a saddle so that it is movable towards and away from the observer on a track. It is important for the last set of mirrors to be movable to allow observers to account for their individual interpupillary distance and thus allow them to achieve proper binocular fusion. In order to aid in fusion, a line-drawn square or rectangle (depending on the stimuli) surround

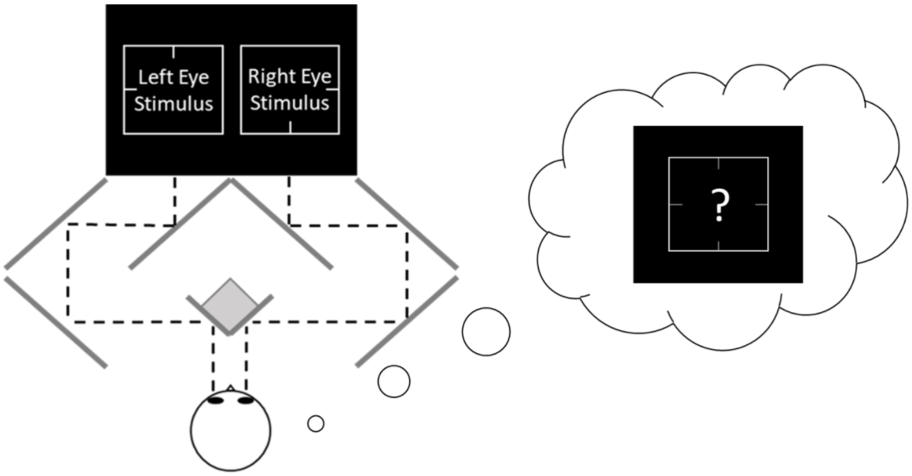

Figure 2.1: The haploscope. The mirrors are represented by the diagonal solid grey lines, and the light path by the dashed black lines. The thought bubble shows the fused percept the observer experiences from viewing the CRT through the haploscope, represented by the black rectangle.

each eye's stimulus. Tick marks known as Nonius lines are positioned at 12 o'clock, 3 o'clock, 6 o'clock, and 9 o'clock on the square or rectangle. The left eye's stimulus has the top and left Nonius lines while the right eye's stimulus has the bottom and right Nonius lines. Perfect fusion is achieved when the Nonius lines appear to align perfectly horizontally and vertically.

2.2 Stimuli

All experiments include stimuli presented dichoptically using the Haploscope, meaning that different stimuli were presented to the left eye and to the right eye at any given moment. These different stimuli were always chromatic, meaning that they produced percepts that had color. The chromaticities used here are defined in MacLeod-Boynton color space defined by relative L, M, and S cone excitation (MacLeod & Boynton, 1979). The equal energy spectrum white (EES white) point is normalized to a value of S/(L+M) of 1.0. The most commonly used chromaticities were [L/(L+M), S/(L+M)] of [0.72,0.3] called "red" and [0.61, 0.3] called "green". Stimuli often had achromatic regions, with chromaticities of [0.665,1.0]. In most cases, dichoptic stimuli were of different chromaticities but sometimes the difference across the two eyes' stimuli was something other than chromatic (orientation of a grating, for example). When ISR was used, all discs swapped at 3.75 Hz. All stimuli were also matched in luminance to each other (set individually for each observer based on heterochromatic flicker photometry, described in Procedure) and set to 5 cd/m^2 for most experiments. This helped ensure processing dominated by the parvocellular pathway and eliminated a need for embedded high-frequency on/off flicker, as needed for ISR with stimuli having luminance contrast (Logothetis, Leopold, & Sheinberg, 1996; Denison & Silver, 2012).

Stimuli from experiments in this dissertation have different configurations based on the specific questions being addressed by the experiment. Since grouping is the process of interest, multiple fragments must be present in the stimuli in order to determine if they are or are not grouped. Here, this is often displayed as a dichoptic stimulus above a fixation cross and another dichoptic stimulus below the fixation cross. These two dichoptic stimuli could be grouped to appear identical, or they could be resolved independently to appear unequal. In order to show grouping, the frequency of seeing both stimuli the same had to exceed the frequency if each ambiguous dichoptic stimulus was resolved independently. Thus, specific measurements of each region or fragment presented *alone* were made to estimate the chance frequency of seeing both stimuli as identical. These measurements were combined using probability modeling to predict how often the regions would appear identical or similar in some way by chance alone. For example, if the prediction is being calculated for how often two solid discs should appear red *together* by chance, the proportion of time the *top alone* is red is multiplied by the proportion of time the *bottom alone* is red. This gives a mathematical prediction for how often the two areas should appear red at the same time if they are resolved independently, based on actual measurements from each observer for each measured percept.

2.3 Procedure

Before participating in any experiments, observers participated in a heterochromatic flicker photometry (HFP) task (Ives, 1912). HFP measures equiluminance using a chromatically flickering disc. Observers report when the disc appears to have the least amount (or no) flicker, which is the point at which the two alternating chromaticities are equiluminant. All observers in each experiment completed this HFP task on three separate days in order to get an accurate and reliable measure. Their equiluminant values were then implemented in every condition to ensure all stimuli were equiluminant to each other.

For every experiment, observers came in on separate days to complete four trials of each condition. The first day was practice and is not reported here. The following three days were used to show all conditions in a randomized order. Instruction screens displayed images to show observers which percepts to report, and these screens were displayed between all runs to ensure observers were completing the required task correctly. Observers were instructed to press and hold buttons on a game pad to report when they perceived the stimuli shown in the instructions. This resulted in dependent-variable measurements of the proportion of time out of the total 60 seconds that the observer had a stable percept of interest, separately for each experimental condition. These measurements, as well as the predictions calculated for independence, were all arcsine transformed prior to analysis of variance in order to better approximate a normal distribution (Kirk, 2013).

Measured percepts were of all regions in view appearing the same in some way. Most often, they all appeared identical in color or form, though other measurements were also gathered depending on the condition. These measured "grouped" percepts are reported individually for each observer in every experiment. In some cases, measurements of percepts where multiple regions were not identical in some way were also taken for comparison to the "grouped" percepts. Also measured were percepts from individual regions in order to build independence probability predictions, as described above.

2.4 Observers

All observers used in the experiments were tested for normal color vision using the Neitz anomaloscope and the Ishihara plates. They were also tested for normal stereo vision using the Titmus Stereo Test. All observers were naïve to the purpose of the experiments except for observer ES, the author. All gave written and signed consent in accordance with the University of Chicago Institutional Review Board.

CHAPTER 3

EXPERIMENT 1:GROUPING DISRUPTED BY PROCESSING AT DIFFERENT LEVELS OF THE VISUAL SYSTEM?

3.1 Rationale

There are many cues present in visual information that neural processes may use to either group together components of a scene or keep as separate components of a scene. Cues exist at every stage of the visual hierarchy, yet once one cue leads to a grouped or ungrouped outcome, the cues at subsequent stages of the hierarchy may become irrelevant. What is left to determine is at what stage is a cue used? Early, such that the cue most faithfully represents the earliest stages of processing, or late, such that the cue represents what is perceptually experienced by the observer?

This experiment tests if resolution of ambiguity at different neural levels of representation eliminates the grouping effect found when neural resolution occurs at the same level (Slezak Shevell, 2018). The earliest neural representations are monocularly-driven. These represent not only the stimulus features, but also the eye to which the stimuli are displayed. Other early representations are binocularly-driven. These represent the stimulus features without any information about to which eye the stimuli were presented. In all dichoptic viewing, both monocularly and binocularly-driven representations can be active, as well as higher level representations that reflect what the observer perceives. The experiment here presents two sets of dichoptic stimuli with conflicting low-level representations but common higher-level representations. This addresses the question of whether the visual system groups things based on how they can appear (from identical stimulus chromaticities) or based on how the information is represented early in visual processing.

Previous research has demonstrated that presenting dichoptic stimuli in Standard Binocular Rivalry (SBR) leads to resolution of ambiguity at a monocular level while presenting dichoptic stimuli in Interocular-switch Rivalry (ISR) leads to resolution of ambiguity at a binocular level (Slezak Shevell, 2018). The present study presents two dichoptic sets of discs together, both chromatically rivalrous, though made such by two different methods. One set of discs rival such that the right eye is always presented a “red” disc while the left eye is always presented a “green” disc (as in SBR). The other set of discs rivals similarly, though swaps the discs at 3.75Hz (as in ISR). Here, cues the visual system may use to group or not group are both present. First, both sets of discs are ambiguous, both with competing neural representations. These competing neural representations, however, may not be at the same level. The neural ambiguity from SBR is thought to be resolved by monocularly-driven processes while the neural ambiguity from ISR is thought to be resolved by binocularly-driven processes. Finally, both discs have competing representations of the same chromaticities: both [L/(L+M), S/(L+M)] of [0.72, 0.3] and of [0.61, 0.3]. Both discs produce higher-level neural representations for the same chromaticities or perhaps the same two color percepts: red and green. Thus, both discs could appear the same color more often than chance if the visual system uses the cues of ambiguous neural representations and matched perceptual outcomes. Alternatively, both discs could appear the same color at chance levels if the visual system uses the cue that the competing neural representations are not identical (monocular vs binocular). The present experiment tests the hypothesis that grouping acts on identical competing neural representations, and the higher-level cue of a shared color percept has no significant effect on this resolution at this lower-level.

To get baseline grouping measurements (and to replicate findings in Kovács, et al., 1996 and Slezak & Shevell, 2018), three single-method conditions were tested: both discs in chromatic ISR (CISR), both discs in conventional SBR, and both discs in patchwork SBR. Conventional SBR refers to the presentation of stimuli of the same color to the same eye for the duration of the trial (for example, both discs “red” in the left eye and both discs “green” in the right eye). Patchwork SBR refers to the presentation of stimuli in opposite colors in the same eye for the duration of the trial (for example, top "red" and bottom "green" to the left eye and top "green" and bottom "red" to the right eye). These conditions are expected to group based on the literature (Kovács, et al., 1996; Slezak & Shevell, 2018), though conventional SBR may lead to higher proportions of the time both discs are perceived to be the same color than patchwork SBR due to the added eye-of-origin grouping effect that can occur when using SBR (monocularly-driven "grouping"; Stuit, Paffen, van der Smagt, & Verstraten, 2011). Though this difference may exist, grouping is still expected for all three single-method conditions.

The important condition is the mixed-method condition in which a disc in CISR is presented with a disc in SBR. Here, grouping could occur if the visual system uses common higher-level representations of chromaticity or color to group regions. Though neural competition may be different between the two discs, they both have binocular-level representations of the two chromaticities and colors. The working hypothesis is, however, that grouping will not occur here due to the discs being resolved at different neural levels of representation. The SBR disc is thought to be resolved through monocular competition while the CISR disc is thought to be resolved through binocular competition. Thus, CISR and SBR are hypothesized to be resolved through independent processes, and the two-disc results will not significantly differ from the independence prediction. If this is the case, then grouping acts on cues given by the low-level representations, and thus would not be in effect here.

3.2 Methods

3.2.1 Stimuli

Stimuli were solid chromatic 1.5 degree (°) diameter discs presented either 1.5° above fixation, 1.5° below fixation, or both 1.5° above and below fixation (Fig. 3.1). Each disc was presented at chromaticities defined in MacLeod-Boynton color space (MacLeod & Boynton, 1979). The chromaticities used were [L/(L+M), S/(L+M)] of [0.72, 0.3] called "red" and [0.61, 0.3] called "green." All discs were dichoptically presented so chromaticity was in rivalry, i.e. when a disc in one location was "green" presented to one eye, the corresponding disc presented to the other eye was "red." The remaining screen was dark (approximately 0.3 cd/m^2) except for the Nonius lines and rectangular frame.

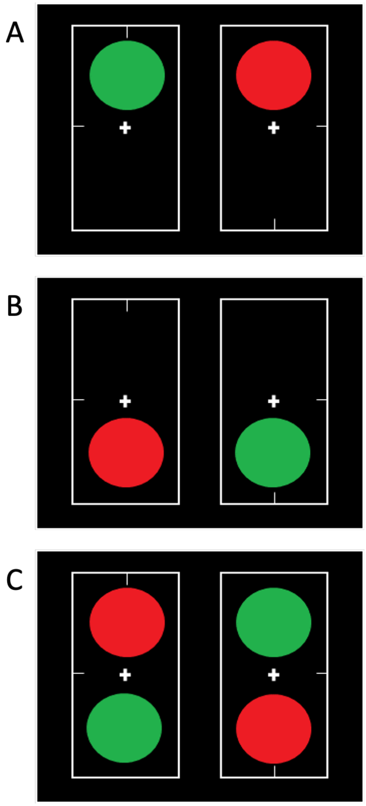

Figure 3.1: Stimuli used in Experiment 1. A) Top disc presented alone centered 1.5° above fixation. B) Bottom disc presented alone centered 1.5 ° below fixation. C) Top and bottom discs presented together, each centered 1.5 away from fixation. These stimuli pictured are in a patchwork array.

Four two-disc conditions were tested along with their component single-disc conditions that were used to calculate the independence predictions. The four conditions were: [1] one disc in SBR with one disc in ISR, [2] both discs in ISR (patchwork only), [3] both discs in SBR conventional rivalry, and [4] both discs in SBR patchwork rivalry (Fig. 3.2). To calculate the independence predictions, top and bottom discs alone were presented both in

ISR and in SBR, meaning four single-disc conditions were run (2 methods x 2 disc locations).

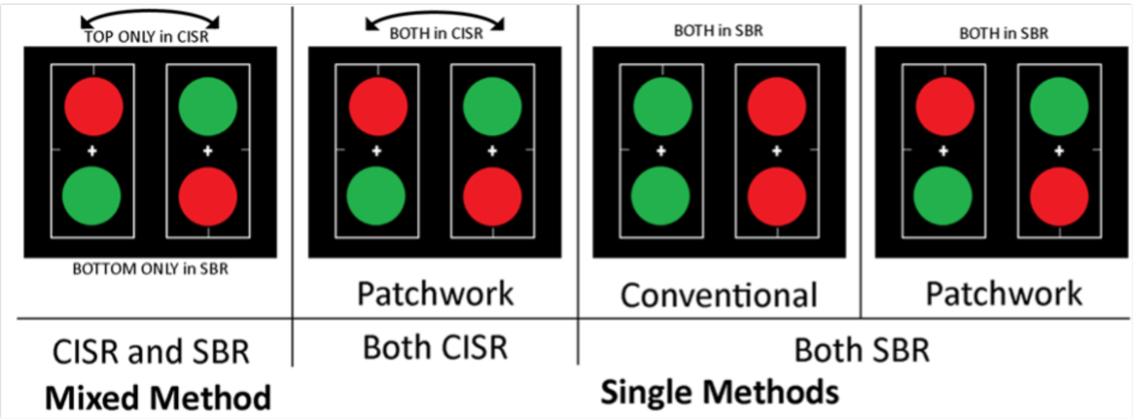

Figure 3.2: Conditions used for Experiment 1, defined both by location of chromatic discs and method used to present the discs. This represents one counterbalance of chromaticity locations for the SBR discs.

Independence predictions were calculated by multiplying the proportion of time the top disc alone was a given color by the proportion of time the bottom disc alone was the same color. This was done separately for both red and green percepts, for each condition and for each observer.

3.2.2 Procedure

On four separate days, observers viewed each condition four times, with chromaticity locations counterbalanced in the SBR trials (e.g., two trials presented “red” to the top left eye and “green” to the top right eye and the other two trials presented “red” to the top right eye and “green” to the top left eye). The first day was treated as practice and excluded from analysis. Observers were instructed to press and hold buttons on a gamepad when both discs appeared to be the same color, with separate buttons for “both red” or “both green.” Observers were instructed not to press any buttons when the percept was mixed or patchy, swapping color quickly (in time with the stimulus swaps within an eye), or if both discs were stable but different colors. Each trial lasted 70 seconds, but the first 10 seconds were not recorded to exclude any onset bias (Carter & Cavanaugh, 2007; Stanley et al., 2011) or differential adaptation between the two eyes. The dependent measure was the proportion of time out of the 60 second trial that either button was held (“red” + “green”).

3.2.3 Observers

Five observers participated in this experiment, four female and one male (ages 21-24). All were naïve to the purpose of the experiment, though two (obs. JA and SW) had some previous experience with ISR.

3.3 Results & Discussion

Data were analyzed separately for each observer. Prior to analysis, all proportional data were transformed using the arcsine transformation in order to approximate the normal distribution as needed for statistical tests (Kirk, 2013). Four planned orthogonal contrasts were performed for each observer comparing each condition to its independence prediction where a significant difference (two-disc measurement higher than predicted) indicates grouping of the two discs (Table 3.1). For the single-method conditions, 14 of the 15 tests (3 conditions x 5 observers) showed grouping significantly above chance (Fig. 3.3). Only one of the five observers, however, showed a significant difference in the mixed method with one dichoptic stimulus presented in standard binocular rivalry (SBR) and the other in chromatic interocular switch rivalry (CISR); this may be due to this observers’s low measurements for both the two-disc measurements and the single-disc measurements. Overall, therefore, observers showed significant grouping for the single-method conditions, but not for the mixed-method condition (Fig. 3.3).

The results show that while discs presented using the same method do group significantly (as expected), discs presented using a mixture of the two methods generally do not. The single-method conditions all presented discs that are resolved by the same kinds of competing representations while the mixed-method condition presented discs that were resolved by

Table 3.1: t values and p values for each contrast performed for each observer. These values represent the comparison between each two-disc measurement and its independence prediction for each separate condition.

