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Extending Levelt's Propositions to perceptual multistability involving interocular grouping

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ABSTRACT

Levelt's Propositions are central to understanding a wide range of multistable perceptual phenomena, but it is unclear whether they extend to perceptual multistability involving interocular grouping. We presented split-grating stimuli with complementary halves of the same color (either red or green) to human subjects. The subjects reported four percepts in alternation: the two stimuli presented to each eye (half red and half green), as well as the two single color (all red or all green), interocularly grouped percepts. Increasing color saturation lead to increased reports of the single color percept in most subjects, indicating increased predominance of grouped percepts (Levelt's Proposition I). This increase in predominance was due to a decrease in the average dominance duration of single-eye percepts, with grouped percept dominance largely unaffected. This agrees with a generalization of Levelt's Proposition II, as the average dominance duration of the stronger (in this case single-eye) percept was primarily affected by changes in stimulus strength. Moreover, in agreement with Levelt's Proposition III the alternation rate between percepts increased as the difference in the strength of the percepts decreased.

1. Introduction

We are remarkably adept at interpreting noisy and ambiguous visual inputs (Fiser, Berkes, Orbán, & Lengyel, 2010; Kersten, Mamassian, & Yuille, 2004). However, sometimes competing interpretations of a stimulus are not disambiguated, and different interpretations are perceived in alternation. For example, binocular rivalry occurs when the two eyes are presented with disparate images. Instead of perceiving a fusion of the two images, one experiences intermittent switching between two distinct percepts (Blake & Logothetis, 2002; Wheatstone, 1838). Multistable perceptual phenomena have been used extensively to study visual awareness and its underlying cortical mechanisms (Leopold & Logothetis, 1996; Polonsky, Blake, Braun, & Heeger, 2000; Sterzer, Kleinschmit, & Rees, 2009; Tong, Meng, & Blake, 2006).

Levelt's observations (Levelt, 1965) have become a touchstone for experimental and modeling studies of perceptual rivalry (Blake, 1989; Moreno-Bote, Rinzel, & Rubin, 2007; Shpiro, Curtu, Rinzel, & Rubin, 2007; Said & Heeger, 2013; Seely & Chow, 2011; Wilson, 2003). Levelt's original Propositions relate *stimulus strength, predominance* (the fraction of time a percept is dominant), and *dominance durations* (the duration of the dominant percept) in bistable binocular rivalry (Brascamp, Klink, & Levelt, 2015): (I) Increasing the strength of the stimulus presented to one eye increases the perceptual predominance of that stimulus; (II) Increasing the difference in stimulus strengths between the two eyes increases the perceptual dominance duration of the stronger stimulus; (III) Increasing the difference in stimulus strength

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between the two eyes reduces the perceptual alternation rate; (IV) Increasing stimulus strength in both eyes while keeping it equal between eyes increases the perceptual alternation rate. Levelt's Propositions also hold in other cases of bistable perceptual rivalry such as bistable rotating structure-from-motion (Klink, Ee, & Wezel, 2008), bistable ambiguous plaids (Moreno-Bote, Shapiro, Rinzel, & Rubin, 2010), and motion-induced blindness (Bonneh, Donner, Cooperman, Heeger, & Sagi, 2014; Carter & Pettigrew, 2003).

However, whether Levelt's Propositions hold in the case of rivalry between more than two percepts is not clear. Such multistable rivalry can occur when multiple patches of two visual scenes are intermingled and the results presented to different eyes simultaneously. In this case, observers intermittently perceive the original, coherent scenes as well as the images presented to each single eye (Kovacs, Papathomas, Yang, & Feher, 1996).

We hypothesized that Levelt's Propositions extend to perceptual multistability involving interocular grouping (Diaz-Caneja, 1928; Kovacs et al., 1996; Suzuki & Grabowecky, 2002). To explore this extension, we categorize percepts into two groups: the stimuli presented to each eye, and interocularly grouped percepts. Following Brascamp et al. (2015) we say that a stimulus parameter that affects a percept's predominance affects its strength. Levelt's Propositions now generalize to: *(I) Increasing grouped percept strength increases the perceptual predominance of those percepts; (II) Increasing the difference between the percept strength of grouped and single-eye percepts increases the perceptual dominance duration of the stronger percepts; (III) Increasing the difference in percept strengths between grouped percepts and single-eye percepts reduces the perceptual alternation rate; (IV) Increasing percept strength in both grouped percepts and single-eye percepts while keeping it equal among percepts increases the perceptual alternation rate* (Brascamp et al., 2015). Here "percept strength" refers to any stimulus parameter that leads to an increase in the relative predominance of a percept.