Condition	t_{16}	p value	t_{16}	p value	t_{16}	p value	t_{16}	p value	t_{16}	p value
Mixed Method	1.63	0.061	4.983	0.00007	0.4135	0.342	0.4939	0.314	1.071	0.15
Both CISR	0.248	0.403	4.983	0.00002	2.4437	0.0132	2.185	0.022	1.775	0.047
Both SBR Conventional	5.218	0.00004	3.6106	0.0012	3.0605	0.0037	3.48	0.0015	2.041	0.029
Both SBR Patchwork	3.041	0.0039	3.763	0.0008	3.0032	0.0042	2.874	0.0055	1.806	0.0448

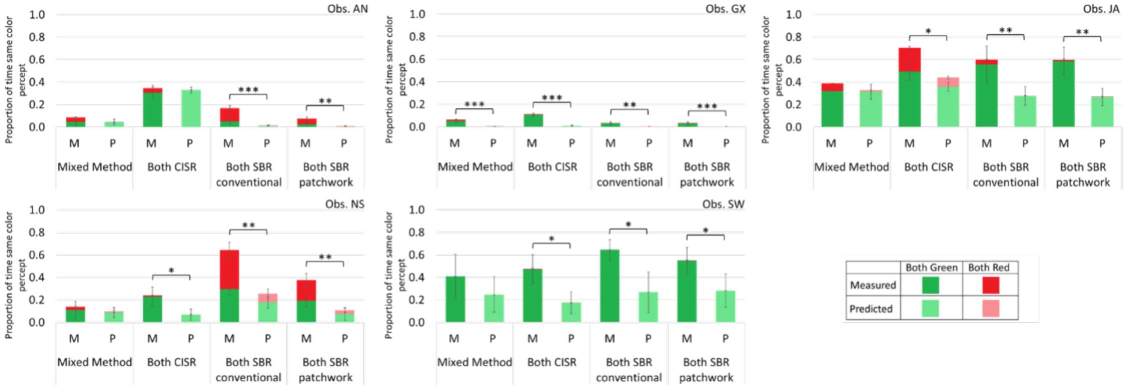

Figure 3.3: Results for Experiment 1. For each graph of individual observer results, the x-axis shows the condition as well as if the data were a two-disc measurement ("M") or a calculated independence prediction ("P"). The y-axis shows the proportion of time each percept was seen. The legend indicates what percepts the colored bars represent, darker for the two-disc measurements and lighter for the predictions. Significance codes: * $p<0.05$, ** $p<0.01$, *** $p<0.001$, and bars not marked are not significant.

different kinds of competing representations. Though both methods resulted in competing representations of the same chromaticities, these representations were of different kinds: monocularly-driven for SBR and binocularly-driven for ISR. The cue of different types of low-level neural competition in the mixed method condition leads to resolution of the discs as the same color not significantly above chance. These results are not consistent with the higher-level cue of the same color representations resulting in grouped percepts. Instead, this supports the hypothesis that grouping acts on competing representations at the same neural level.

CHAPTER 4

EXPERIMENT 2: CAN BINOCULARLY-INTEGRATED REPRESENTATIONS GROUP?

4.1 Rationale

Conscious perception is constructed by combinations of many different neural representations. Take for instance a solid red disc stimulus. A percept from this stimulus is achieved from neural representations of long wavelengths and of neural representations of curved edges. The information from these representations are combined and create the percept of a solid disc that is red. In the case of dichoptic stimuli, neural representations from each stimulus compete because two different objects cannot appear in the same place at the same time. What this means is that two neural representations with different tunings within the same feature domain are active at the same time and compete for dominance which leads observers to perceive one of the multiple possible percepts at a time. Take for instance dichoptic solid red and green discs. Here, an object cannot be completely red *and* completely green *simultaneously*, so the neural representations of red compete with those of green, leading to the percept of a solid disc (because both conflicting stimuli signal the same form) that alternates between appearing red and appearing green (Christiansen, D'Antona, & Shevell, 2017).

This is, of course, a simplification of all the neural representations active when an observer views a scene. Adding multiple features to rivalrous stimuli increases complexity and allows us to begin to understand how the visual system determines what components across the visual field combine to create the percept of one object. To address this complexity, instead of solid dichoptic discs, stimuli in the following experiment were discs containing orthogonal gratings of the same spatial frequency in either the same or opposite chromaticities. These stimuli can activate more competing neural representations than the solid discs, and they can be combined in various ways to produce different percepts. The percept of interest here is plaids.

Plaids are percepts that contain elements from both eyes' grating stimuli. Representations of these integrated plaid patterns must exist later in the visual system than the representations of the individual gratings that contribute to the plaid. Typically, experiments using dichoptic presentation ignore the predominance of plaid percepts, lumping plaid together with “mixed” or “patchy” percepts (Logothetis, Leopold, & Sheinberg, 1996; Lee & Blake, 1999; Papathomas, Kovács, & Conway, 2005). This misses an opportunity to learn about the visual system because plaid percepts differ from mixed and patchy percepts in that they are simultaneous predominance of both eye's component gratings.

The present experiment aimed to determine if two plaids appear together more often than chance, implying a third representation competing with the two, most-often-studied representations of the component gratings. This experiment aimed also to examine the other features that may be competing or not in the gratings (i.e., rivalrous or consistent chromaticity) and how that affects percepts of plaid and grouped plaids.

As in Experiment 1, conditions presenting top discs alone and bottom discs alone were also tested in order to calculate the independence predictions for each condition. Following from the results from Exp. 1, the individual gratings were expected to group in conditions where the competing neural representations completely matched one another. For instance, neural representations of “red” rightward tilted gratings competing with “green” leftward tilted gratings both above and below fixation should group due to strong cues (both chromaticity and orientation) that their ambiguity should be resolved non-independently. The same is true when chromaticity is identical across all dichoptic gratings, though chromaticity here is an uninformative cue as even gratings of different orientation also share chromaticity. Other conditions pair gratings that differ in their competition in some way, for instance pairing dichoptic stimuli with both chromatic and orientation rivalry with dichoptic stimuli with only orientation rivalry. In another condition, pairing dichoptic stimuli both with only orientation rivalry, but each dichoptic pair presented in a different chromaticity than the other pair. If these conditions with non-identical competition in each region result in grouped individual gratings, then grouping is dependent on a shared competing neural representation (here, orientation) and is not limited by a non-shared neural representation (here, chromaticity). If these conditions do not result in grouped percepts, then this would suggest that all neural representations from the dichoptic stimuli (i.e., representations of chromaticity, orientation, and spatial frequency) may need to be identical for grouping to occur.

The novel percept measured here is the simultaneous percept of two plaids. This is expected if [1] the visual system combines input from the two dichoptic gratings and [2] the neural representations of the combined gratings (plaids) compete with the representations of the individual gratings for dominance. No grouping of plaids is predicted if grouping cannot act on representations of binocularly-integrated information as it can for representations of the physical stimuli presented.

4.2 Methods

4.2.1 Stimuli

Stimuli were 3.3 cpd gratings oriented at both ±45° within 1.5° diameter discs. The gratings were equiluminant and their form was defined by chromatic contrast. All gratings included "grey" regions at [0.665, 1.0] and either "red" regions at [0.72, 0.3] or "green" regions at [0.61,0.3]. The rivalrous gratings presented to corresponding retinal locations always rivaled in orientation (i.e. one eye presented a 45° grating and the other a 135° grating) and sometimes rivaled in chromaticity (i.e. either both "red/grey" gratings in one location, for instance, or "red/grey" to one eye and "green/grey" to the other). Three stimulus

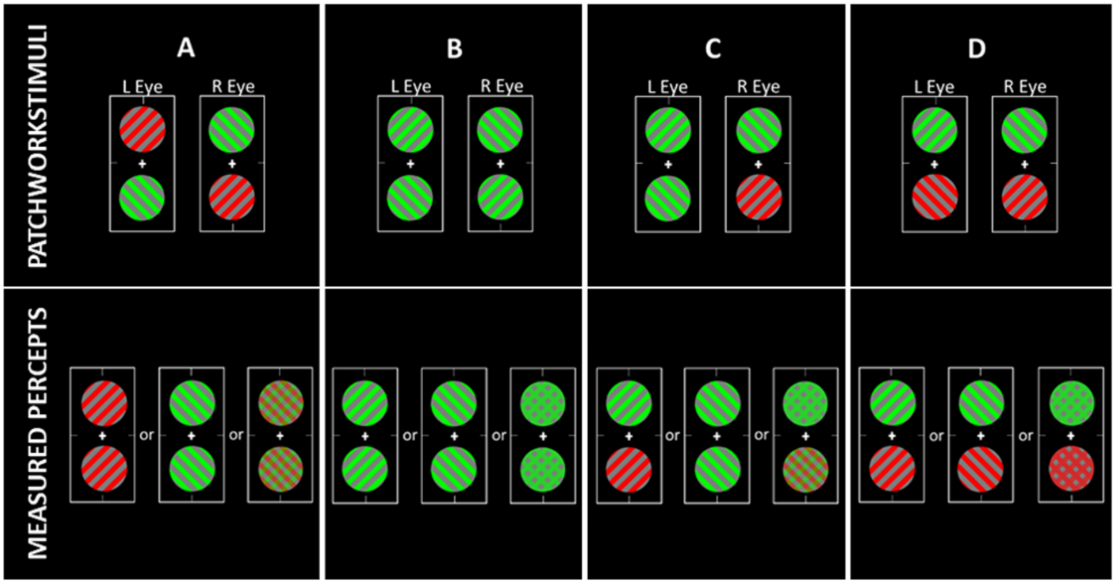

Figure 4.1: Stimuli and percepts measured in Exp. 2. The top of the figure shows the ISR stimuli, all orthogonal gratings of either the same or different chromaticity as its dichoptic pair. The bottom shows the measured percepts for each condition, including both grouped individual gratings and grouped plaids. All gratings were presented in a patchwork array, eliminating the possibility that two identical gratings would be presented together to one eye in order to avoid a 'grouped percept' from one dominant eye.

configurations were used to test for grouping: two discs, one above and one below fixation; one disc above fixation; and one disc below fixation. The configurations with single discs were used to calculate the independence predictions for each condition. The method to create this model is the same as described above.

The conditions were defined by how the chromaticities were assigned, and thus what kind of plaid could be perceived in each location. The four conditions were: [A] each rivalrous disc had rivalrous chromaticity, [B] all four rivalrous discs were presented at the same chromaticity, [C] the two rivalrous discs in one location had rivalrous chromaticities and the other discs were presented at the same chromaticity, and [D] both rivalrous discs in one dichoptic set were presented in the same chromaticity, but opposite chromaticity from the other dichoptic set (Fig. 4.1). The chromaticity/orientation pairings were counterbalanced.

4.2.2 Procedure

For all conditions, observers reported three possible percepts with separate button presses on a gamepad. The percepts measured here were of both discs appearing to be tilted in the same direction, regardless of color. For all conditions, observers held one button when both gratings appeared to be tilted toward the right (45 °), a second button when both gratings appeared to be tilted toward the left (135°), and a third button when both gratings appeared to be superimposed as a plaid (Fig. 4.1). When only one disc was present, button assignments remained the same and observers reported their percept of the single disc alone.

Observers made settings on four different days, with the first day treated as practice and not reported. Each day, observers viewed each condition four times (including chromaticity/orientation counterbalances), for a total of eight blocks per day (4 with both discs present, 2 with just the top disc present, and 2 with just the bottom disc present).

4.2.3 Observers

Six observers participated in this experiment. Four were female and two were male, all naïve as to the purpose of the study and without experience viewing rivalrous stimuli before the practice sessions.

4.3 Results & Discussion

Four planned orthogonal contrasts and two planned non-orthogonal contrasts were performed separately on the individual grating results and the plaid results (Table 4.1). The four orthogonal contrasts compared each of the four conditions' two-discs measurement to its independence prediction. The two non-orthogonal contrasts compared the two-discs measurements from specific conditions to each other. The first non-orthogonal contrast compared the condition with all four discs in the same chromaticity (condition B) to the condition with all four discs with chromatic rivalry (condition A) to test if having chromaticity also rivaling influenced ambiguity resolution. The second non-orthogonal contrast compared the condition with all four discs in the same chromaticity (condition B) to the condition with each pair of discs in the same chromaticity (condition D) to test if grouping is disrupted by a non-shared, non-rivalrous representation of chromaticity.

Observers perceived the individual gratings to be grouped by orientation consistently across all conditions (Fig. 4.2a). Measurements below 5% of the total viewing time (below 3 sec in the 60 sec viewing period) were not analyzed to eliminate the influence of occasional random button presses. For gratings grouped by color and orientation (condition A), five of the six observers showed a significant difference between the two-discs measurement and the independence prediction in the direction supporting grouping. For gratings of all the same color grouped by orientation (condition B), four of the five observers above the 5% criterion showed a significant difference between the two-discs measurement and the independence prediction in the direction supporting grouping, and though the fifth observer (ST) did not reach significance the results were in the direction of grouping. These results were expected based on the findings in Exp. 1 because the neural representations in competition are identical in these conditions.

Table 4.1: t values and p values for the contrasts performed for each observer. The top half of the table reports comparisons between the two-disc measurements and the independence predictions for the individual grating data. The bottom half of the table reports comparisons between the two-disc measurements and the independence predictions for the plaid data, as well as the two non-orthogonal* comparisons in the last two rows.

Condition	AT		BP		LH		SK		SL		ST	
Individual Grating	t_{16}	p value	t_{16}	p value	t_{16}	p value	t_{16}	p value	t_{16}	p value	t_{16}	p value
A	2.767	0.0069	3.996	0.0005	3.876	0.0006	9.091	0.00000005	0.606	0.276	4.435	0.0002
B	3.338	0.0021	5.337	0.00003	2.081	0.0269	9.974	0.00000001	0	1	1.289	0.107
C	3.527	0.0013	4.260	0.0003	1.004	0.1651	6.427	0.000004	1.081	0.148	2.497	0.012
D	4.104	0.0004	4.155	0.0004	2.581	0.0101	10.07	0.00000001	1.705	0.054	3.210	0.002
Plaid	t16	p value	t16	p value	t16	p value	t16	p value	t16	p value	t16	p value
A	3.953	0.0005	0.462	0.325	1.378	0.093	4.510	0.00017	1.309	0.104	1.332	0.101
B	2.404	0.0143	1.604	0.064	2.989	0.004	5.539	0.00002	0.697	0.247	3.209	0.0027
C	1.890	0.0385	0.339	0.369	1.557	0.069	6.126	0.000007	1.787	0.046	3.064	0.0037
D	2.598	0.0097	0.184	0.428	3.554	0.001	6.740	0.000002	1.211	0.121	4.901	0.00008
A < B *	0.122	0.904	2.303	0.035	6.263	0.00001	3.288	0.0046	2.510	0.023	2.815	0.012
B > D *	0.187	0.854	1.420	0.175	0.561	0.583	1.201	0.2473	0.514	0.614	1.689	0.111

[a]

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[a] The values displayed here were averaged over three experimental days.

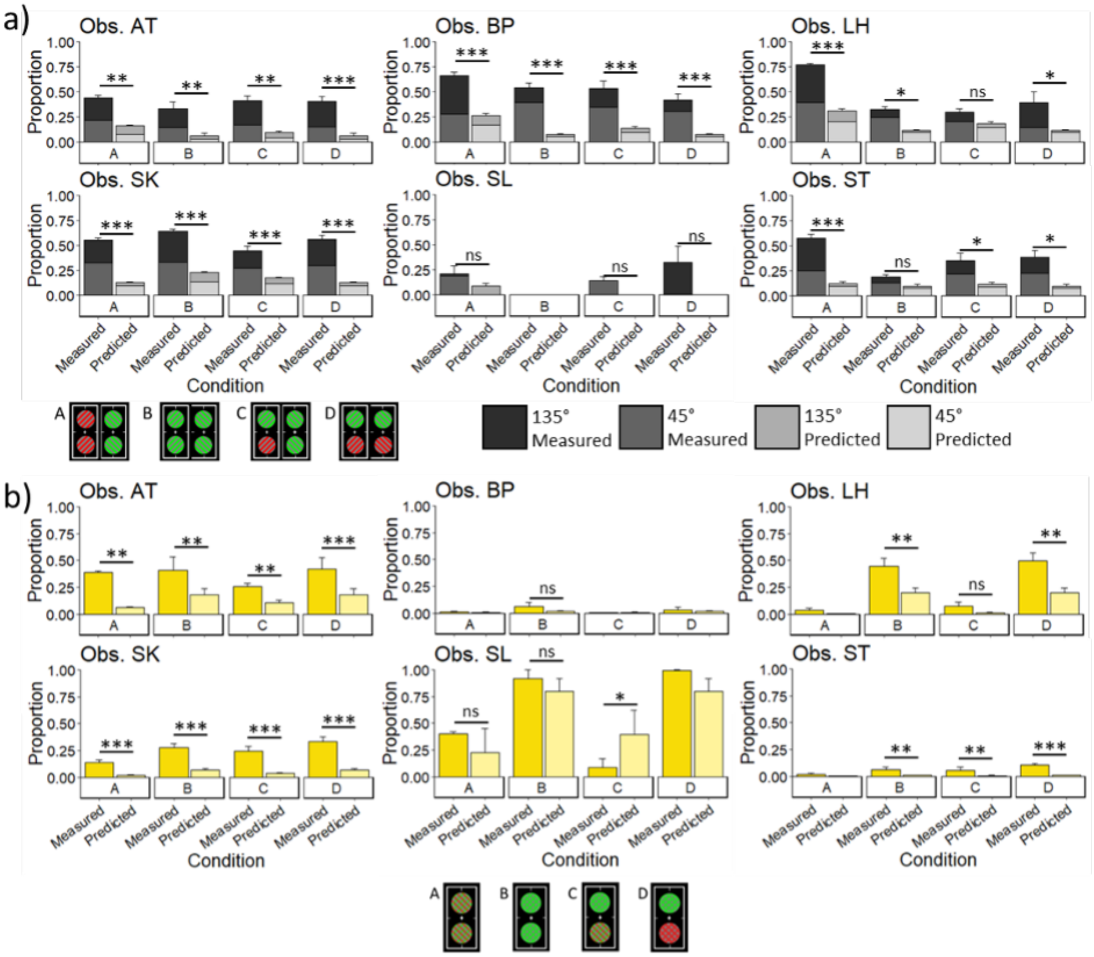

Figure 4.2: Results for Exp. 2, figure adapted from Slezak, Coia, & Shevell, 2019. a) Individual grating results with percepts and color legend shown below graphs. b) Plaid results with percepts shown below graphs. Significance codes: ns $p>0.05$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$, unmarked comparisons were below the 5% criterion (see text) and not tested.

For gratings of the same color paired with opposite-colored gratings grouped by orientation (condition C), four of the six observers showed a significant difference between the two-discs measurement and the independence prediction in the direction supporting grouping (the two non-significant results were both in the direction of grouping). For gratings never matching in color grouped by orientation (condition D), five of the six observers showed a significant difference between the two-discs measurement and the independence prediction in the direction supporting grouping (and the sixth non-significant result in the direction of grouping). These results demonstrated that grouping follows from shared competing neural representations (here, orientation) and was not eliminated by a non-shared neural representation for another feature (here, chromaticity). This is true even when the non-shared neural representations of chromaticity are also in competition (condition C).

Observers perceived grouped plaids to varying degrees across the conditions (Fig. 4.2b). Again, measurements below 5% of the total viewing time were not analyzed to potential intrusion from random button processes. Here, measurements above 95% of the total viewing time were also not analyzed to eliminate a ceiling effect that could misrepresent the results. For two bi-colored plaids (condition A), two of the three observers with results above 5% showed a significant difference between the two-discs measurement and the independence prediction, supporting grouping. For two single-colored plaids of identical chromaticity (condition B), four of the six observers showed a significant difference between the two-discs measurement and the independence prediction in the direction supporting grouping (with the two non-significant results in the direction of grouping). For single-colored plaids paired with bi-colored plaids (condition C), three of the five observers showed significantly greater time with the two discs appeared the same compared to the independence prediction. For two single-colored plaids of two different colors (condition D), four of the four observers above the 5% and below the 95% criterion showed significantly greater time the two discs appeared the same compared to the independence prediction (with the fifth non-significant observer in the direction of grouping). Overall, these results with plaids show that grouping acts on representations of binocularly-integrated information and that these binocularly-integrated representations compete with the representations from the individual gratings. Again, grouping is not limited by a non-shared neural representation of chromaticity across the regions in conditions C and D.

The non-orthogonal contrasts reveal some differences between conditions. Two bi-colored plaids (condition A) are seen less often than two single-colored plaids (condition B): Five of six observers perceived more same-color single-colored plaids than bi-colored plaids (Obs. BP: $p<0.05$; Obs. LH: $p<0.001$; Obs. SK: $p<0.001$; Obs. SL: $p<0.05$; Obs. ST: $p<0.05$; Obs. AT $p>0.05$; comparison not shown in Fig. 4.2b). This shows that rivalrous chromaticity can affect how the ambiguity is resolved. It may be that the chromatic contrast between the competing representations in condition A lead to more dominance and suppression between the two gratings than when there is a lack of chromatic contrast, thus leading to less plaid. The two conditions with single-colored plaids (conditions B and D) were never significantly different from each other (all observers $p>0.15$). This suggests that grouping is not limited by a non-shared neural representation (chromaticity), and is in accord with the idea of less suppression with no chromatic contrast within a plaid.

Overall, two dichoptic gratings group to produce percepts of identically oriented individual gratings and also percepts of binocularly-integrated plaids. These groups are not limited by differences in chromaticity across the dichoptic stimuli (i.e., just the top or bottom dichoptic discs) or between the two separate dichoptic pairs (i.e., the top and bottom set of dichoptic discs). This indicates that the shared neural competition of neural representations of orientation, or more broadly, of texture, lead to grouping despite non-shared representations of chromaticity. This happened even in the case of condition C where neural competition in the top disc, for instance, was between representations of only orientation and competition in the bottom disc of both chromaticity and orientation. This result is distinct from Exp. 1 because two dichoptic discs grouped despite non-identical neural competition. The difference here lies in the fact that these gratings were resolved at a shared binocular level of neural representation and both gratings always had shared competition between representations of the same orientations.

CHAPTER 5

EXPERIMENT 3: RULING OUT GROUPED PLAIDS CAUSED BY INHIBITION OF INTEROCULAR SUPPRESSION

5.1 Rationale

When dichoptic stimuli are shown to an observer, their visual system will experience both dominance and suppression. Dominance leads the observer to have a percept from the dominant, or stronger of the competing representations. Suppression occurs simultaneously to the other representation or representations that are not perceived. This dominance and suppression fluctuate over time and lead to slow alternations in what the observer perceives. In Experiment 2, plaids are thought to be perceived due to dominance of a third, binocularly-integrated representation of both individual gratings together. It could be, however, that plaids occur because there is an *inhibition* of the suppression that typically occurs between the dichoptic stimuli. Under this alternative hypothesis, instead of competition between the representations leading to suppression of one and dominance of the other, there would be no suppression (and thus no dominance) and both gratings would be perceived (plaid). Two follow-up experiments were conducted here to rule out the alternative hypothesis that plaids were perceived together due to an inhibition of interocular suppression.

5.2 Experiment 3a

Experiment 3a tests the idea that an inhibition of suppression across the whole visual field could cause both eyes' gratings to appear together as plaids in both locations more often than chance. To test this hypothesis, rivalrous stimuli that were different from the orthogonal gratings in Exp. 2, but with matched spatial frequency and chromaticity to the original gratings, were used. These new rivalrous stimuli were paired with the ±45° gratings to test if fused percepts would occur together more often than chance. The new rivalrous stimuli had different orientations and other form cues, and thus created fused percepts that were not the same as the original plaids. If an inhibition of suppression across the whole visual field is what led to the simultaneous percept of two plaids in the original experiment, then here the new fused percepts should be seen with the original plaids just as often as in the previous experiment. If, instead, the simultaneous perception of two plaids is due to two identical binocularly-integrated representations competing in both regions, then these new fused percepts should not group with the original plaids because they have different binocularly-integrated representations from each other.

5.2.1 Methods

Stimuli

Three conditions were run to test the inhibition of suppression hypothesis: two new conditions and one replication condition for comparison. In each condition, one disc contained orthogonal 3.3 cpd gratings as in Exp. 2. The other discs paired with these gratings were one of two sets: [1] radial bars originating at the center of the disc paired with concentric rings (Fig. 5.1a), and [2] vertical and horizontally oriented gratings (Fig. 5.1b). These new rivalrous gratings were also 3.3 cpd (on average for the radial stimulus) and all the same chromaticity (all four discs at [L/(L+M), S/(L+M)] of [0.72, 0.3] or all four at [0.61,0.3]), just as in Exp. 2. The radial and concentric stimuli both have a black central circle (0.6 degrees in diameter) to keep the spatial frequency information as similar as possible to the other stimuli. The condition from Exp. 2 that measured grouped, same chromaticity single-colored plaids was run again for comparison to the new conditions and new inhibition of suppression model (Fig. 5.1c).

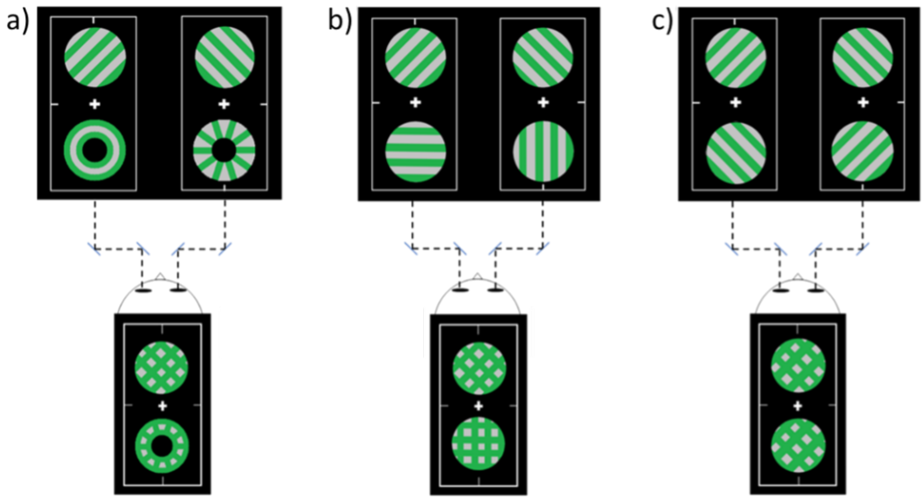

Figure 5.1: Stimuli and percepts for Experiment 3a. The top of the figure shows the ISR stimuli and the bottom shows the measured fused percepts. a) radial bars and concentric rings paired with diagonal gratings; b) vertical and horizontal gratings paired with diagonal gratings; c) two sets of identical diagonal gratings, as in Exp. 2 Condition B. The location of each pair of rivalrous stimuli, as well as the chromaticity all discs presented, was counterbalanced.

As in previous experiments, three stimulus configurations were used to test for grouping and calculate independence predictions: two discs, one above and one below fixation; one disc above fixation; and one disc below fixation. The configurations with a single disc were used here to calculate inhibition of suppression predictions for each condition as well as the independence predictions as before.

Inhibition of Suppression Model

The global inhibition-of-interocular-suppression prediction is created taking the amount of time there *is* suppression on top (1-time top is a fused percept); this is the amount of time the top dichoptic pair did not cause global inhibition of interocular suppression. This value is multiplied by the time there *is* suppression on the bottom (1-time bottom is a fused percept). The product is the amount of time neither dichoptic pair would cause global suppression of inhibition, assuming independence. Because this model predicts the results if there is global inhibition of interocular suppression, this final product is subtracted from 1.0 to give the final inhibition-of-interocular-suppression prediction value.

1.0 - ((1.0 - P(top is a fused percept)) × (1.0 - P(bottom is a fused percept)))

Procedure

For all conditions, observers reported only fused percepts with a button press on a gamepad. Only fused percepts were measured because there were no clear delineations of "groups" for the individual rivalrous stimuli. When only one disc was present, the response button remained the same and observers reported their percept of the single disc alone.

Observers made settings on four different days with the first day was treated as practice and not reported. Each day, observers viewed each condition four times (including chromaticity/location counterbalances), with a total of nine separate blocks per day (3 with both discs present, 3 with just the top disc present, and 3 with just the bottom disc present).

Observers

Six observers participated in this experiment, all female. Two of the six observers (Obs. AT and LH) participated in the main experiment prior to participating in this experiment, though all remained naïve as to the purpose of the experiment. One observer, WZ, only completed conditions 1 and 2.

5.2.2 Results & Discussion

Two contrasts were conducted for each condition: one comparing the two-discs measurement to the independence prediction and one comparing the two-discs measurement to the inhibition of suppression prediction. These planned, non-orthogonal contrasts were Bonferroni corrected (Table 5.1). A significant difference from the independence prediction indicated that the resolution of ambiguity for the two discs is linked in some way. A significant difference from the inhibition of suppression prediction indicated that the two discs are not linked due to an inhibition of suppression across the whole visual field. If the two-discs measurement is significantly different from both predictions, then grouping of binocularly-integrated representations is supported.

Condition 3 (both sets of diagonal gratings) was expected to show results consistent with grouping, and three of the five observers showed a significant difference between both predictions compared to the two-discs measurements (Fig. 5.2). The results are consistent with neither the inhibition of suppression prediction nor the independence prediction. Observer LC showed no significant difference between either prediction and the two-discs result, though had measurements too close to ceiling to be informative. Obs. AR had data in the correct direction to support grouping, but had a p-value of 0.10 comparing the two-disc measurement to the independence prediction (though had a significant difference between the two-disc measurement and the inhibition of suppression prediction). For the other two conditions, Radial & Concentric and Horizontal & Vertical, the results failed to show grouping for eight of 12 cases (2 conditions x 6 observers), as expected for two *non*-identical binocularly-integrated representations. Of the four that were significantly different from chance independence, three were not significantly different from the inhibition of suppression prediction (Fig. 5.2).

As expected if two plaids were perceived simultaneously due to a grouping mechanism that operates on identical binocularly-integrated representations, the two identical plaids group (that is, there is a significant difference between the measurement and independence prediction and also between the measurement and inhibition of suppression prediction). Two fused percepts that are not identical, however, do not appear together simultaneously at rates consistent with grouping (no significant difference between the measurements and independence predictions, or no significant difference between the measurements and inhibition of

Table 5.1: *t* values and *p* values for the contrasts performed for each observer. The table reports comparisons between the two-disc measurements and the independence predictions for each condition and comparisons between the two-disc measurements and the inhibition of interocular suppression prediction (label shortened to “Inhibition” in the table).

	Observers	AR		AT		LC		LH		WZ		XZ	
		t_{18}	p val	t_{18}	p val	t_{18}	p val	t_{18}	p val	t_{18}	p val	t_{18}	p val
Radial & Concentric	Independence	1.7725	0.093	4.161	0.0002	0.705	0.489	1.788	0.0904	0.4529	0.6587	4.32	0.0004
	Inhibition	2.3948	0.027	0.937	0.1805	2.205	0.0406	3.896	0.0010	1.965	0.0729	4.405	0.0003
Horizontal & Vertical	Independence	4.3625	0.0003	6.910	0.0000009	0.187	0.8534	1.656	0.1149	1.0547	0.3123	1.736	0.099
	Inhibition	0.1909	0.8507	1.86	0.079	2.146	0.0457	3.295	0.0040	1.2325	0.2413	6.946	0.0000017
Both Diagonal Grating	Independence	1.7283	0.1010	2.579	0.0094	0.067	0.947	2.888	0.0097			2.863	0.0103
	Inhibition	3.1960	0.0050	2.651	0.008	1.709	0.1045	2.666	0.0157			5.820	0.000016

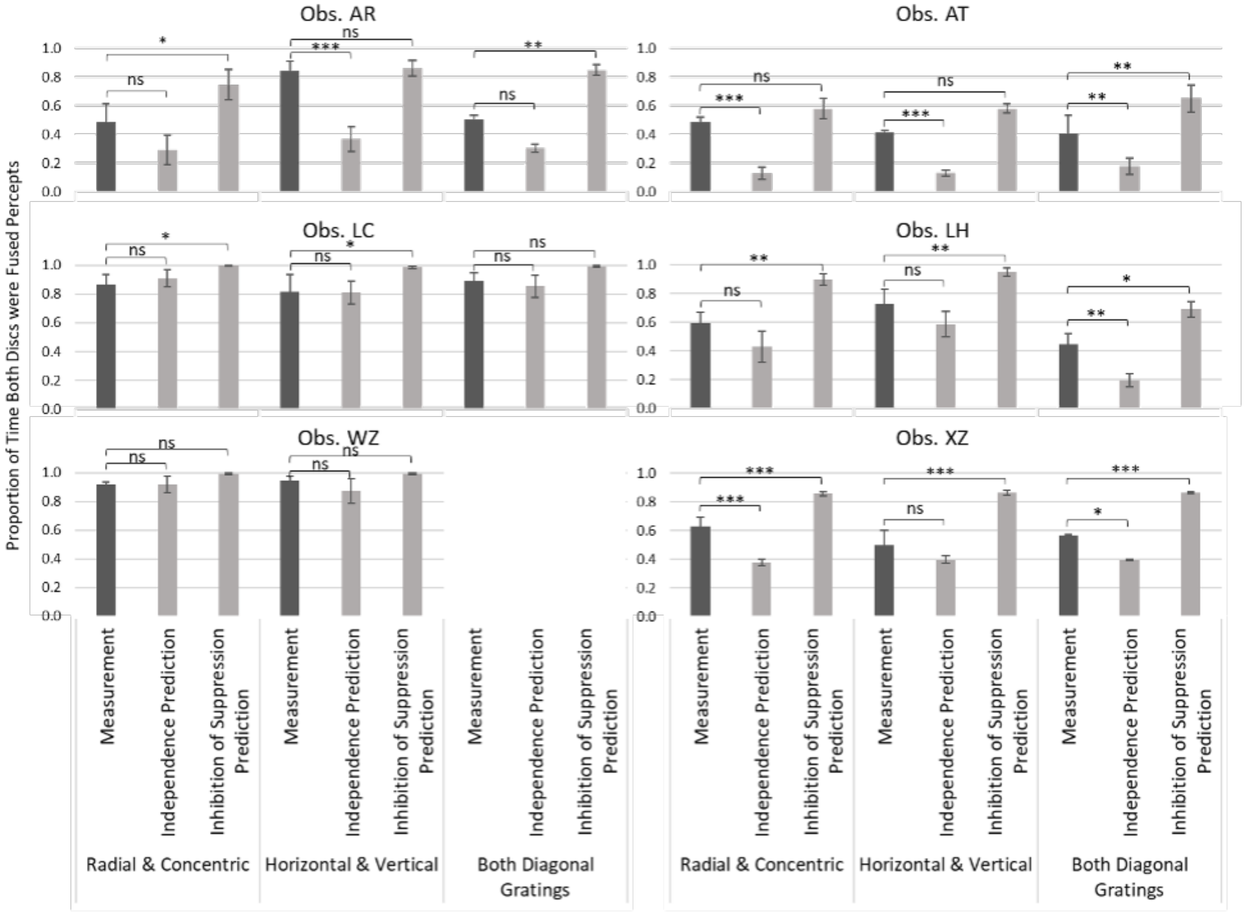

Figure 5.2: Results for Exp. 3a. The x-axis shows the condition and whether the bars represent the two-disc measurement, the independence prediction, or the inhibition of suppression prediction. The y-axis shows the proportion of time fused percepts were seen together. Significance: * $p<0.05$, ** $p<0.01$, *** $p<0.001$, ns $p>0.05$.

suppression predictions). Overall, the results show that inhibition of suppression across the whole visual field can account for the grouped plaid percepts in the previous experiment.

5.3 Experiment 3b

Exp. 3a showed that there was not an overall inhibition of suppression over the whole visual field. Here, experiment 3b tested the alternative hypothesis that inhibition of suppression could be driven by just one area of the visual field yet affect the other area. Exp. 2 demonstrated that more dichoptic plaid is perceived when the component gratings are matched in chromaticity than when they are in different chromaticities, perhaps due to the chromatic contrast from chromatically rivalrous gratings causing more suppression (more rivalry of individual gratings and less plaid) than the rivalrous gratings without chromatic contrast. If suppression in one area of the visual field can determine the behavior of another area, then having chromatically rivalrous discs in one area of the visual field should induce the other to have more suppression as well. Similarly, rivalrous discs of the same chromaticity causing inhibition of suppression in one area should induce inhibition of suppression in the other area.