To test this generalization of Levelt's Propositions we used split-grating stimuli (See Fig. 1A) for which subjects reliably reported four percepts in alternation: single-eye percepts – the two stimuli presented to each eye (percepts 1 and 2 in Fig. 1B), as well as two interocularly grouped, single color percepts (3 and 4 in Fig. 1B). We hypothesized that an increase in color saturation[2] increases the strength of the coherent, grouped percepts. Indeed, we found that for most subjects an increase in color saturation lead to increased predominance of grouped percepts (Proposition I). At the same time the dominance duration of single-eye (stronger) percepts decreased, while that of grouped (weaker) percepts remained largely unaffected (Proposition II). As a consequence, the alternation rate increased with a reduction in the difference of percept strengths (Proposition III). A more detailed analysis showed that these effects are primarily due to the increased strength of all red percepts (percept 3 in Fig. 1B). In addition, we found that an increase in the predominance of grouped percepts was partly due to an increase in the fraction of visits to grouped percepts.

Color has been previously reported to affect interocular grouping (Kovacs et al., 1996). However, to our knowledge the changes in the predominance of grouped images due to changes in color saturation, and the corresponding extensions of Levelt's Propositions to multistable rivalry have not been explored before. We have reported these results previously on a preprint server and at a confeernce (Jacot-Guillarmod et al., 2016; Wang et al., 2016).

[2] Throughout the paper, we use the term 'saturation' defined as one of the axes of the HSV color space. We manipulated percept strength by changing the stimulus only along the S (saturation) axis of the HSV space. However, as discussed in details in the Methods section, note that a change along a single axis in one color space corresponds to changes along multiple axis in other color spaces.

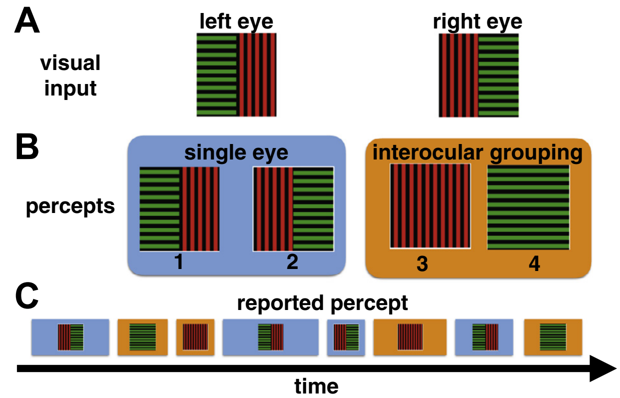


Fig. 1. (A) An example of the stimuli presented to the left and right eyes. Gratings were always split so that halves with the same color and orientation could be matched via interocular grouping, but were otherwise randomized across trials and blocks (see Methods). (B) Subjects typically reported seeing one of four percepts – two single-eye and two grouped – at any given time during a trial. (C) A typical perceptual time series reported by a subject, showing the stochasticity in both the dominance times and the order of transitions between percepts.

2. Methods

2.1. Experiment

Observers Nine observers with normal or corrected-to-normal vision, including three of the authors (AJ, ZK, YW), participated in this experiment. Six were naive to the experimental hypotheses and three were not. The experiments were conducted according to a protocol approved by the University of Houston Committee for the Protection of Human Subjects and in accordance with the federal regulations 45 CFR 46, the ethical principles established by the Belmont Report, and the principles expressed in the Declaration of Helsinki. All participants provided their written informed voluntary consent following the consent procedure approved by the University of Houston Committee for the Protection of Human Subjects. Data are presented for all nine subjects.

Apparatus The visual stimuli used in the experiment were generated using a VSG visual stimulus generator card (VSG 2/5, Cambridge Research Systems). The stimuli were displayed on a calibrated 19" high resolution color monitor with a 100 Hz frame rate. Monitor calibration was carried out using CRS colorCAL colorimeter. A head/chin rest was used to stabilize observers' head position. The distance between the monitor and the observer was set to 108 cm. We used a stereoscopic mirror arrangement (haploscope) in order to present the left and right stimuli separately to the left and right eyes. It consisted of four mirrors, whose horizontal/vertical positions and inclinations could be adjusted using screws.

Stimuli Subjects were presented with variations of the stimulus depicted in Fig. 1A. A square composed of two orthogonal gratings was presented to each eye using the haploscope. The orthogonal gratings were arranged so that interocular grouping resulted in a percept with single, i.e., uniform orientation (horizontal or vertical). In order to have a stimulus parameter to control the percept strength for this interocular grouping we have added color to our stimuli. As a result interocular grouping lead not only to a uniform orientation but also to a uniform color of the percept (Fig. 1A). Stalmeier and de, 1988 studied the contribution of color and luminance contrast to binocular rivalry. In their experiments, the stimulus to one eye consisted of achromatic concentric rings whereas the stimulus to the other eye consisted of radial patterns made of isoluminant color pairs. They showed that the dominance duration of the colored radial pattern, hence the strength of the chromatic input, increased as the chromatic distance, $d(u,v)$, between the colors in the CIE 1960 space increased up to $d(u,v) \approx 0.1$, and saturated thereafter. There were also significant differences in dominance durations depending on the criterion for isoluminance (flicker photometry vs minimal distinct border (MDB) criterion), and the direction of change in the color space. Finally, their results showed inter-subject variability both in the effectiveness of pure chromatic contrast and achromatic contrast.