This alternative hypothesis was tested using one set of rivalrous discs that has chromatic rivalry and the other set presented in one shared chromaticity (as in Condition C from Exp. 2). If an inhibition of suppression driven by one area of the visual field is inducing "grouped" plaids, then the proportion of time plaid is seen when presenting both discs but only asking about one should differ from the proportion of time plaid is seen when only a single disc is presented. If instead, grouping is acting on shared competing representations, then the unique suppression/fusion profiles of the rivalrous discs should not change when one disc or both discs are presented.

5.3.1 Methods

Stimuli

The stimuli used in this experiment were the same as used in condition 3 of Experiment 2 (pairing single-colored plaid with bi-colored plaid). Gratings were 3.3 cpd and could be either “red” or “green” ([L/(L+M), S/(L+M)] of [0.72,0.3] or [0.61, 0.3], respectively) always paired with grey ([0.665, 1.0]). All three stimulus configurations were used: both discs present, top disc only, and bottom disc only. When both discs were presented, one disc (either above or below fixation) contained rivalrous gratings of the same chromaticity and the other disc contained rivalrous gratings of opposing chromaticities. Both the top and bottom discs alone were presented in rivalrous chromaticities and in the same chromaticity on separate runs (Fig. 5.3). Locations and chromaticities were counterbalanced.

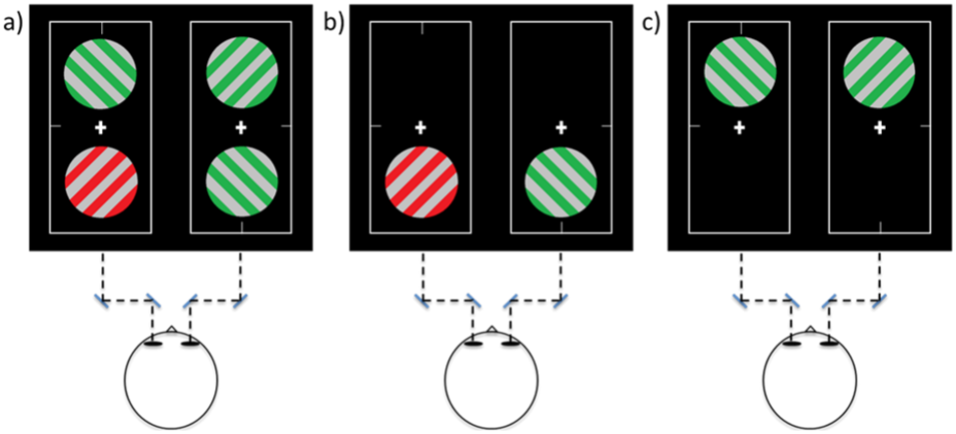

Figure 5.3: Stimuli for the second follow-up experiment. Only plaid percepts were measured (not shown). a) Stimuli shown for two separate conditions with different instruction: either [1] report single-colored plaid only or [2] report bi-colored plaid only. b) Stimuli for the comparison condition for [1]. c) Stimuli for the comparison condition for [2].

Procedure

For all stimulus arrangements, observers held down a button on a gamepad when a plaid percept was seen. When each disc was presented alone, observers used the button to respond when they saw a plaid of either a single color or of two colors. When both discs were presented, observers followed one of two sets of instructions. In one condition [1], observers were told to hold down the button when they saw the single-colored plaid *regardless* of how they perceived the other disc. In a separate condition [2], observers were told to hold down the button when they saw the bi-colored plaid *regardless* of how they perceived the other disc.

Observers made settings on four different days, with the first day treated as practice and not reported. Each day, observers viewed each of the four conditions four times (including chromaticity/location counterbalances).

Observers

Four observers participated in this experiment, all female. All four participated in Exp. 3a, and two had also participated in Exp. 2 (Obs. AT and LH). Despite previous experience with viewing rivalrous stimuli, all observers remained naïve as to the purpose of the study.

5.3.2 Result & Discussion

An arcsine transformation was applied to the data before analysis was conducted (Kirk, 2013). Two planned, orthogonal contrasts were performed: [1] comparing the results from showing both discs but reporting only the single-colored plaid to the results from the single-colored plaid alone, and [2] comparing the results from showing both discs but reporting only the bi-colored plaid to the results from the bi-colored plaid alone (Table 5.2). Significant results for either contrast would indicate that the fusion/suppression profile of one kind of rivalry (chromatic vs. non-chromatic) can influence the other.

There were no significant differences between the proportion of time single-colored plaid alone was reported compared to reporting single-colored plaid when both discs were present for all observers (Fig. 5.4). Likewise, there were no significant differences between the

Table 5.2: *t* values and *p* for the contrasts performed for each observer. The table reports comparisons between plaids reported when viewing two discs and plaids reported when viewed alone.

Observers	AR		AT		LH		WZ	
	t_{12}	p value	t_{12}	p value	t_{12}	p value	t_{12}	p value
Condition								
Bi-colored Plaid	1.529	0.076	0.3726	0.357	0.4738	0.3221	1.354	0.1003
Single-colored Plaid	0.048	0.48	0.7110	0.2453	1.0019	0.1680	0.0344	0.4865

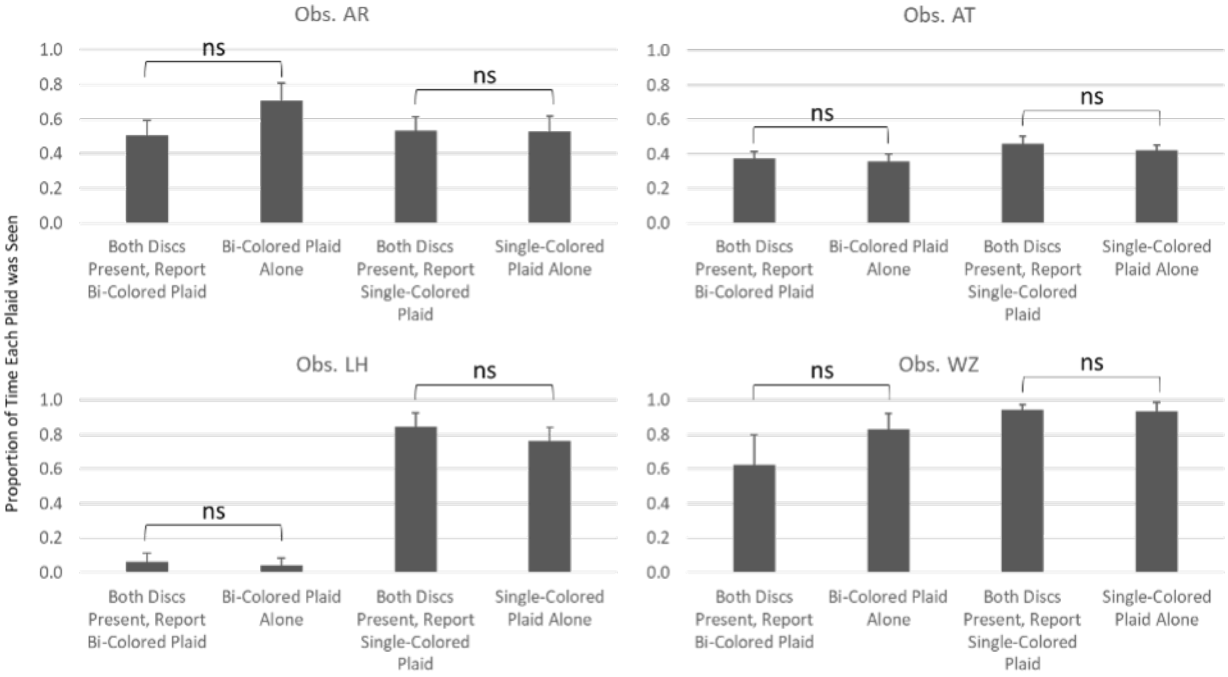

Figure 5.4: Results from Experiment 3b. The x-axis shows the condition the observer viewed and specific set of instructions. The y-axis shows the proportion of time plaid was seen. Significance: ns p>0.05.

proportion of time bi-colored plaid alone was reported compared to reporting bi-colored plaid when both discs were present for all observers (Fig. 5.4). This pattern of results was expected if grouped plaid percepts are not due to an inhibition of suppression driven by one area of the visual field affecting the other, but are instead due to dominance of a binocularly-integrated representation.

The results are not consistent with the hypothesis that the suppression or inhibition of suppression in one area of the visual field influences the suppression or inhibition of suppression in another. This result, coupled with Exp. 3a, supports the main hypothesis that there is a grouping process acting on the shared competing representations, including those binocularly-integrated representations of plaid.

CHAPTER 6

EXPERIMENT 4: DOES PERCEIVED COLOR OR PHYSICAL CHROMATICITY DRIVE GROUPING?

6.1 Rationale

When multiple chromatically ambiguous regions are presented together in the same manner (i.e. all using SBR or all using ISR, as in Exp. 1), observers tend to perceive all regions as identical in color significantly more often than chance. How monocularly- and binocularly-driven neurons play a role in this grouping process has been studied in-depth (Kovacs, Papathomas, Yang, & Feher, 1996; Papathomas, Kovacs, & Conway 2005; Slezak & Shevell, 2018; Slezak, Coia, & Shevell, 2019), but there remains a key question yet to be addressed: what neural cues does the visual system use to group regions together? When multiple chromatically ambiguous discs are presented together and appear to an observer to be all the same color, this grouping phenomenon could be driven by either all regions having 1) the same two competing physical chromaticities in each location (the stimulus), or 2) the same two color percepts in each location (the hue seen). The study here aimed to disentangle physical chromaticity and perceptual color experience through chromatic induction to determine which of these two cues the visual system uses to group together separate regions in view.

Chromatic induction classically has been defined as color appearance shifts due to simultaneous contrast or chromatic assimilation (Monnier, 2008). Here, chromatic induction is used to describe changes in the color percept of a test area through both contrast and assimilation (as in Xian & Shevell, 2004). Patterned surrounds of specific spatial frequencies can induce strong color-appearance shifts when a test ring or region is surrounded by two sets of other chromatic areas (Monnier & Shevell, 2003; refer back to Fig. 1.4 in the Introduction).

A previous study has made use of chromatic induction in dichoptic presentation, though not to test for grouping. Identical achromatic test regions were presented within dichoptic surrounds with inverse chromaticities such that the achromatic test regions appeared as different colors on each surround. In line with physically different dichoptic chromaticities, these physically identical but perceptually different colors alternated in perceived color (Hong & Shevell, 2008). This showed that resolution of chromatic ambiguity could occur after induced color-appearance shifts. These results might suggest that shared color appearance determines whether regions with neural ambiguity are grouped or resolved independently. As an alternative, Exp. 1 of this proposal showed that the low-level competing representations determine if grouping can occur, indicating the possibility that grouping might be driven by neural representations of the low-level physical chromaticities of the stimuli.

In this experiment, chromatic induction was used to disentangle perceived color from physical chromaticity by [1] inducing different color percepts from identical physical chromaticities within unequal inducing surrounds, and [2] presenting unequal chromaticities within different inducing surrounds chosen so that the unequal chromaticities appeared to match each other in color. The aim here was to test whether two chromatic regions were grouped based on shared color percepts or shared physical chromaticity. A final condition presented two regions that did not match in chromaticity or color as a negative control with neither of the tested cues matching.

6.2 Methods

6.2.1 Stimuli

Two separate sets of stimuli were used for this experiment, both using strong chromatic induction (as in Monnier & Shevell, 2003). First were stimuli used to obtain observer color matches. These stimuli were 3.3 cycles per degree (cpd) horizontal gratings, both for the inducing surround and the test regions within a 2.25° square. The test region was a 1.5°

square at 20 cd/m^2 with intervening inducing lines set to 15 cd/m^2 along with the background inducing lines, all on an otherwise dark (0.3 cd/m^2) background (Figs. 6.1a,b). The chromaticities used for the inducing surround were [L/(L+M), S/(L+M)] of [0.665, 2.0] called "purple" and [0.665, 0.16] called "lime." The test regions were one of two possible chromaticities: [0.71, 1.0] called "red" or [0.62, 1.0] called "green." The other stimuli were used to measure grouping using ISR. These stimuli were 4.5° squares with two test regions, one centered 1.5° above and one centered 1.5° below a fixation cross. Along with these two-region stimuli, their single-region components were tested to build independence predictions. The test regions were always dichoptic "red" and "green" with L/(L+M) values as above, but the S/(L+M) value was different depending on the condition (below) and the observer's color match.

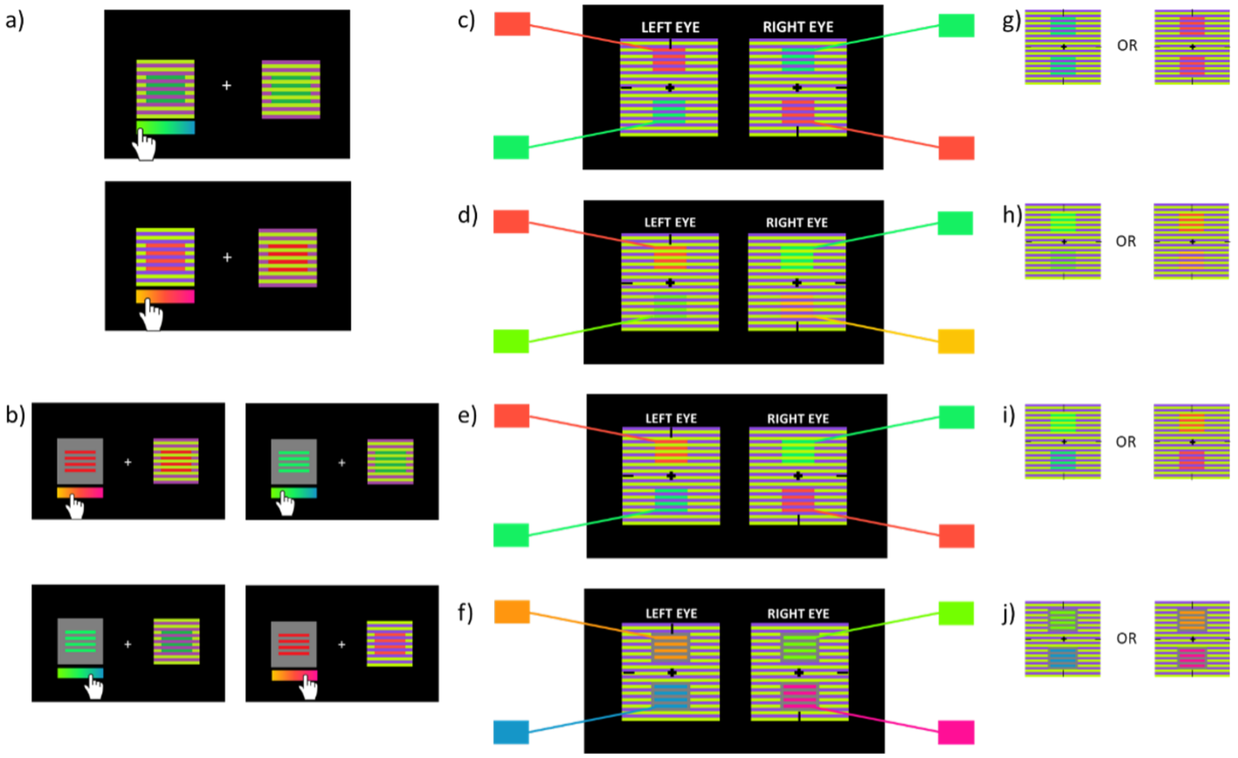

Figure 6.1: Stimuli and percepts for Experiment 4. a) and b) show color matching tasks that were used to obtain chromaticities used in d) and f), respectively. The test region is shown on the side with the color scale and finger picker. Only the two square stimuli and fixation cross were displayed on the trials. c) - f) show the ISR grouping conditions: c) same (confounded) color and chromaticity, d) same color, different chromaticity, e) different color, same chromaticity, f) different color, different chromaticity. Conditions with only the top and only the bottom of each condition were also run but not pictured. g) – j) show the percepts measured for each condition c) – f) respectively: g) percepts grouped by color and chromaticity corresponding to the same color and chromaticity condition, h) percepts grouped by color corresponding to the same color, different chromaticity condition, i) percepts grouped by chromaticity corresponding to the different color, same chromaticity condition, j) percepts grouped by the original chromaticities used in b) to obtain the color matches corresponding to the different color, different chromaticity condition. These show one possible counterbalance of each condition, but all possible counterbalances of chromaticity locations were run.

Four conditions are tested in this experiment, each a different combination of two parameters: the perceived colors could either be identical above and below fixation or different above and below fixation, and the chromaticity of the regions could either be identical above and below fixation or different. First, the top and bottom regions with the same (confounded) color appearance and chromaticities. Second, the top and bottom regions with the same color appearance but different chromaticities (same-color condition). Third, the top and bottom regions with different color appearances but the same chromaticities (same-chromaticity condition).And fourth, the top and bottom regions with different color appearances and different chromaticities (both-different condition). Every condition had the test regions in inducing bars that differed depending on the condition. Condition 1 used identical chromaticities in identical inducing backgrounds above and below fixation (Fig. 6.1c). Condition 2 used different chromaticities in opposite induction above and below fixation in order to have the color appearance match between the two regions (Fig. 6.1d). To obtain the color matches for this condition, observers viewed the "red" in lime induction and made changes in the S/(L+M) axis to a "red" in purple induction until they appeared to be identical colors (Fig. 6.1a)). Condition 3 used identical chromaticities in opposite induction above and below fixation in order to have different color appearances in the two regions (Fig. 6.1e). No color matches were needed in this condition. Condition 4 used different chromaticities in neutral inducing backgrounds in order to maintain a difference in both color appearance and in stimulus chromaticity (Fig. 6.1f). To obtain the chromaticities used here, observers viewed the "red" on lime induction and made changes in the S/(L+M) axis to a "red" on a grey background until they appeared to be identical colors (Fig. 6.1b). In addition to these four conditions, trials with only the top and bottom regions alone were presented to calculate the independence predictions as in previous experiments.