In preliminary observations, we found color saturation effectively controlled percept strength for interocular grouping. Hence, grating halves were assigned a color – either red or green – at two different saturation levels, 0.4 or 0.9. The HSV color space coordinates for red and green were (0.497, 0.4/0.9, 0.7) and (120.23, 0.4/0.9, 0.7), respectively, with the pair of values 0.4/0.9 referring to two different levels of color saturation. At low saturation ($S = 0.4$), the corresponding CIE 1960 (u,v) coordinates for red were $(0.214, 0.3)$ and $L = 57.7\ \text{cd/m}^2$; whereas for green they were $(0.169, 0.315)$ and $L = 72\ \text{cd/m}^2$. At high saturation ($S = 0.9$), the corresponding CIE 1960 (u,v) coordinates for red were $(0.333, 0.329)$ and $L = 25.4\ \text{cd/m}^2$ whereas for green they were $(0.127, 0.360)$ and $L = 57.6\ \text{cd/m}^2$. At low saturation, the chromatic distance $d(u,v)$ between the two colors was $d(u,v) = 0.05$ and the achromatic distance in terms of Michelson Contrast (MC) was $MC = 0.11$. At high saturation, these values were $d(u,v) = 0.21$ and $MC = 0.388$. Hence, by changing color saturation from 0.4 to 0.9, stimulus strength was increased significantly both in chromatic and achromatic dimensions. It is also noteworthy that the chromatic distance values of 0.05 and 0.21 fall to the left and right of the critical distance $d(u,v) \approx 0.1$ at which the strength of the chromatic stimulus for binocular rivalry starts to saturate as observed by Stalmeier and de Weert (1988).

To allow for interocular grouping of complementary patches, the two halves with the same orientation always shared the same color at the same saturation level, and were shown to opposite hemifields of either eye. For example, the combination horizontal green/vertical red presented to the left eye determined the combination vertical red/horizontal green presented to the right eye, as well as the two grouped percepts – vertical red and horizontal green (See Fig. 1B). In total, there were four possible stimulus arrangements, all completely determined by any half of a stimulus presented to one eye. The two squares were displayed on a grey background (0.0, 0.0, 0.2): $(u,v) = (0.188, 0.442)$ and $L = 23.88\ \text{cd/m}^2$ and were contained within a square frame with a protruding horizontal and vertical line to help image alignment.

Experimental procedure Each *session* was divided into six 3-min trials separated by a 90-s resting period. To account for the time it took subjects to adjust to the stimuli and form stable percepts, the first 30 s of each trial were not analyzed. Eye preference (the tendency to prefer visual input from one eye to the other) is common in human observers: approximately two-thirds of the population is right-eye dominant and one-third left-eye dominant (Chaurasia & Mathur, 1976). We therefore have designed our experiment so that the association between color and orientation was maintained within a single session, but was randomized across sessions to reduce possible effects due to eye preference among subjects. For example, we used a vertical red/horizontal green left eye stimulus across some sessions (Fig. 1A). In contrast, saturation and the position of the horizontal grating was randomized across the six trials. Within one session, each saturation level appeared in three trials and each grating positioning occurred in three trials.

Four subjects finished 6 total sessions (AJ, MA, ZK, ND), three subjects finished 5 sessions (FG, YW, ML), one subject finished 4 sessions (AB) and the remaining one finished 7 sessions (ZM). Therefore, after discarding the initial 30 s of each trial, a total of about 90 min of data over about 36 trials was collected per subject: about 18 trials for each saturation conditions, with 3 trials per level and color/orientation pairing. See Github deposit (https://github.com/YunjiaoWang/multistableRivalry.git) for more details.

Subjects were asked to indicate the dominant percept by holding down one of four different buttons (1, 2, 3, 4) on a gamepad. They were instructed to press button 1 when perceiving a split grating with left part red; button 2 when perceiving split grating with left part green; button 3 when perceiving an all red grating; and button 4 when perceiving an all green grating. When the perceived image did not correspond to one of these four options, subjects were instructed to release all buttons. We also recorded the times during which no stable percept was reported, and labeled these times as "percept 0". Such a report typically marked a transition between percepts, but could also be followed by a transition to the same percept. The average duration of percept 0 ranged from 0.2–0.9 s. Before the beginning of the experiment, subjects were familiarized with the controller. The distribution of the times of different percepts, including no stable percepts (percept '0'), and further details are presented in the Supplementary Material (Data analysis: Section 'Distribution of time duration without stable percept') in our Github repository.

2.2. Data analysis

We performed the statistical analysis in R and provide a description of the analysis below. Commented code, as well as all collected data are available in the Github repository.