If grouping acts on representations of physical chromaticity, then conditions [1] and [3] should show significant grouping effects. If grouping acts on representations of perceived colors, then conditions [1] and [2] should show significant grouping effects. No grouping is expected from condition [4] because both chromaticity and color do not match between the two regions.

6.2.2 Procedure

This experiment consisted of two parts: first a color-matching task, then a grouping measurement. The color matching task was done on two separate days with eight repetitions of each color match. Observers sat with their chin in a chin rest to ensure proper viewing distance for the CRT screen without the haploscope. A trial consisted of a black screen with a white fixation cross at the center. The two chromatic induction and test squares were then displayed for 80 ms on either side of fixation. One side was the comparison chromatic induction and the other side was the test that changed in chromaticity along the S/(L+M) axis depending on the observer's response from trial to trial. The side of the test, as well as observer instructions, was counterbalanced. Observers were instructed to respond with a button press to indicate which side was "more blue," "more green," "more orange," or "more pink," depending on the trial. Once they reached a point that they thought both sides appeared identical, they pressed a "match" button and that chromaticity was recorded. These values were used for the second part of the experiment.

The second part used ISR to present two regions, one above and one below a fixation cross, in order to measure grouping. Here, observers viewed the screen through a haploscope with their chin in the chin rest to ensure the correct viewing distance. Each condition was viewed four times in a single day, and the whole experiment lasted five days with the first as practice (four averaged measurements with four repetitions total). The trials lasted 70 seconds total, but only the last 60 seconds were recorded in order to control for onset effects and an initial difference in adaptation between the two eyes. Conditions [1] and [3] used the same dichoptic chromaticities for all observers while conditions [2] and [4] used chromaticities from the color-matching task that were unique to each observer. Observers reported via gamepad buttons "grouped" percepts when both areas above and below fixation appeared the same color (conditions [1] and [2]); the colors associated with the same chromaticity (but different in appearance; condition [3]); or different colors derived from color matches made to identical chromaticities with opposite induction (different in both color appearance and chromaticity; condition [4]). Observers also reported stable percepts that were specifically not grouped: when both areas above and below fixation appeared opposite colors (conditions [1] and [2]; top "pink" and bottom "blue" or top "blue" and bottom "pink," for instance); the colors associated with opposite chromaticities (condition [3]; top "orange" and bottom "blue," for instance); or different colors derived from color matches made from opposite chromaticities in opposite induction (condition [4]; top "orange" and bottom "blue," for instance). Observers were instructed not to press any buttons when their percepts were mixed or patchy, or swapped in time with the rapid stimulus swaps between eyes.

6.2.3 Observers

Three observers participated in this experiment, all female. Two were naïve to the purpose of the study and one was the author. All had previous experience with ISR stimuli.

6.3 Results

Two sets of analyses were completed: [1] planned, orthogonal contrasts comparing each condition to its independence prediction in order to test for grouping (Table 6.1), and [2] a two-way ANOVA on only the two-region measurements to test for any effect of color percept or physical chromaticity on grouping (Table 6.2).

For the "grouped" percepts, all three observers showed significantly larger measurements than their corresponding predictions for every condition ($p<0.05$ for each of the 12 tests; Fig. 6.2). All two-way ANOVAs for the three observers showed no significant effect of color or of chromaticity, indicating that there were no significant differences across the four conditions. Thus, chromatically ambiguous regions need not be identical in color or in chromaticity to be grouped.

For the "non-grouped" percepts, two of the three observers showed a significant differ-

Grouped Percepts	**Observers**					
		ES		JA		SB
	t_{24}	p value	t_{24}	p value	t_{24}	p value
Same color same chromaticity	9.2909	0.000000001	4.7486	0.000039	4.5385	0.000067
Same color different chromaticity	9.4896	0.0000000006	4.2217	0.00015	3.558	0.000797
Different color same chromaticity	7.5146	0.000000046	3.8846	0.00035	2.440	0.01122
Different color different chromaticity	9.9819	0.0000000002	3.4261	0.0011	3.623	0.00067
Non-Grouped Percepts						
Same color same chromaticity	14.197	0.0000000000002	7.2266	0.00000009	1.7419	0.047
Same color different chromaticity	12.639	0.000000000002	5.7022	0.00000355	1.449	0.0801
Different color same chromaticity	11.368	0.00000000002	4.208	0.00015	0.410	0.34
Different color different chromaticity	10.916	0.00000000004	6.53	0.00000046	1.350	0.094

Table 6.1: t values and p values from the contrasts performed on each observers' data. The top half of the table reports values from comparisons between the "grouped" percept measurements and their independence predictions, and the bottom half of the table reports values from comparisons between the "non-grouped" percepts and their independence predictions.

Main Effects	ES		JA		SB	
	$F_{1,12}$	p value	$F_{1,12}$	p value	$F_{1,12}$	p value
Color	3.0593	0.1058	0.7558	0.4017	2.2030	0.1635
Chromaticity	0.2136	0.6522	0.4862	0.4989	0.1670	0.6900

Table 6.2: *F* values and *p* values from the two-way ANOVA conducted on only the "grouped" percept two-disc measurement data. The table shows both the results for the main effect of color and the main effect of chromaticity.

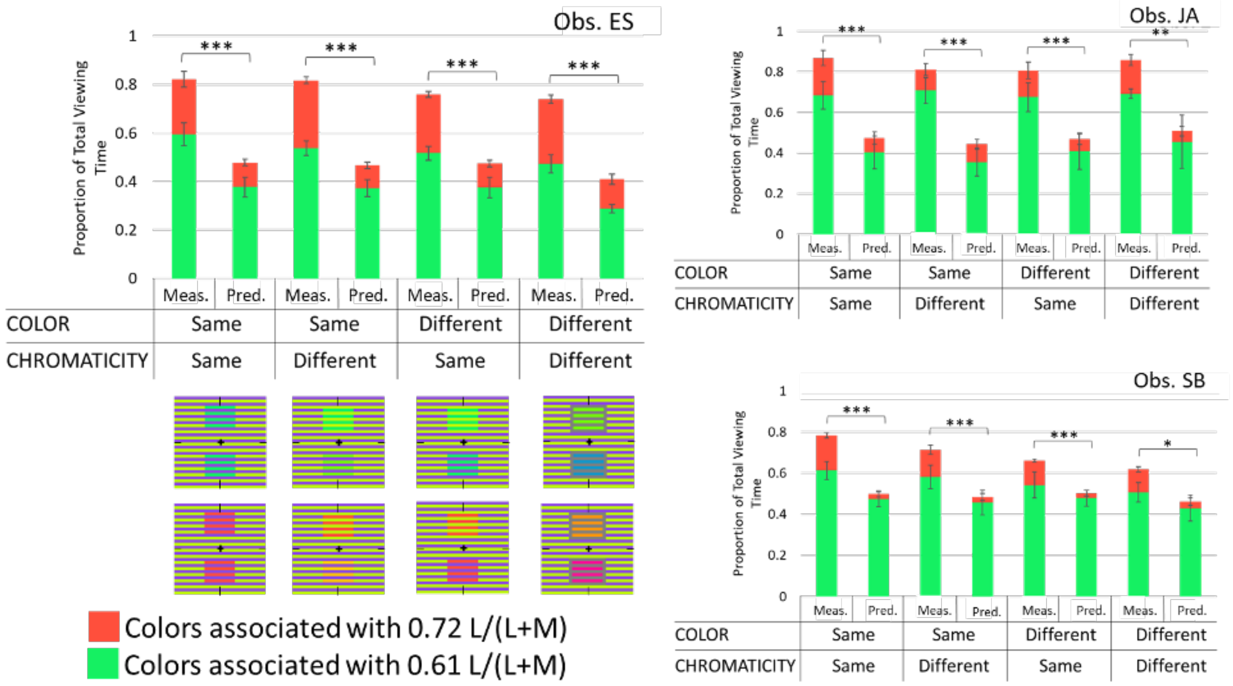

Figure 6.2: "Grouped" percept results from Exp. 4. The x-axis shows the condition and whether the bars represent the two-region measurements ("Meas.") or the calculated predictions ("Pred."). The y-axis shows the proportion of time each percept was seen, with the example percepts shown under their corresponding conditions under the first observer's plots. Significance codes: * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

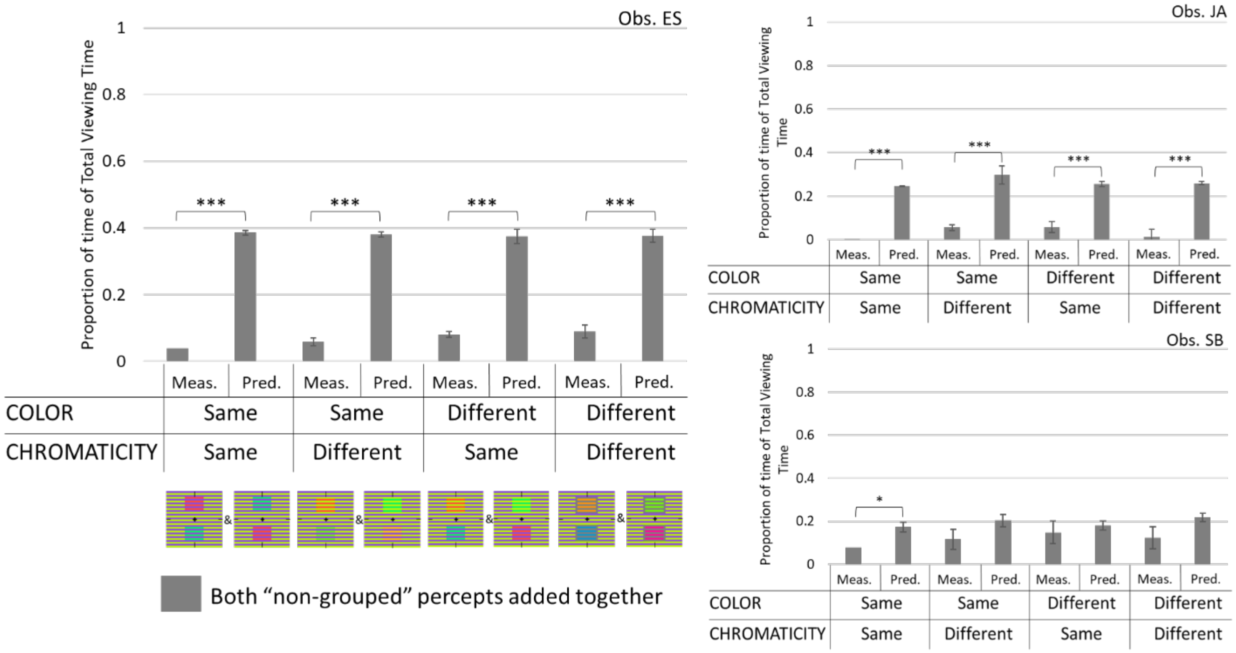

Figure 6.3: “Non-grouped” percept results from Exp. 4. The x-axis shows the condition and whether the bars represent the two-region measurements (“Meas.”) or the calculated predictions (“Pred.”). The y-axis shows the proportion of time each percept was seen, with the example percepts shown under their corresponding conditions under the first observer's graph. Significance codes: * $p<0.05$, ** $p<0.01$, *** $p<0.001$, and comparisons without marks are not significant.

ence between the measurements and predictions for all conditions such that the two regions appeared in non-grouped colors significantly *less often* than chance ($p<0.001$; Fig. 6.3). The third observer showed no significant differences between the measurements and predictions for conditions [2], [3], and [4] (meaning the two regions appeared in non-grouped colors for a duration not significantly different from chance levels, $p<0.05$) but did show a significant difference between the measurement and prediction for condition [1], also in the direction of both regions appearing in non-grouped colors less often than chance ($p<0.05$; Fig. 6.3).

If chromatically ambiguous regions need not be identical in color nor chromaticity to group, this begs the question of what the groups really are? The fourth condition with neither identical color nor chromaticity was originally tested in order to measure how often two things appear together when they have no matching feature to promote grouping, i.e.

a negative control. It is, therefore, surprising that grouping was found here at levels not significantly different from those found when perceived color, physical chromaticity, or both were identical.

To further unpack this finding, it is important to consider how the chromaticities for condition [4] were obtained. Observers were able to change the chromaticity of a comparison test region only along the S/(L+M) axis, meaning that the L/(L+M) values for the redder and greener stimuli never changed (they were always 0.71 and 0.62, respectively). So while the exact chromaticity, both S/(L+M) and L/(L+M), was not identical in condition [2] and [4], the L/(L+M) values were identical in all four conditions. The possibility that a shared L/(L+M) value led to the grouping found here was tested in the following experiment.

CHAPTER 7

EXPERIMENT 5: IS GROUPING DRIVEN BY EITHER A SHARED L/(L+M) OR S/(L+M) VALUE?

7.1 Rationale

Experiment 4 found grouping of chromatically ambiguous discs not matched in color percept or chromaticity. Though unexpected, this result speaks to the flexibility of grouping mechanisms. Here, Experiment 5 aimed to rule out an explanation based on the stimuli used in Exp. 4. To obtain color matches used in conditions [2] and [4] of Exp. 4, observers reported when two pulsed regions on different surrounds appeared identical in color. These color matches were made by changing the S/(L+M) stimulus value based on the observer's response before the final setting was made (through button presses meaning "left region is more pink," for instance). As a function of this procedure, the test regions used in conditions [2] and [4] always shared a common L/(L+M) value while the S/(L+M) value would differ. In the case where conditions [2] and [4] show significant grouping, this effect could be driven by the common L/(L+M) value. This potential explanation was tested in the present experiment.

Four conditions were tested to measure grouping in cases with both matched and unmatched L/(L+M) values and S/(L+M) values. The main aim was to determine if only a shared L/(L+M) value would drive grouping, as Exp. 4 might indicate. A second condition held the S/(L+M) value constant and had only the L/(L+M) value differ to determine if grouping occurs in this case (the compliment to condition [4] in Exp. 4). Grouping in this case was expected because existing evidence suggests that grouping with s-cone defined stimuli should not be different from l-cone defined stimuli (Christiansen, D'Antona, Shevell, 2017). The final two conditions mirrored the perceived colors used in the first two conditions but now without shared chromatic information above and below fixation. Here, grouping was not expected because there were no identical competing neural representations for any chromatic information – that is, both the L/(L+M) values and S/(L+M) values were unequal.

7.2 Methods

7.2.1 Stimuli

Stimuli for all four conditions were solid chromatic discs presented dichoptically. Condition 1 presented chromaticities that could be grouped by their L/(L+M) values – either 0.71 L/(L+M) or 0.62 L/(L+M) (Fig. 7.1a). Condition 2 presented chromaticities that could be grouped by their S/(L+M) values – either 0.6 S/(L+M) or 1.2 S/(L+M) (Fig. 7.1b). In these first two conditions, the other chromatic values (S/(L+M) for condition 1 and L/(L+M) for condition 2) were non-identical. The final two conditions used the same four chromaticities, but paired them differently in their dichoptic display to mirror the perceived color sets from conditions 1 and 2 (Fig. 7.1c). Condition 1 had a disc rivaling between orange and lime and a separate disc rivaling between blue and pink; thus, condition 3 mirrored this color arrangement while having both the L/(L+M) and S/(L+M) values different from each other above and below fixation. Condition 2 had a disc rivaling between orange and pink and a separate disc rivaling between blue and lime; thus, condition 4 mirrored this color arrangement while also having both the L/(L+M) and S/(L+M) values different from each other above and below fixation. The stimuli could be in one of three stimulus arrangements as in previous experiments: one disc above fixation, one disc below fixation, or a disc above and below fixation. These were used to calculate independence predictions for each condition.

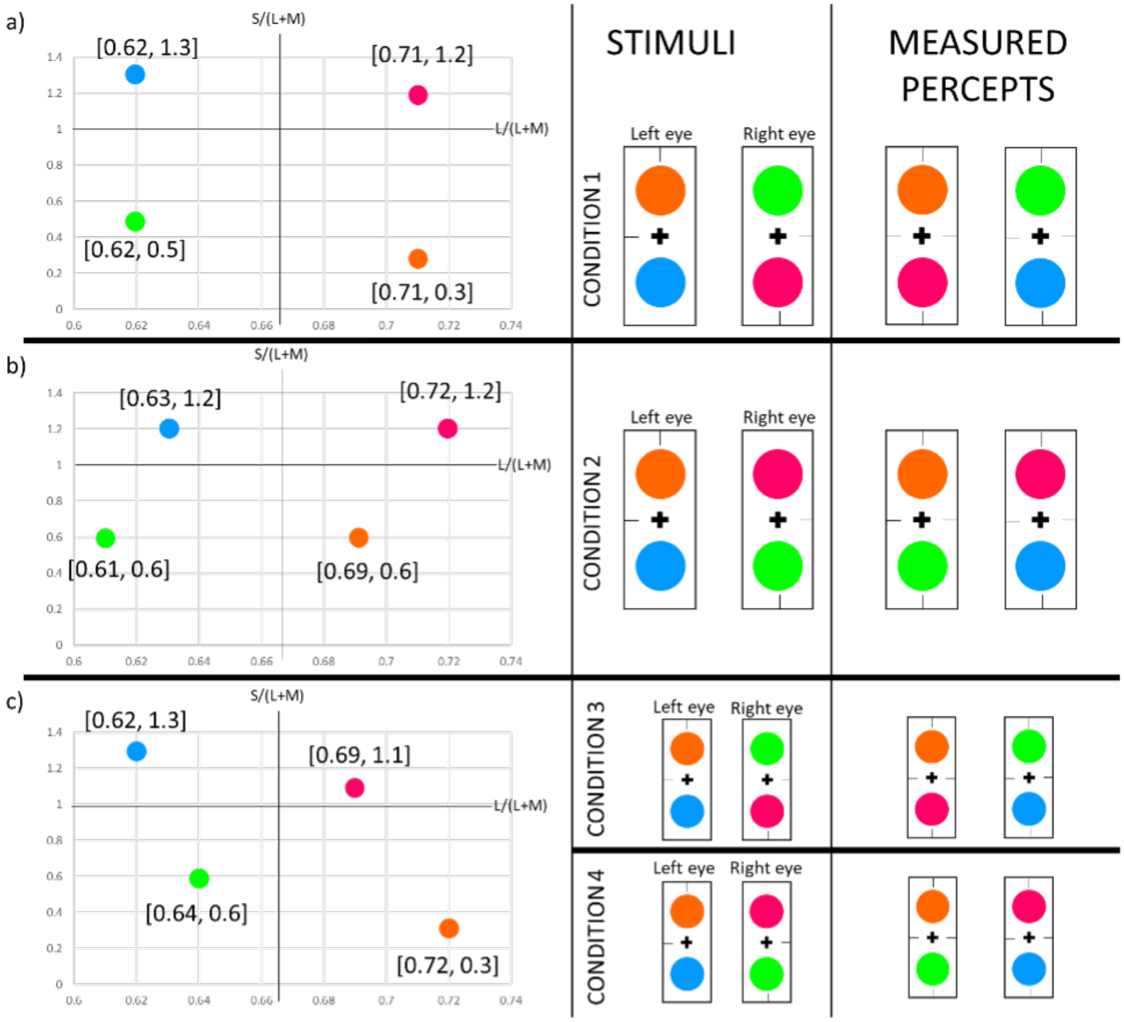

Figure 7.1: Stimuli and measured percepts used in Exp. 5. Each section shows the chromaticities for each disc plotted in L/(L+M, S/(L+M) coordinate space with the values called out next to each marker. To the right of each plot is the stimuli and the measured percepts, each with the condition number labeled on the left. Note that c) has two conditions using the same four chromaticities, thus two conditions are shown to the right of the coordinate plot. a) Condition 1 with shared L/(L+M) values denoting the groups. b) Condition 2 with shared S/(L+M) values denoting the groups. c) Conditions 3 and 4 with no shared chromatic information, but condition 3 mirroring the perceived colors from condition 1 and condition 4 mirroring the perceived colors from condition 2.

7.2.2 Procedure

Each condition was viewed four times in a single day, and the whole experiment lasted four days with the first as practice. The trials lasted 70 seconds total, but only the last 60 seconds were recorded in order to control for onset effects and initial differential adaptation between the two eyes.

For condition 1, observers reported when they perceived the colors above and below fixation to be grouped by L/(L+M) value, or orange with pink and lime with blue (Fig. 7.1a). For condition 2, observers reported when they perceived the colors above and below fixation to be grouped by S/(L+M) value, or orange with lime and pink with blue (Fig 7.1b). For condition 3, observers reported when they perceived the colors above and below fixation to be grouped as in condition 1 (Fig. 7.1c). For condition 4, observers reported when they perceived the colors above and below fixation to be grouped as in condition 2 (Fig. 7.1c). Observers were instructed not to press any buttons when their percepts were mixed or patchy, swapped in time with the stimulus swap rate within a single eye, or were some combination of colors that were not one of the two measured percepts. Observers reported when the disc appeared as one of two colors in the conditions with single discs alone.

7.2.3 Observers

Seven observers (five female) participated in this experiment. Five were naïve to the purpose of the study, one was the author, and one was a member of the lab with some prior knowledge about the experiment (though due to the nature of the conditions, this observer could not determine which condition they were viewing at any given time). Two observers had previous exposure to ISR stimuli and the other five did not. One observer was eliminated from the study because overall they did not perceive any steady colors for longer than 5

7.3 Results & Discussion

Prior to analysis, total dominance times for the two color percepts for each condition were added together (i.e., the orange/pink measurements were added to the lime/blue measurements, for instance). Two sets of analyses were completed: [1] planned, orthogonal contrasts comparing each condition to its independence prediction in order to test for grouping, and [2] planned, non-orthogonal Bonferroni-corrected contrasts to test for differences between conditions (Table 7).

For the first set of contrasts, grouping was found across all conditions for some of the observers, which broadly indicates that having shared chromatic information is not a prerequisite for grouping. Instead, grouping can occur significantly for conditions that have no common L/(L+M) or S/(L+M) value. This is directly opposed to the possible explanation that a shared L/(L+M) value caused the grouping found in Experiment 4.

Table 7.1: t values and p values for the contrasts performed for each observer. The top half of the table reports comparisons between the two-disc measurements and the independence predictions for the individual grating data. The bottom half of the table reports comparisons between the two-disc measurements and the independence predictions for the plaid data, as well as the two non-orthogonal* comparisons in the last two rows.

Condition	ES		JP		KO		DB		JL		NZ	
Grouping Tests	t_{16}	p value	t_{16}	p value	t_{16}	p value	t_{16}	p value	t_{16}	p value	t_{16}	p value
Same l	6.98	0.00000155	5.3135	0.000034	2.702	0.0078	7.7433	0.00000042	1.9129	0.0369	3.8912	0.00064
Same s	2.254	0.0192	1.246	0.115	2.7033	0.0078	6.3589	0.00000474	2.002	0.0312	4.8765	0.000084
No Match A	1.769	0.0479	3.154	0.003	2.461	0.0127	6.5574	0.0000032	1.679	0.056	4.59144	0.00015
No Match B	3.808	0.00077	1.630	0.061	1.329	0.1012	4.762	0.000106	0.353	0.364	3.4426	0.00167
Comparisons*	t_{16}	p value	t_{16}	p value	t_{16}	p value	t_{16}	p value	t_{16}	p value	t_{16}	p value
Same l >Same s	6.1564	0.000006	3.036	0.0156	4.856	0.00035	1.093	0.5808	1.072	0.599	0.4856	1.0
NoA >NoB	6.0789	0.000007	5.304	0.000142	2.5706	0.041	1.2096	0.488	0.57208	0.287	0.8377	0.829
Same l >NoA	5.58767	0.00002	0.8185	0.848	0.2668	0.39	1.417	0.3512	0.1244	0.451	0.8465	0.819
Same s >NoB	5.5102	0.000023	3.0855	0.014	2.019	0.12	1.537	0.2876	1.5201	0.295	1.1969	0.497

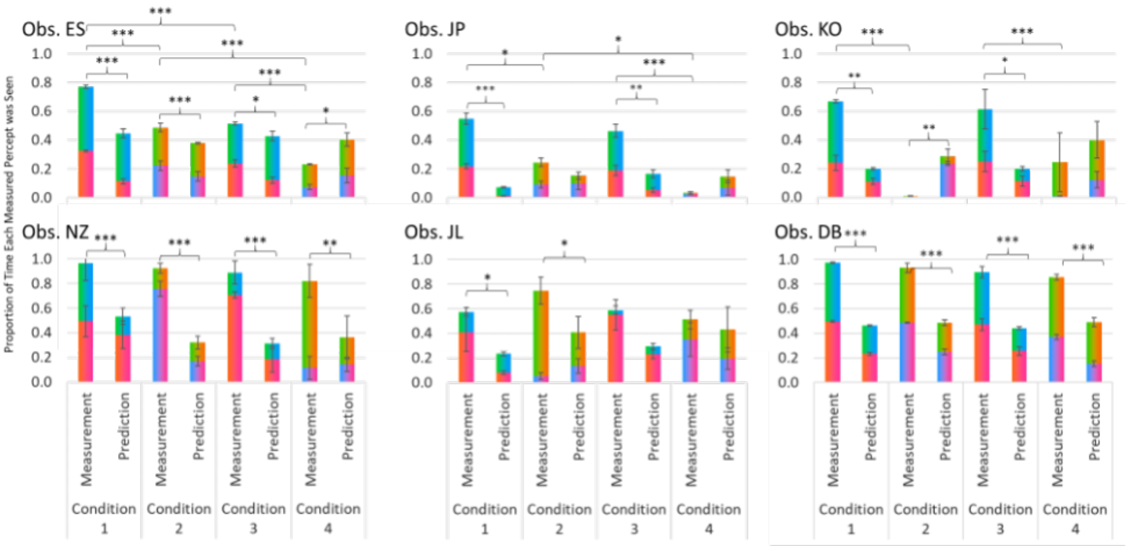

Figure 7.2: Results for all six observers for Experiment 5. Each graph shows the condition and whether the data is a two-disc measurement or an independence prediction along the x-axis and the total proportion of time each percept was seen up the y-axis. The colors in the bars represent the grouped colors perceived: a pink/orange bar represents the time the observer perceived one disc as pink and the other as orange, and so on. Error bars are standard errors across the three days of measurements. Significance bars show both the orthogonal contrasts testing for grouping and the non-orthogonal contrasts testing for differences between condition measurements. Significance codes: * $p<0.05$, ** $p<0.01$, *** $p<0.001$, and comparisons without marks are not significant.

Specifically, all six observers showed significant grouping in condition 1, which was expected and essentially a replication of Exp. 4 condition 4 with solid discs instead of the chromatic induction stimuli (Fig. 7.2). Also, four of the six observers showed significant grouping for condition 2, indicating that grouping could occur for colors that shared S/(L+M) values, also as expected (Fig. 7.2). The last two conditions also showed significant grouping for some of the observers, which was not expected. For condition 3, which mirrored condition 1, five of the six observers showed significant grouping (Fig. 7.2). And finally, in condition 4, two of the six observers showed significant grouping (Fig. 7.2). Condition 4 had the most differences across observers, with one showing a significant effect and two showing a non-significant effect in the opposite direction from grouping – i.e., the observers saw orange with lime and pink with blue significantly less often than predicted by independence. This may be due to the very high proportions of time these observers perceived blue and orange, which were not part of a grouped set, and thus not measured in the grouping measurements.

The non-orthogonal contrasts revealed some significant differences between conditions. Though all conditions showed significant grouping for some observers, the conditions with shared chromatic information (conditions 1 and 2) were predicted to have higher total grouping times than the conditions without shared chromatic information (conditions 3 and 4). This was only the case for one of the six observers for condition 1 and two of the six observers for condition 2 (Fig. 7.2). More observers showed a significant difference between grouping for orange and pink or lime and blue (conditions 1 and 3) than for orange and lime or pink and blue (conditions 2 and 4). Three observers showed a significant difference between conditions 1 and 2 such that condition 1 with shared L/(L+M) values had more total dominance time than condition 2 with shared S/(L+M) values (Fig. 7.2). The same three observers showed a significant difference between conditions 3 and 4. Here, condition 3, with the same perceived colors as condition 1, had more total dominance time than condition 4, with the same perceived colors as condition 2. Thus, overall "redder" and "greener" colors grouped more often than "yellower" and "bluer" colors.

Altogether, these results show that chromatically ambiguous discs do not need to have a shared L/(L+M) value in order to group. Instead, discs will also group based on a shared S/(L+M) value or based on similarity of color in either the l or s dimension. As a post-hoc inference, these surprising results may be due to mechanisms associated with color constancy, a topic that is similar to grouping. In natural viewing, the visual system links together regions of a uniform surface despite changing illumination across the surface (Foster, 2011; Nascimento & Foster, 2000; Fine, MacLeod, & Boynton, 2003; Barbur & Spang, 2008). This suggests a role for color constancy, a perceptual phenomenon in which viewing a uniform surface under varying illumination yields a perceived uniform color surface ("relational" color constancy; Foster, 2011). This holds true both for surfaces at a single time under different illumination (e.g., caused by shadows, highlights, etc.) and for surfaces over time with a changing illuminant (e.g., changes over the course of a day due to varying angles of the sun or changes in artificial lighting). Although the chromaticity varies across an object, these differences can be reconciled so the observer perceives the object as having a constant surface color, even if the observer can perceive the variations in color over the object caused by shadows or highlights. Though the chromaticity hitting the retina is physically different from each region across the surface, the observer is still able to group it together. The same mechanisms that drive color constancy may have driven the results of conditions 3 and 4, where the chromaticity is physically different, but the observers can group them nonetheless.

CHAPTER 8

EXPERIMENT 6: DOES GROUPING ACT ON COMPETING NEURAL REPRESENTATIONS THAT HAVE ONLY ONE SHARED PERCEPTUAL OUTCOME?

8.1 Rationale

The results from the five experiments thus far point to joint resolution of ambiguity, i.e. grouping, that is dependent on common competing representations. Take for instance two discs that were chromatically ambiguous with the same two possible color percepts. The ambiguity from these discs will be resolved as a grouped percept, meaning an observer will perceive both discs as the same color more often than chance. In Exp. 1, grouping was eliminated when competition was between two different kinds of neural representation (monocular vs binocular) even though what they were representing was identical ("red" and "green"). In Exp. 2 and 3, two plaids appeared together more often than chance despite an unshared color. In that case, only competing representations of orientation and pattern were common between the two regions, thus those competing representations drove the grouped resolution of ambiguity. In Exp. 4 and 5, two regions appearing different colors and having different physical chromaticities were grouped based on similarity of chromaticity and color. These results suggest that the neural process for grouping components of the visual field together may depend on their neurally ambiguity itself. Prior to resolving ambiguity, multiple perceptual outcomes are possible from these multistable stimuli. In the previous experiments here, the perceptual outcomes were always matched in some regard in both locations, e.g., both discs could appear "redder" above and below fixation or "greener" above and below fixation. Here, the question tested is whether grouping can occur when some perceptual outcomes are not possible in both locations, and thus the specific neural representations competing are not identical.

Focusing again on Exp. 1, the two discs did not appear the same color more often than chance even though they shared ambiguous chromaticity and perceptual colors. This was due to neural competition for the two discs at different levels of the visual system, as induced by different presentation methods (SBR vs ISR). The present experiment tested a related pairing. Here, all ambiguity was created using the same method (ISR), thus ensuring a shared neural level of resolution (binocular). The difference here lies in the ambiguous chromaticity and color percepts. Instead of *both* regions rivaling between "red" and "green," one region rivaled, for instance, in "red" and "purple". Here, both regions had the same level of neural competition: a binocularly-driven representation of "red" competing with a binocularly-driven representation of "green" in one location, and a binocularly-driven representations of "red" competing with a binocularly-driven representations of "purple" in another location.

There are two possible outcomes here. [1] Resolution of ambiguity based on neural competition of two identical or similar neural representations predicts no grouping will occur (i.e., observers see both discs as "red" at the level of chance) because the competing representations themselves are not matched in their specific chromatic representations. That is, for grouping to occur, both representations competing for dominance must be shared in the two separate regions. [2] Grouping based on competition between neural representations of the same feature without identical feature identities predicts grouping does occur (i.e., observers perceive both discs as "red" significantly more than chance) because one of the neural representations is of the same chromaticity (here, both discs can appear "red" because of the binocularly-driven representations of "red" in both locations) and both regions have the same ambiguous feature (i.e., competing chromaticities).

Based on the experiments presented in this dissertation, the working hypothesis was that no grouping would occur. As summarized above, the previous findings presented here indicate that common neural competition drives grouping and that potential perceptual outcomes do not significantly impact resolution. Also, previous work in the lab indicated that no grouping was found with a shared ambiguous feature if none of the specific feature values were shared by the sets of dichoptic stimuli. Specifically, this was shown by pairing an ambiguously “red”/”green” disc with an ambiguously “blue”/”yellow” disc; no color was seen with any other significantly more often than chance, even though both regions had competing chromaticities (Wang, 2016).

8.2 Methods

8.2.1 Stimuli

Stimuli for the two conditions were solid chromatic discs presented dichoptically. Three chromaticities were used: [L/(L+M), S/(L+M)] of [0.72, 0.3] called “red,” [0.61, 0.3] called “green,” and [0.665, 1.7] called “purple.” The “control” condition replicated the main grouping finding from both sets of chromatic discs alternating between the same two chromaticities above and below fixation. These chromaticities could be “red” rivaling with “green” in both locations, “red” rivaling with “purple” in both locations, or “green” rivaling with “purple” in both locations (Fig. 6.1a). The “mismatch” condition presented all six possible combinations of discs such that the top and bottom disc could only appear identical in one color but not another. The combinations were: “red”/”green” rivalry above or below fixation paired with “red”/”purple” rivalry in the other location; “green”/”red” rivalry above or below fixation paired with “green”/”purple” rivalry in the other location; and “purple”/”red” rivalry above or below fixation paired with “purple”/”green” rivalry in the other location (Fig. 6.1b). The location of each disc was counterbalanced for six total trials. Conditions with top and bottom discs alone were included to calculate independence predictions as before.

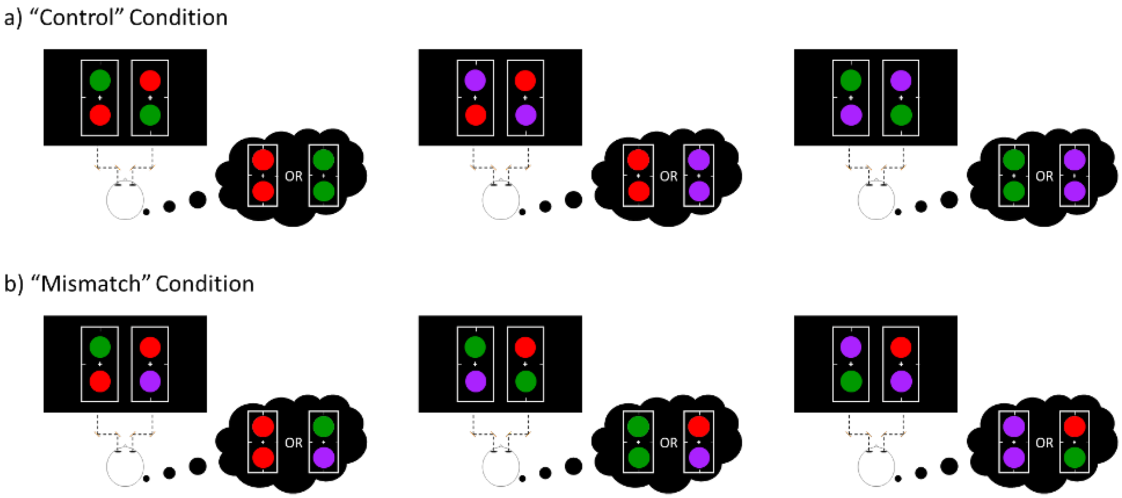

Figure 8.1: Stimuli and measured percepts for Exp. 6. Each image shows the dichoptic discs used for each color set of each condition in the black rectangle representing the CRT screen. The thought bubbles show the two measured percepts for each condition. a) Stimuli for the control condition. Each of the three color sets had the possibility to match in both colors above and below fixation, as shown in the thought bubbles depicting the measured percepts. b) Stimuli for the mismatch condition. Each of the three color sets is one of two location counterbalances. The measured percepts shown in the thought bubbles were of either both discs appearing the same color or both discs appearing different colors (and different from the first, "grouped" color).