We conducted all data analyses under a Bayesian framework. Standard significance tests would allow us to reject the null hypothesis that a color saturation change has no effect on dominance time, but would not allow us to accept the alternative hypothesis. In contrast, a Bayesian approach allows us to conclude that for some subjects a change in color saturation did affect percept dominance. We believe that showing the probabilities that this effect was present is more informative than concluding that a null hypothesis is rejected at some (arbitrary) significance level. Our use of Bayesian statistics means that confidence intervals are replaced by credible intervals, and traditional notions of "significance" do not apply. Instead of using a fixed threshold for significance, we provide the probabilities that a change in color saturation affects the perception of the stimuli, given the data (Wasserstein & Lazar, 2016).

Importantly, in our analysis we use a hierarchical model to analyze concurrently the data from all subjects in the experiment (Gelman & Hill, 2006). Such models address the issue of multiple comparisons and provide efficient estimates (Gelman, Hill, & Yajima, 2012).

Predominance of grouped percepts Using the time series recorded from each trial, we computed the predominance of grouped percepts. Predominance is the fraction of time that subjects reported a grouped percept, T_{grouped}, by pressing the corresponding gamepad button, out of the total time they reported any percept (percepts 1, 2, 3 or 4), i.e.

$$r(i) = \frac{T_{\text{grouped}}(i)}{T_{\text{grouped}}(i) + T_{\text{single}}(i)}.$$

Here i is the number of the trial, with 18 trials at each color saturation level (0.4 and 0.9). This is equivalent to the fraction of time that buttons 3 or 4 were pressed out of the total time any button was pressed during trial i. In our analysis, we partitioned trials based on the color saturation level used for each trial, grouping across all other conditions. We analyzed changes in predominance using a linear Student-t regression model to account for skewness in the data. We included the condition (low/high color saturation) as a covariate and set the degrees of freedom of the t distribution to

4 to provide robust inference while avoiding computational difficulties often encountered when using a prior for the degrees of freedom (Fonseca, Ferreira, & Migon, 2008). Letting r_{ij} be the predominance for subject j in trial i, the model is specified as:

$$\begin{aligned} & r_{ij} \sim t_4(\mu_{ij}, \sigma^2), \\ & \mu_{ij} = \beta_{0j} + \beta_{1j} x_{ij}, \\ & \beta_{0j} \sim \text{Normal}(\beta_0, \tau_0^2), \quad \beta_{1j} \sim \text{Normal}(\beta_1, \tau_1^2), \end{aligned} \tag{1}$$

where x_{ij} is the color saturation indicator (1 for 0.9, 0 for 0.4). The random regression coefficients β_{0j} and β_{1j} allow the effects of color saturation to vary across subjects. This hierarchical model assumes that the effects from different subjects are similar but not identical and come from the same population with overall means of β_0 and β_1. Prior distributions for the overall saturation effects β_0 and β_1 were independent and normal with mean 0, and variance 10^4. We used Uniform(0, 100) priors for the standard deviation of the random effects, τ_0 and τ_1, and Uniform(0, 1000) for σ. We estimated the mean difference in the fraction of time between the two saturation levels and its 95% credible interval (CI) and the probability that the difference is greater than 0. We performed an equivalent analysis to examine whether the mean dominance time of the single eye or grouped percepts changed across conditions.

From the ith trial in each condition, we also computed ratios of the number of visits to grouped percepts, N_{grouped}, over the number of all visits to either single-eye or grouped percepts,

$$n(i) = \frac{N_{\text{grouped}}(i)}{N_{\text{grouped}}(i) + N_{\text{single}}(i)}.$$

We used the model specified in Eq. (1) to analyze $n(i)$ and determine the change in the fraction of visits to the grouped or single-eye percepts across conditions.

Single-color images To examine the effect of saturation of the colors green and red individually we divided the grouped percepts into two sets – a set of all green (percept 4) and a set of all red (percept 3). We then analyzed the effect of color saturation on predominance, and dominance duration for each color individually using the same statistical approach and models as in the case of grouped percepts.

Transition probabilities To estimate the transition probabilities between percept types, we classified percepts into two states: single-eye, S, corresponding to percepts 1 and 2, and grouped, G, corresponding to percepts 3 and 4. For each trial, we converted the data into two binary sequences: One sequence contained all transitions from state S with transitions from S to S denoted by 1, and from S to G by 0. The second sequence contained transitions from G, those from G to G denoted by 1, and from G to S by 0. We used all data obtained by each subject in a given condition (low/high color saturation) to estimate the transition probability from S to S, and from G to G. The model is specified as

$$\begin{aligned} & y_{t,ij} \sim \text{Bernoulli}(p_{ij}), \\ & p_{ij} = \theta_{0j} + \theta_{1j} x_{ij}, \\ & \theta_{0j} \sim \text{Beta}(\omega * (\kappa - 2) + 1, (1 - \omega) * (\kappa - 2) + 1)), \\ & \theta_{1j} \sim \text{Normal}(\theta_1, \tau_1^2), \end{aligned} \tag{2}$$

where $y_{t,ij}$ is the binary sequence of transitions described above, t is the sequence index, i the color saturation index, and j the subject index. Here p_{ij} is the probability of $y_{t,ij} = 1$ in condition i for subject j, and x_{ij} is the color saturation indicator (0 for saturation 0.4, and 1 for saturation 0.9). We used vague priors: a uniform prior on the interval $[0, 1]$ for the mode, ω, and a Gamma prior with rate and shape both equal to 0.01 for the concentration parameter, κ. The prior distribution for the overall saturation effect, θ_1, was normal with mean 0, and variance 10^4, and independent of all other parameters. We used a Uniform(0, 100) prior for the standard deviation of the random effect τ_1.

Model implementation All Bayesian models were implemented via Markov Chain Monte Carlo methods in JAGS. We used 3 MCMC chains with at least 20,000 iterations after an initial burn-in of 4000 iterations. We assessed convergence by calculating the Gelman-Rubin diagnostic, $\widehat{R}$ for all parameters.

3. Results

Nine observers were presented with two split-grating images simultaneously to each eye using a haploscope (See Methods). Subjects reported one of four possible percepts by pressing buttons on a game pad. We examined how the fraction of time subjects perceived grouped images (the *predominance* of grouped images) depended on color saturation.

Dominance durations follow a gamma distribution The dominance duration, the total time that a subject reported seeing a percept for single-eye and grouped percepts had the shape of a gamma distribution (See Fig. 2 and Supplementary Material in Github deposit.) This is consistent with previous studies of perceptual multistability (Blake & Logothetis, 2002; Brascamp, van Ee, Pestman, & van den Berg, 2005; van Ee, 2009).

For some, but not all subjects, the mean of single-eye percept times decreased with an increase in color saturation (Fig. 2). A more thorough analysis was therefore needed to determine the effect of color saturation on percept predominance.

Predominance of grouped percepts We first examined whether an increase in color saturation affected the fraction of time grouped percepts were reported. We hypothesized that predominance of grouped percepts increases with color saturation, as a result of a stronger visual cue to bind the two complementary halves of the stimuli presented to each eye into a coherent percept (Wagemans et al., 2012). The data supports this in five out of nine subjects (Fig. 3): For five out of the nine subjects there was a 0.92 or higher probability that the difference in mean predominance times increased with color saturation given the reported observations (See Table in Fig. 3). According to Levelt's Proposition I, we

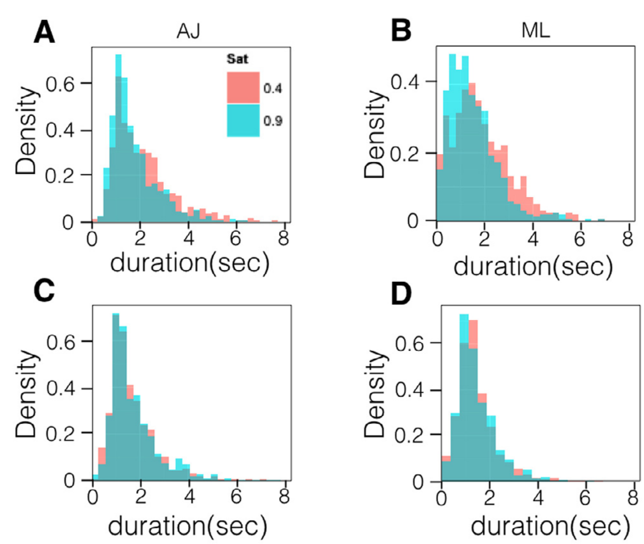
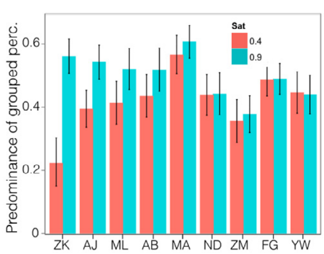


Fig. 2. Dominance times for two subjects, ML and AJ, approximately follow a gamma distribution. (A,B) Histograms of single-eye percept durations are unimodal, but somewhat different between the two saturation conditions. (C,D) Histograms of the grouped percept durations are closer to each other. Each histogram contains data collected from 18 trials of 2.5 min each, amounting to approximately 1200 dominance duration reports (See Methods and Supplementary Material in Github deposit for more details).

thus treated color saturation as a parameter that affected percept strength. There was no evidence that changes in color saturation impacted predominance in the remaining subjects.