8.2.2 Procedure

Each condition was viewed six times in a single day, and the whole experiment lasted four days with the first as practice. The trials lasted 70 seconds total, but only the last 60 seconds were recorded in order to control for onset effects and differential adaptation between the two eyes.

For the control condition, observers reported when they perceived the colors above and below fixation to be identical (Fig. 6.1a). There were three color sets, each run twice in a day to have six measurements from one day. For the mismatch condition, observers reported two kinds of percepts: both discs identical in color and both discs their other color. For instance, if the top disc was rivaling between "red" and "green" and the bottom disc was rivaling between "red" and "purple," then the two percepts measured were [1] both discs "red" and

[2] top disc "green" and bottom disc "purple" (Fig. 6.1b). Observers were instructed not to press any buttons when their percepts were mixed or patchy, swapped in time rapidly with the stimulus swap within a single eye, or were some combination of colors that were not one of the two measured percepts.

8.2.3 Observers

Five observers (three female) participated in this experiment. Four observers were naïve to the purpose of the study, and one was the author. All observers had first participated in Exp. 5 so had previous exposure to ISR stimuli. This included participant GK who was eliminated from Exp. 5 because of very low dominance times.

8.3 Results & Discussion

Prior to analysis, the results from each color set was averaged. For the mismatch condition, the results were averaged separately for the two types of color percepts (both same color and different colors). Three orthogonal contrasts were performed to test for a grouping effect for the three percept types (both discs same color for the control condition and for the mismatch condition, and both discs different colors for the mismatch condition). One non-orthogonal contrast compared the "both same color" measurements for the control with the mismatch conditions (Table 8.1).

The control condition showed significant grouping for both discs appearing the same color for all five observers, as expected (Fig. 8.2). The same percept measurement for the mismatch condition is in contrast to this result, supporting the hypothesis that identical neural competition does affect whether grouping will occur. Only one observer showed significant grouping for both discs appearing the same in the mismatch condition (Fig. 8.2). One observer showed a significant effect in the opposite direction: less total time when both discs appeared the same than predicted by independence (Fig. 8.2). The remaining

Table 8.1: t values and p for the contrasts performed separately for each observer. The first three rows of values represent the grouping comparisons between the two-disc measurements and their independence predictions, separately for each percept type for the mismatch condition. The last row of values represents the contrast between the two listed two-disc measurements.

	Observers										
		ES		DB		GK		KO		JL	
		t_{12}	p value	t_{12}	p value	t_{12}	p value	t_{12}	p value	t_{12}	p value
Grouping Tests											
	Control	6.5753	0.0000131	8.625	0.00000086	1.824	0.0465	4.4432	0.000401	1.9195	0.0395
	Mismatch Same	1.039	0.159	4.908	0.00018	0.4089	0.3449	9.2009	0.000000436	0.0840	0.467
	Mismatch Different	3.7048	0.0015	11.423	0.0000000417	3.9785	0.00091	5.724	0.0000477	2.908	0.0065
	Comparison	t_{12}	p value	t_{12}	p value	t_{12}	p value	t_{12}	p value	t_{12}	p value
	Control>Mismatch Same	4.8484	0.000199	3.090	0.0046	2.8272	0.0076	9.508	0.000000307	1.477	0.0827

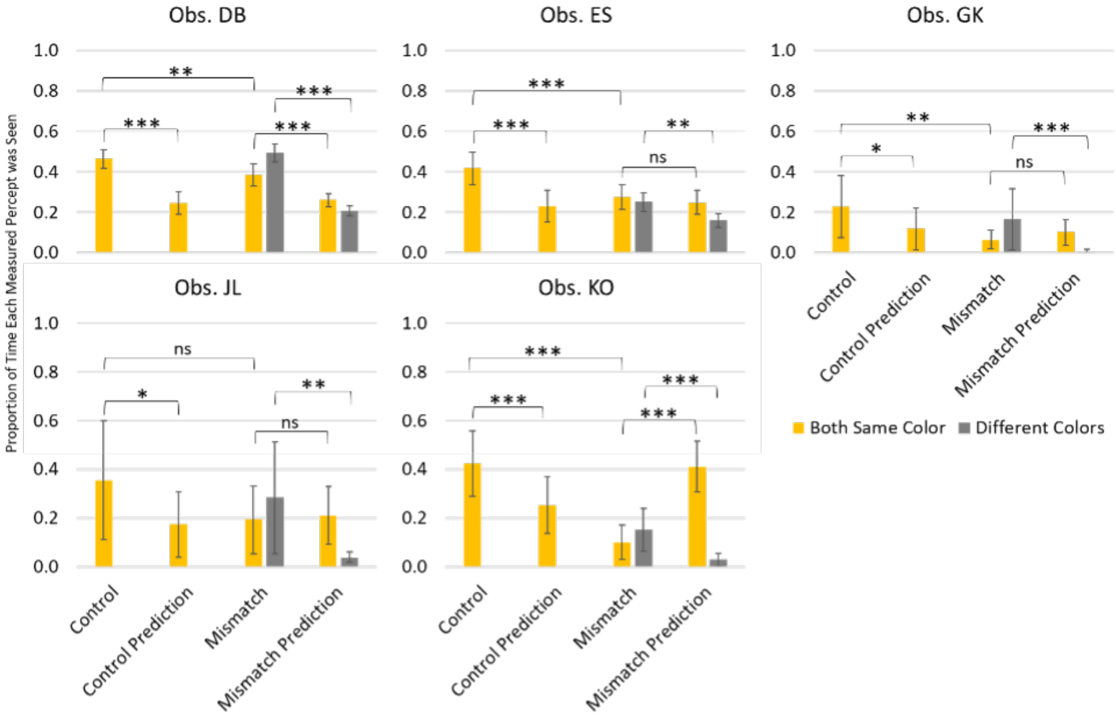

Figure 8.2: Results for Exp. 6. Each observer's graph shows the condition along the x-axis and the proportion of time each measured percept was seen on the y-axis. Yellow bars show when observers perceived both discs as the same color for both conditions and grey bars show when observers perceived both discs as different colors for the mismatch condition. Error bars are standard errors of the mean. Significance codes: * $p<0.05$, ** $p<0.01$, *** $p<0.001$, and ns $p>0.05$

three observers showed no significant differences between the measurement from both discs appearing the same and its independence prediction (Fig. 8.2). This result is in contrast also with the different color measurement from the mismatch condition: all five observers showed significant grouping of the different colors (Fig. 8.2). Finally, the contrast comparing when both discs appeared the same between the control and mismatch conditions was significant for four of the five observers. Overall, there is less time when both discs appear the same in the mismatch condition compared to the control condition.

These results show that grouping occurs when there is identical neural competition from the discs above and below fixation such that *both* representations competing must be the same. When the chromaticities rivaling above and below fixation are not *both* identical, this grouping occurs less often (significantly for four of five observers, and trending in the same direction for the fifth). Further, unequal neural competition results in observers perceiving the maximally different percepts more often than chance (significantly for every observer). This was a novel finding found with grating stimuli (Peiso & Shevell, 2020) and is now replicated here. These results support the hypothesis that the visual system groups based on identical neural competition in not only the feature domain (here, chromaticity) but also the specific identity of the feature (i.e., “red” and “green” and “purple” here) must be identical above and below. Grouping does not significantly occur when some perceptual outcomes are not possible in both locations, and thus the specific neural representations competing are not identical.

CHAPTER 9

DISCUSSION

Multiple neurally ambiguous regions of the visual field will group to be resolved non-independently, thus forming coherent percepts. This finding has been shown numerous times using a multitude of methods and stimuli aiming to answer many different questions about the visual system's grouping mechanisms (e.g., Adams & Haire, 1957; Kovács, Papathomas, Yang, & Fehér, 1996; Alais & Blake, 1999; Ngo, Miller, Liu, & Pettigrew, 2000; de Weert, Snoeren, & Koning, 2005). The experiments in this dissertation aimed to answer a fundamental question: what level of visual processing drives this ubiquitous grouping? Specifically, what are the competing neural representations that evoke grouping? The overarching hypothesis for all experiments presented here was that identical competing neural representations from the dichoptic stimuli drive grouping. The representations could be identical in the features they represented (orientation of gratings or chromaticity, for instance), specific levels within a feature domain (specific chromaticities, for instance), or the neural level of representation for grouping to occur (monocular vs. binocular).

Experiment 1 found that having a shared level of neural competition determined if two regions could group or not. Consistent with the overarching hypothesis, results support that two regions did group together when their neural competition was at the same level of the visual system, whether that be monocular (as from discs in SBR) or binocular (as from discs in ISR), but did not group when neural competition was at different levels (as from discs in presented in SBR paired with discs in ISR).

Experiment 2 found that grouping could act on binocularly-integrated representations. Dichoptic grating stimuli that always had rivaling orientations could fused to form plaids, a binocularly-integrated percept. Observers perceived grouped plaids at the same time as they perceived gratings grouped by orientation, indicating competition between three binocular-level representations grouped based on a common pattern. This is consistent with the overarching hypothesis because the neural competition was between representations that were identical in the features they represented: pattern broadly, but orientation and binocularly-integrated plaid specifically. This grouping persisted even when one region had competing representations of chromaticity and the other region did not.

Experiment 3 found that grouped plaids were not reported due to inhibition of interocular suppression, but instead due to binocular-level competition between three representations: those from 45-degree gratings, 135-degree gratings, and binocularly-integrated plaid. Prior to these results, it was plausible that plaids occurred only due to inhibition of the typical suppression that takes place when viewing dichoptic stimuli. Experiment 3a tested whether a global inhibition of suppression could produce results that looked like grouped plaids. Instead, it was found that two dichoptic regions would group only when their binocularly-integrated representations were identical. Two regions with different binocularly-integrated representations, and thus different fused percepts, never produced results consistent with grouping and instead had total dominance times that were either not significantly different from the independence predictions or not significantly different from the inhibition-of-suppression predictions. Experiment 3b tested whether inhibition of suppression could occur in one region of the visual field that is induced by a stimulus in another region. This was not found and results instead indicated that different kinds of plaids (single-colored or bi-colored) retained their individual predominance (high for single-colored plaids and low for bi-colored plaids) when alone or paired together. All together, these two sets of results show that the grouped plaid finding from Experiment 2 was not due to inhibition of suppression.

Experiment 4 determined what neural level of representation in the visual system mediated grouping when the neural level of competition was identical (unlike in Exp. 1 with different neural levels of competition). This experiment tested if grouping would act on neural representations of the stimulus (low-level competition between representations of chromaticity) or of the percept (higher-level competition between representations of color). The results indicate that grouping can act on both representations of chromaticity and color and, in fact, neither has to be identical in order to group. Analysis of the stimuli post-hoc gave rise to a hypothesis that having simply some chromatic information shared across the competing stimuli could drive grouping, here specifically matching L/(L+M) values. Either way, common competition between neural representations of chromaticities, either identical or not, was able to produce grouped percepts for all observers.

Experiment 5 tested whether grouping was dependent on a shared L/(L+M) value. Instead, a surprising result showed that grouping could occur for chromatically ambiguous discs when they shared an L/(L+M) value, or an S/(L+M) value, or neither! This demonstrated that common competition of chromatically ambiguous discs results in grouping even when the specific chromaticities themselves are not exactly identical. Instead, the grouping here was based only on similarity of chromaticities and colors rather than necessitating identical neural representations of color or chromaticity.

Experiment 6 further investigated how precisely matched the competing neural representations must be in order for grouping to occur. As in Exp. 4 and 5, here there was common competition between representations of chromaticity, but again, the chromaticities were not identical. This experiment addressed the question of whether grouping occurred for two regions with only one shared competing neural representation within the same feature domain. Here, unlike in Exp. 4 and 5, one of the competing neural representations of chromaticity was identical above and below fixation while the other dichoptic counterpart was not. For all observers, this significantly diminished or eliminated the grouping found when both neural representations of chromaticity were identical above and below fixation; moreover, the single shared possible percept did not significantly lead to grouped percepts. This suggests grouping occurs when both neural representations are identical above and below fixation, and is consistent with the overarching hypothesis that identical neural competition leads to grouping.

The specific aims of this dissertation focused on what kinds of neural representations grouping could act on. These six experiments show that grouping occurs for low-level neural representations that have common competition. The visual system can group the ambiguous regions based on that common competition and resolves that they are identical; if there is no common competition, then the joint resolution of ambiguity occurs at levels not significantly different from chance. The experiments presented here indicate that lower-level neural representations significantly influence grouping, again supporting the hypothesis that grouping is an early process that then leads to specific grouped percepts rather than the percepts driving the grouping. This is demonstrated with observers perceiving grouped colors in Exp. 1, 4, 5, and 6. Exp. 2 and 3 demonstrate that though resolution occurs at a lower level, binocularly-integrated representations also group. This may indicate that grouping can be mediated by multiple levels of the visual system, with an emphasis on equal competition rather than the level at which that competition takes place.

9.1 Grouping based on identical competing neural representations

The experiments in this dissertation show that grouping for dichoptic stimuli occurs when the competing neural representations are identical. In the case of Exp. 1, the neural representations had to be at identical neural levels, such as a binocular level for ISR stimuli. In the case of Exp. 2, 3, 4, and 5, the neural representations had to be identical in what feature they were representing, such as orientation. In the case of Exp. 6, the neural representations had to be identical in both competing representations despite a common feature the neural populations represented (chromaticity).

Several results found may seem counter to this overarching hypothesis. First, consider the finding of grouped individual gratings and plaid in Exp. 2, condition C. This condition paired two dichoptic gratings with orthogonal orientations, but one had competing chromaticity and the other did not. In other words, one disc had competing representations of chromaticity and of orientation while the other had competing representations of only orientation. Previous work has shown that observers do not experience feature misbinding when viewing the first kind of ambiguous gratings, which suggests that the features are linked and the competition occurs between representations of the whole grating rather than separate competition between representations of chromaticity and competition between representations of orientation (Slezak, Coia, & Shevell, 2019). This especially follows from grouping acting on representations of these complete gratings with representations of plaids simultaneously (i.e. competition between three kinds of representations rather than only two as is typically thought). Generally speaking, these results indicate that grouping is acting on identical competition between representations for patterns and whether or not those patterns have different chromaticities is irrelevant (in regards to grouping, not in regards to total dominance time) because all the features of the patterns have already been linked.

Second, Exp. 4 and 5 showed that the specific chromaticities and colors that were represented by the competing neural populations did not need to be identical. Instead, grouping occurred for discs matched only in L/(L+M) values, only in S/(L+M) values, or neither. The groups, however, never differed by a large amount in either the L/(L+M) or S/(L+M) direction (only ever up to 0.03 L/(L+M) and 0.3 S/(L+M)). This coupled with the nature of neural representations in general could explain how grouping was found in these cases. Neural representations are never as specific as coding for one singular stimulus parameter, like the famed “grandmother cell” (Bowers, 2009; Quian Quiroga & Kreiman, 2010; Bowers, 2011). Instead, there is a distribution of neural responses for every stimulus (Erickson, 1984; Averbeck, Latham, & Pouget, 2006). In the case of chromaticity, though a neural population may respond best to a certain chromaticity, it will also respond to similar chromaticities nearby in color space (Gegenfurtner & Kiper, 2003; Emery et al., 2017). Essentially, neural representations are continuous rather than discrete and that may account for the grouping of non-identical but similar chromaticities.

Third, Exp. 5 and 6 have seemingly conflicting results when considering that Exp. 5 found grouping without common chromaticities and Exp. 6 did *not* find grouping without common chromaticities. Here the difference lies in the neural competition in each of these cases. Exp. 5 had competition that was not identical in chromaticity in either location. Instead, there was a competition between similar chromaticities in both locations. Essentially, there was either rivalry between “reddish” and “greenish” discs or “blueish” and “yellowish” discs, but the rivalry above and below fixation was always of the same kind. Exp. 6 very specifically had only one identical chromaticity above and below fixation but the chromaticities it rivaled with in each location were specifically not similar in any way (very different in both the L/(L+M) dimension and S/(L+M) dimension – chromaticities similar to those used when no grouping was found for “red”/”green” rivalry paired with “blue”/”yellow” rivalry (Wang, 2016)). This key difference between the two experiments may speak to the flexibility of the neural mechanisms of grouping in the case of Exp. 5 while also emphasizing that all four competing neural representations (two on top, two on bottom) need to be identical/similar for maximal grouping to occur in the case of Exp. 6.

These nuances do not contradict the overarching hypothesis, but instead show how robust the support is here. In each of the cases described above, grouping persisted in key instances where the competing neural representations were the same (as with representations of plaids and feature-linked gratings, and with various similar chromaticities) and was not found significantly where the competing neural representations were substantially different (as with specifically mismatched chromatic rivalry).