We also performed a secondary analysis of the predominance of grouped red and grouped green percepts, and found a larger effect for the grouped red percepts (Fig. 4). This cannot be explained by a strengthening of luminance or image contrast since at high saturation the green color had higher luminance. A similar trend held for achromatic contrast (See Methods). However, it has been reported that in several contexts the color red tends to be more salient than green (Emmanouil, Avigan, Persuh, & Ro, 2013; Lindsey et al., 2010; Stromeyer & Eskew., 1992). Red images may promote a strong top-down attentional signal from higher order areas processing object color (Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998). Furthermore, unlike single-eye percepts, the predominance of grouped green percept did not decrease. Indeed there is some evidence that in three out of the first five subjects, there is a slight increase in the predominance of the grouped green percepts. Thus there is strong evidence that increasing color saturation increases the predominance of the all red percept, and weaker evidence that it increases the predominance of the all green percept. If the strength of the grouped green percept did not increase, we would expect its predominance to decrease, as for single-eye percepts (Fig. 3).



ID	diff.	95% CI	prob.
ZK	0.31	(0.20, 0.41)	0.999
AJ	0.14	(0.06, 0.22)	0.999
ML	0.11	(0.02, 0.20)	0.989
AB	0.09	(-0.01, 0.18)	0.966
MA	0.06	(-0.02, 0.13)	0.928
ND	0.01	(-0.09, 0.10)	0.550
ZM	0.01	(-0.07, 0.10)	0.629
FG	0.01	(-0.06, 0.08)	0.597
YW	-0.00	(-0.09, 0.08)	0.489

Fig. 3. (Plot) Predominance of grouped percepts: here and in all subsequent figures each colored bar indicates the mean at a given color saturation level in a given subject and black error bars denote the 95% credible intervals (See Methods). (Table) Differences between ratios at the two color saturation levels: diff. = difference of predominance means at saturation 0.9 and 0.4; here and in all subsequent (Table) % CI stands for 95% credible interval; 'prob.' is the probability that the predominance of grouped percepts is higher at saturation level 0.9 (See Methods). We use the same ordering of subjects in all subsequent tables and figures, so that the five subjects sensitive to changes in color saturation are listed first.

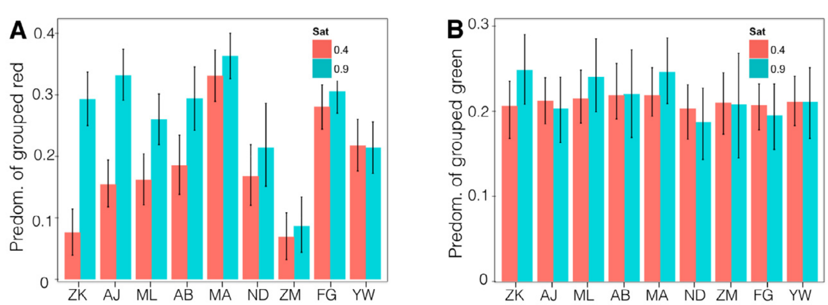
We next examined how this change in predominance was related to both changes in average dominance time and the frequency of visits to single-eye versus grouped percepts.

3.1. Causes of predominance changes

In the case of only two percepts, the number of visits to each percept will differ by at most one per trial (van Ee, 2009), and dominance duration is closely related to predominance. When there are more than two percepts, they do not simply alternate, and the order in which multiple percepts appear can affect predominance (Huguet, Rinzel, & Hupé, 2014; Naber, Gruenhage, & Einhuser, 2010). Thus, to understand changes in predominance we must examine how color saturation influences dominance duration, as well as the number of visits to each percept.

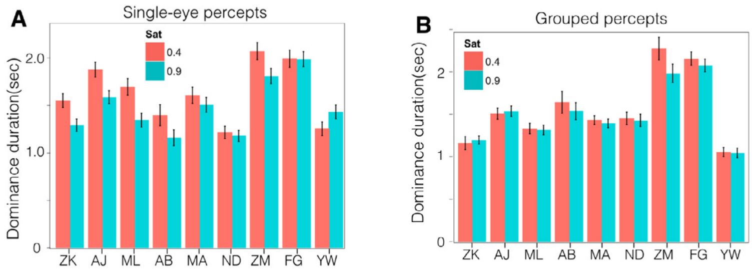
Single-eye percept durations decrease with color saturation We compared the average dominance durations of single-eye and grouped percepts for the two different color saturation conditions in Fig. 5. In six out of nine subjects, there was a higher than 0.95 probability that dominance duration of single-eye percepts decreased as color saturation increased (subjects ZK, AJ, ML, AB, MA, ZM, See Fig. 5A). These included the five subjects for which the predominance of grouped percepts increased. There was no strong evidence that increased color saturation increased the dominance duration of all grouped percepts in any subjects.

The generalization of Levelt's Proposition II states that increasing the difference between the percept strength of grouped and single-eye percepts increases the average perceptual dominance duration of the stronger percepts (Brascamp et al., 2015). By increasing color saturation, we decreased the difference in stimulus strength between single-eye and grouped percepts: In the low color saturation case, the single-eye percepts were stronger, as their predominance was higher than that of grouped percepts



grouped red				grouped green			
ID	diff.	95% CI	prob.	ID	diff.	95% CI	prob.
ZK	0.22	(0.16, 0.28)	0.999	ZK	0.04	(-0.01, 0.10)	0.955
AJ	0.18	(0.12, 0.23)	0.999	AJ	-0.01	(-0.06, 0.03)	0.353
ML	0.10	(0.04, 0.15)	0.999	ML	0.03	(-0.02, 0.08)	0.848
AB	0.11	(0.04, 0.18)	0.999	AB	0.00	(-0.06, 0.05)	0.530
MA	0.03	(-0.02, 0.09)	0.876	MA	0.03	(-0.01, 0.07)	0.885
ND	0.05	(-0.03, 0.13)	0.878	ND	-0.02	(-0.07, 0.03)	0.262
ZM	0.02	(-0.04, 0.08)	0.738	ZM	-0.00	(-0.07, 0.06)	0.499
FG	0.03	(-0.03, 0.08)	0.836	FG	-0.01	(-0.06, 0.03)	0.301
YW	-0.01	(-0.06, 0.05)	0.439	YW	-0.00	(-0.05, 0.04)	0.498

Fig. 4. (A) Predominance of grouped red percept: there is a pronounced increase in predominance with the color saturation in the first six subjects with probability around 0.9. (B) Predominance of grouped green percept: predominance is largely unchanged, with two subjects (ZK, MA) showing a slight increase. (Table) Differences between predominance at the two color saturation levels: values in the table are computed in the same way as in Fig. 3.

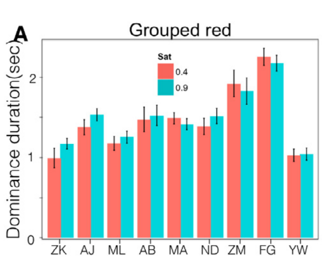


single-eye perc.				grouped perc.			
ID	diff.	95% CI	D-prob.	ID	diff.	95% CI	prob.
ZK	-0.23	(-0.32, -0.14)	0.999	ZK	0.04	(-0.05, 0.13)	0.777
AJ	-0.26	(-0.36, -0.15)	0.999	AJ	0.03	(-0.06, 0.11)	0.714
ML	-0.32	(-0.43, -0.21)	0.999	ML	-0.02	(-0.10, 0.07)	0.333
AB	-0.21	(-0.34, 0.08)	0.999	AB	-0.10	(-0.26, 0.04)	0.075
MA	-0.09	(-0.20, 0.02)	0.950	MA	-0.04	(-0.11, 0.03)	0.142
ND	-0.03	(-0.12, 0.06)	0.743	ND	-0.02	(-0.12, 0.08)	0.303
ZM	-0.21	(-0.32, -0.09)	0.999	ZM	-0.29	(-0.47,-0.08)	0.000
FG	-0.01	(-0.12, 0.11)	0.552	FG	-0.08	(-0.19, 0.02)	0.052
YW	0.16	(0.06, 0.27)	0.001	YW	-0.01	(-0.09, 0.07)	0.396

Fig. 5. Average dominance durations of (A) single-eye percepts and (B) grouped percepts. The average dominance duration of single-eye percepts decreases as color saturation is increased for the subjects who also experience increased grouped percept predominance. (Table) Values in the table are computed in the same way as in Fig. 3. Here 'D-prob.' (on left) is the probability that the dominance duration of single-eye percepts decreases and 'prob.' (on right) is the probability that the dominance duration of grouped percepts increases.

(Fig. 3, for seven of the nine subjects the predominance of grouped percepts was below 0.5 with a probability of 0.94 or higher. See Supplementary Material in Github). At higher color saturation the grouped percepts had a mean predominance of near 0.5 or below for eight subjects. We therefore concluded that the single-eye percepts are stronger. Thus, for most subjects who were sensitive to a change in percept strength the stronger percepts' (single-eye) mean dominance duration decreased, while the weaker percepts' (grouped) durations remained roughly the same. We explore further comparisons with Propositions II-IV in the Discussion.

A separate analysis of dominance duration changes of the grouped green and red percepts showed that changes were less pronounced than those of single-eye percepts (Fig. 6): There was a slight increase in the dominance duration of the grouped red percept (compare corresponding values of the first five subjects in the tables in Fig. 5 on single-eye percepts and Fig. 6 for grouped red case), but this is in line with Proposition II, which allows for slight increases in the dominance duration of percepts whose stimulus strength increases (Brascamp et al., 2015). Furthermore, the decrease in the dominance duration of grouped green percepts was smaller than the decrease for single-eye percepts for four of the first five subjects (compare corresponding values of the first five subjects in the tables in Fig. 7 and also Fig. 7(B)). Thus, in line with Proposition II, the substantial increase in the predominance of the grouped percept was accompanied by a slight to no increase in the dominance duration.