Previous work in the literature speaks to these conclusions, as well. Though multiple cues that could drive grouping were often confounded in past studies, their results are in line with the findings presented here. Multiple chromatically ambiguous discs group and are all resolved to be the same color when they are presented in SBR (Kovács et al., 1996), when they are presented in either SBR or ISR (Slezak & Shevell, 2018), when they are in CISR and swapped at different frequencies, at different stereoscopic depths, and with onset asynchronies (Wang, 2016). While these studies confound perceived color and physical chromaticity, this dissertation shows that the distinction has no significant bearing on grouping. Other work examined how the visual system grouped multiple dichoptic regions that could form one coherent percept. Though this grouping could be driven by the low-level cues of similarity in each feature domain (like color, orientation, or spatial frequency) or by the higher-level interpretation of the Gestalt formations, grouping was found at significant rates. This was shown for concentric ring stimuli (forming a coherent bulls-eye) paired with horizontal bar stimuli (forming coherent stripes; Ngo et al., 2000) and for half fields that could form coherent arrows, crosses, or diamonds of the same or different colors (de Weert, Snoeren, & Koning, 2005).

Different kinds of ambiguous stimuli like random dot clouds and bistable images with and without motion have been used to test for coupled swap rates, which would indicate non-independent ambiguity resolution. Two or more similarly ambiguous stimuli have tightly coupled swap rates, indicating that when ambiguity is shared between different stimuli, they are grouped. This grouping did not occur for stimuli that were not similarly ambiguous (e.g., random dot clouds with different axes of rotational motion; Maier et al., 2003). This fits in well with the findings presented here because Exp. 1 and 6 showed that stimuli that were not similarly ambiguous did not significantly lead to grouping. These findings especially dovetail with each other because of the difference in methods and stimuli used for each of the experiments – the results are not limited to one kind of ambiguity but instead speak to a broader mechanism.

Other research delves into degree of ambiguity affecting grouping, pairing ambiguous stimuli with unambiguous stimuli to determine if stable interpretations of the input influence how the neural ambiguity from competing neural representations are resolved. It was found that unambiguous input has no significant influence on the resolution of ambiguity from CISR discs (Lee, Slezak, & Shevell, 2018) or ambiguity from a diverse set of stimuli (Grossmann & Dobbins, 2003). In the latter case, grouping occurred for dissimilar physical stimuli if their ambiguity was equal. Grouping was not found for ambiguous stimuli paired with unambiguous stimuli, even if their physical forms were similar, like with a Necker cube paired with an unambiguous rendering of a three-dimensional cube (Grossmann & Dobbins, 2003).

One previous study that is analogous to Exp. 1 may seem to provide conflicting conclusions to those presented here. A single circular stimulus split into three segments, each with a different kind of rivalry (orthogonal gratings in SBR, ISR, and Monocular Rivalry (MR)), was perceived to be a coherent grating significantly more often than chance (chance as modeled in this dissertation; Pearson & Clifford, 2005). To put these findings into context, another study provides evidence of different resolution of ambiguity within the different visual pathways (Denison & Silver, 2012). There, stimuli that were biased towards processing in the parvocellular pathway tended to be resolved at a binocular level while stimuli biased towards processing in the magnocellular pathway tended to be resolved at a monocular level. This is relevant here because the SBR, ISR, and MR stimuli described above had luminance contrast and the ISR stimuli had to be embedded in a 20 Hz flicker (as in Logothetis, Leopold, & Sheinberg, 1996). It may be that the luminance contrast made the ISR stimuli analogous to the SBR stimuli in its processing in the magnocellular pathway, resulting in grouped percepts that were not necessarily resolved together across different neural levels. The monocular rivalry seems to be a unique case considering its dominance profile increased by about 60% of its total dominance time when the other two forms of rivalry were added to it (Pearson Clifford, 2005). Exp. 1 in this dissertation did not make use of monocular rivalry, so this result cannot be put in context here.

Altogether, the findings from this dissertation add specificity to previous findings about how multiple regions with neural ambiguity can group. Here, percept-level and stimulus-level neural representations were disentangled where previously they were confounded (Kovács et al., 1996; Ngo et al., 2000; de Weert, Snoeren, & Koning, 2005; Wang, 2016; Slezak & Shevell, 2018), though evidence here points specifically to color percepts and physical chromaticity having no significant differential effect on grouping. The primary finding that neural ambiguity must be similar or identical in two or more regions for grouping to occur fits in seamlessly with previous findings from motion (Maier et al., 2003), bistable image (Grossmann & Dobbins, 2003), and CISR disc (Lee, Slezak, & Shevell, 2018) ambiguity resolution.

9.2 General implications of grouping

The experiments laid out in this dissertation all make use of very carefully selected stimuli and present them to observers through a special apparatus. All this may make it seem as though the results found here are not applicable to the real world, especially considering how often a lay person views anything through a haploscope. Despite this perception, these results speak to how the visual system resolves everyday ambiguity that exists from almost every visual scene. Observers are able to perceive whole objects as coherent even when they are visually broken up (like viewing something past a partial occluder) or part of a greater whole. These experiments speak to how the visual system can both group a visual scene together as part of a garden, for instance, and also differentiate the specific plants in the garden from one another. The visual system uses cues of how similar the multiple neural representations from such a scene are and thus can group them. It also detects how the multiple neural representations are different in order to not group together distinct objects, or plants in this example. In fact, the visual system can both group by similarity so that different regions appear the same and also perceptually enhance the differences between the regions (see Peiso & Shevell, 2020). Both are important for an observer acting on a visual scene, and this dissertation shows that the ways in which the scene is ambiguous actually contributes to determining what visual components belong together and which should remain separate.

9.3 Conclusion

The visual system's task is to take ambiguous neural input and combine it a way such that coherent objects are perceivable. Evidence presented here points to common competing neural representations determining whether the ambiguity for multiple regions is resolved together (grouping). The features represented by the competing neural populations (chromaticity or pattern, for example) and the neural level of competition (monocular or binocular, for example) determines if two regions that *can* appear the same, *do* appear the same. In the larger context of perceiving a coherent world, the manifestation of the inherent ambiguity is key – *how* are neural representations similar or different from one another.

Exp. 1 showed that grouping does not persist significantly when neural competition is at different neural levels. Exp. 2 showed that two binocularly-integrated neural representations of the same patterns group. Exp. 3 showed that the phenomenon of perceiving plaids together more than chance in Exp. 2 was not due to inhibition of suppression. Exp. 4 showed that chromatically ambiguous discs need not be identical in color or chromaticity to group. Exp. 5 showed that this grouping was not reliant on a shared L/(L+M) value. Exp. 6 showed that grouping is diminished or eliminated when the specific neural representations that are competing within a feature domain are not identical. All support the overarching hypothesis that grouping occurs when competing neural representations from dichoptic stimuli that are identical or at least very similar in some way, and was not found when the competition is sufficiently different.

REFERENCES

[1] Adams, P. A., & Haire, M. (1958). Structural and conceptual factors in the perception of double-cube figures. The American journal of psychology, 548-556.

[2] Alais, D., & Blake, R. (1999). Grouping visual features during binocular rivalry. Vision research, 39(26), 4341-4353.

[3] Barbur, J. L., & Spang, K. (2008). Colour constancy and conscious perception of changes of illuminant. Neuropsychologia, 46(3), 853-863.

[4] Barlow, H. B. (1981). The Ferrier lecture, 1980. Proceedings of the Royal Society of London. Series B. Biological Sciences, 212(1186), 1-34.

[5] Barlow, H. B. (1986). Why have multiple cortical areas?. Vision research, 26(1), 81-90

[6] Blake, R. (2001). A primer on binocular rivalry, including current controversies. Brain and mind, 2(1), 5-38.

[7] Blake, R., & Logothetis, N. K. (2002). Visual competition. Nature Reviews Neuroscience, 3(1), 13.

[8] Bowers, J. S. (2009). On the biological plausibility of grandmother cells: implications for neural network theories in psychology and neuroscience. Psychological review, 116(1), 220.

[9] Bowers, J. S. (2011). What is a grandmother cell? And how would you know if you found one?. Connection Science, 23(2), 91-95.

[10] Brascamp, J., Sohn, H., Lee, S. H., & Blake, R. (2013). A monocular contribution to stimulus rivalry. Proceedings of the National Academy of Sciences, 110(21), 8337-8344.

[11] Buck, S. L., & DeLawyer, T. (2014). Dark versus bright equilibrium hues: rod and cone biases. JOSA A, 31(4), A75-A81.

[12] Burke, D., Alais, D., & Wenderoth, P. (1999). Determinants of fusion of dichoptically presented orthogonal gratings. Perception, 28(1), 73-88.

[13] Carter, O., & Cavanagh, P. (2007). Onset rivalry: Brief presentation isolates an early independent phase of perceptual competition. PloS one, 2(4), e343.

[14] Christiansen, J. H., D'Antona, A. D., & Shevell, S. K. (2017). Chromatic interocular-switch rivalry. Journal of vision, 17(5), 9-9.

[15] de Weert, C. M., Snoeren, P. R., & Koning, A. (2005). Interactions between binocular rivalry and Gestalt formation. Vision Research, 45(19), 2571-2579.

[16] Denison, R. N., & Silver, M. A. (2012). Distinct contributions of the magnocellular and parvocellular visual streams to perceptual selection. Journal of Cognitive Neuroscience, 24(1), 246-259.

[17] D'Zmura, M., & Lennie, P. (1986). Mechanisms of color constancy. JOSA A, 3(10), 1662-1672.

[18] Emery, K. J., Volbrecht, V. J., Peterzell, D. H., & Webster, M. A. (2017). Variations in normal color vision. VI. Factors underlying individual differences in hue scaling and their implications for models of color appearance. Vision research, 141, 51-65.

[19] Erickson, R. P. (1984). On the Neural Bases of Behavior: Thomas Young's early nineteenth–century theory of color vision serves as a unifying principle for understanding how the brain works. American Scientist, 72(3), 233-241.

[20] Fine, I., MacLeod, D. I., & Boynton, G. M. (2003). Surface segmentation based on the luminance and color statistics of natural scenes. JOSA A, 20(7), 1283-1291.

[21] Finlayson, G. D., & Trezzi, E. (2004, January). Shades of gray and colour constancy. In Color and Imaging Conference (Vol. 2004, No. 1, pp. 37-41). Society for Imaging Science and Technology.

[22] Foster, D. H. (2011). Color constancy. Vision research, 51(7), 674-700.

[23] Gegenfurtner, K. R., & Kiper, D. C. (2003). Color vision. Annual review of neuroscience, 26(1), 181-206.

[24] Grossmann, J. K., & Dobbins, A. C. (2003). Differential ambiguity reduces grouping of metastable objects. Vision Research, 43(4), 359-369.

[25] Hong, S. W., & Shevell, S. K. (2006). Resolution of binocular rivalry: Perceptual misbinding of color. Visual neuroscience, 23(3-4), 561-566.

[26] Hong, S. W., & Shevell, S. K. (2008). Binocular rivalry between identical retinal stimuli with an induced color difference. Visual neuroscience, 25(3), 361-364.

[27] Hong, S. W., & Shevell, S. K. (2009). Color-binding errors during rivalrous suppression of form. Psychological science, 20(9), 1084-1091.

[28] Hurlbert, A., & Wolf, K. (2004). Color contrast: a contributory mechanism to color constancy. Progress in brain research, 144, 145-160.

[29] Ives, H. E. (1912). On heterochromatic photometry. Philosophical Magazine, 24(845), 53.

[30] Kanizsa, G. (1976). Subjective contours. Scientific American, 234(4), 48-53.

[31] Kellman, P. J., & Shipley, T. F. (1991). A theory of visual interpolation in object perception. Cognitive psychology, 23(2), 141-221.

[32] Kingdom, F. A., Kardous, N., Curran, L., Gheorghiu, E., & Bell, J. (2014). Saliency interactions between the ‘L-M’and ‘S’cardinal colour directions. Vision research, 95, 36-42.

[33] Kirk, R. E. (2013). Experimental design: Procedures for the behavioral sciences. Thousand Oaks, CA: SAGE Publications, Inc. doi: 10.4135/9781483384733

[34] Kovacs, I., Papathomas, T. V., Yang, M., & Fehér, Á. (1996). When the brain changes its mind: Interocular grouping during binocular rivalry. Proceedings of the National Academy of Sciences, 93(26), 15508-15511.

[35] Lee, H. C. (1986). Method for computing the scene-illuminant chromaticity from specular highlights. JOSA A, 3(10), 1694-1699.

[36] Lee, R. J., & Smithson, H. E. (2016). Low levels of specularity support operational color constancy, particularly when surface and illumination geometry can be inferred. JOSA A, 33(3), A306-A318.

[37] Lee, S. H., & Blake, R. (1999). Rival ideas about binocular rivalry. Vision research, 39(8), 1447-1454.Lee, S. M., Slezak, E., & Shevell, S. (2018). Ambiguity contributes to grouping of color objects. Journal of Vision, 18(10), 586-586.

[38] Levelt, W. J. (1965). On binocular rivalry (Doctoral dissertation, Van Gorcum Assen).

[39] Liu, L., Tyler, C. W., & Schor, C. M. (1992). Failure of rivalry at low contrast: evidence of a suprathreshold binocular summation process. Vision research, 32(8), 1471-1479.

[40] Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivalling during binocular rivalry?. Nature, 380(6575), 621.

[41] MacLeod, D. I., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. JOSA, 69(8), 1183-1186.

[42] Maier, A., Wilke, M., Logothetis, N. K., & Leopold, D. A. (2003). Perception of temporally interleaved ambiguous patterns. Current Biology, 13(13), 1076-1085.

[43] Marr, D., & Hildreth, E. (1980). Theory of edge detection. Proceedings of the Royal Society of London. Series B. Biological Sciences, 207(1167), 187-217.

[44] Monnier, P. (2008). Standard definitions of chromatic induction fail to describe induction with S-cone patterned backgrounds. Vision research, 48(27), 2708-2714.

[45] Monnier, P., & Shevell, S. K. (2003). Large shifts in color appearance from patterned chromatic backgrounds. Nature neuroscience, 6(8), 801.

[46] Nascimento, S. M., & Foster, D. H. (2000). Relational color constancy in achromatic and isoluminant images. JOSA A, 17(2), 225-231.

[47] Necker, L. A., 1832. Observations on some remarkable Optical Phenomena seen in Switzerland; and on an Optical Phenomenon which occurs on viewing a Figure of a Crystal or geometrical Solid The London and Edinburgh Philosophical Magazine and Journal of Science, 1(5), 329-337.

[48] Ngo, T. T., Miller, S. M., Liu, G. B., & Pettigrew, J. D. (2000). Binocular rivalry and perceptual coherence. Current Biology, 10(4), R134-R136.

[49] Papathomas, T. V., Kovács, I., & Conway, T. (2005). Interocular grouping in binocular rivalry: Basic attributes and combinations. Binocular rivalry, 155-168.

[50] Pearson, J., & Clifford, C. W. (2005). When your brain decides what you see: Grouping across monocular, binocular, and stimulus rivalry. Psychological science, 16(7), 516-519.

[51] Peiso, J. R., & Shevell, S. K. (2020). Seeing fruit on trees: enhanced perceptual dissimilarity from multiple ambiguous neural representations. JOSA A, 37(4), A255-A261.

[52] Quian Quiroga, R., & Kreiman, G. (2010). Measuring sparseness in the brain: comment on Bowers (2009).

[53] Rubin E, 1921. Visuell wahrgenommene Figuren (Copenhagen: Gyldendals) Rubin, N. (2003). Binocular rivalry and perceptual multi-stability. Trends in Neurosciences, 26(6), 289-291.

[54] Shevell, S. K., & Wang, W. (2016). Color-motion feature-binding errors are mediated by a higher-order chromatic representation. JOSA A, 33(3), A85-A92.

[55] Slezak, E., & Shevell, S. K. (2018). Perceptual resolution of color for multiple chromatically ambiguous objects. JOSA A, 35(4), B85-B91.

[56] Spelke, E. S. (1990). Principles of object perception. Cognitive science, 14(1), 29-56.

[57] Stanley, J., Forte, J., Cavanagh, P., & Carter, O. (2011). Onset rivalry: The initial dominance phase is independent of ongoing perceptual alternations. Frontiers in Human Neuroscience, 5, 140.

[58] Stuit, S. M., Paffen, C., van der Smagt, M., & Verstraten, F. (2011). What is grouping during binocular rivalry?. Frontiers in human neuroscience, 5, 117.

[59] Tong, F., Meng, M., & Blake, R. (2006). Neural bases of binocular rivalry. Trends in cognitive sciences, 10(11), 502-511.

[60] Treisman, A. (1962). Binocular rivalry and stereoscopic depth perception. Quarterly Journal of Experimental Psychology, 14(1), 23-37.

[61] Treisman, A. (1985). Preattentive processing in vision. Computer vision, graphics, and image processing, 31(2), 156-177. Van Essen, D. C., Anderson,

[62] C. H., & Felleman, D. J. (1992). Information processing in the primate visual system: an integrated systems perspective. Science, 255(5043), 419-423.

[63] Wang, W. (2016). Grouping in resolving chromatic interocular-switch rivalry (Doctoral dissertation, The University of Chicago).

[64] Wang, W., & Shevell, S. K. (2014). Do S cones contribute to color-motion feature binding?. JOSA A, 31(4), A60-A64.

[65] Wertheimer, M. (1923/1938). Laws of organization in perceptual forms. In A Source Book of Gestalt Psychology, ed. & trans. Ellis, W., (pp. 71–88). London: Routledge & Kegan Paul. (Original work published in 1923 as Untersuchungen zur Lehre von der Gestalt II, in Psychologische Forschung 4, 301–350.)

[66] Wheatstone, C. (1838). XVIII. Contributions to the physiology of vision.—Part the first. on some remarkable, and hitherto unobserved, phenomena of binocular vision. Philosophical transactions of the Royal Society of London, 128, 371-394.

[67] Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. Proceedings of the National Academy of Sciences, 100(24), 14499-14503.

[68] Wilson, H. R. (2007). Minimal physiological conditions for binocular rivalry and rivalry memory. Vision research, 47(21), 2741-2750.

[69] Wu, D. A., Kanai, R., & Shimojo, S. (2004). Vision: Steady-state misbinding of colour and motion. Nature, 429(6989), 262.

[70] Xian, S. X., & Shevell, S. K. (2004). Changes in color appearance caused by perceptual grouping. Visual Neuroscience, 21(3), 383-388.