ID	diff.	95% CI	prob.
ZK	0.18	(0.04, 0.32)	0.997
AJ	0.15	(0.04, 0.27)	0.995
ML	0.08	(-0.03, 0.19)	0.915
AB	0.05	(-0.13, 0.22)	0.713
MA	-0.07	(-0.17, 0.02)	0.062
ND	0.13	(0.00, 0.27)	0.976
ZM	-0.09	(-0.32, 0.10)	0.204
FG	-0.08	(-0.22, 0.05)	0.126
YW	0.01	(-0.09, 0.12)	0.605

Fig. 6. The average dominance duration of grouped red shows increases in some subjects and decreases in some others. However, the magnitude of the changes overall are less pronounced as that in single-eye percepts.

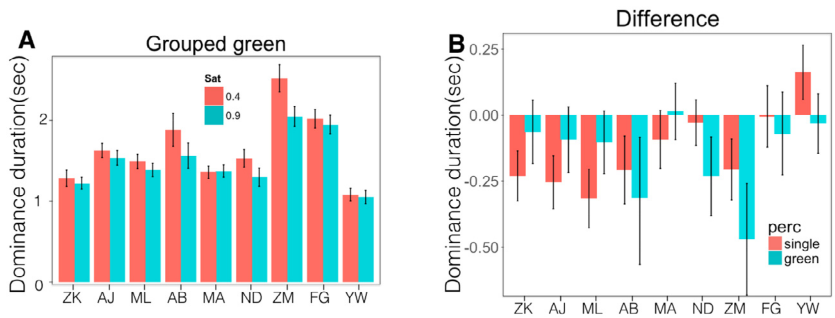
Grouped percept visit frequency increases with color saturation With multiple percepts, each can occur with a frequency between 0% to 50%, excluding self-transitions. This frequency impacts predominance (Naber et al., 2010; Huguet et al., 2014). We therefore examined how the frequency of visits to single-eye and grouped percepts depended on color saturation. Consistent with our results for grouped percept predominance (Fig. 3), the frequency of visits to grouped percepts increased with color saturation in most subjects (Fig. 8, see Methods for details about the analysis): Subjects ZK, AJ, ML and AB (probability > 0.94), and to a lesser degree MA (prob. > 0.82), show a consistent increase in the number of visits to grouped percepts.

We conclude that two main factors contributed to increased predominance of grouped percepts: the average dominance duration of single-eye percepts decreased, while the dominance durations of grouped percepts remained approximately unchanged, and the grouped percepts were visited more frequently when color saturation was high.

3.2. Transitions to grouped percepts increase with color saturation

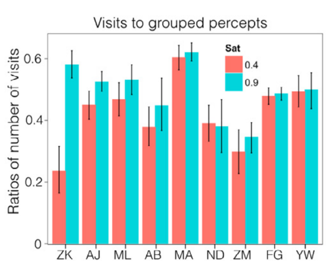
We also analyzed the transition probability between percepts. We focused on the frequency of transitions between each percept type: single-eye or grouped percepts (See Fig. 9A). In doing so, we reduced the number of possible transitions to four: single-eye to grouped, grouped to single-eye, grouped to grouped, and single-eye to single-eye (See Methods).

Our analysis of the frequency of visits to grouped percepts (Fig. 8) suggests an increase in transitions to grouped percepts in the high color saturation condition. Consistent with this trend, we found that the ratio of transitions from single-eye to single-eye percepts decreased in the first five subjects (ZK, AJ, ML, MA, and ZM in Fig. 9B). This implies that the ratio of the transitions from single-eye to grouped percepts increased as color saturation increased. In addition, the ratio of grouped percepts to grouped percepts transitions increased as the color saturation for four out of those five subjects (prob. > 0.94, see Fig. 9C). Thus, there was an increase in the frequency of transitions between grouped percepts. This phenomenon has previously been referred to as



single-eye perc.				grouped green.			
ID	diff.	95% CI	D-prob.	ID	diff.	95% CI	D-prob.
ZK	-0.23	(-0.32, -0.14)	0.999	ZK	-0.06	(-0.18, 0.06)	0.843
AJ	-0.26	(-0.36, -0.15)	0.999	AJ	-0.09	(-0.22, 0.03)	0.929
ML	-0.32	(-0.43, -0.21)	0.999	ML	-0.10	(-0.22, 0.02)	0.956
AB	-0.21	(-0.34, 0.08)	0.999	AB	-0.32	(-0.57, -0.09)	0.998
MA	-0.09	(-0.20, 0.02)	0.950	MA	0.01	(-0.09, 0.12)	0.394
ND	-0.03	(-0.12, 0.06)	0.743	ND	-0.23	(-0.38, -0.08)	0.999
ZM	-0.21	(-0.32, -0.09)	0.999	ZM	-0.47	(-0.68, -0.26)	0.999
FG	-0.01	(-0.12, 0.11)	0.552	FG	-0.07	(-0.23, 0.08)	0.819
YW	0.16	(0.06, 0.27)	0.001	YW	-0.03	(-0.14, 0.08)	0.716

Fig. 7. (A) Average dominance duration of grouped green; (B) Average difference of dominance duration of grouped green and single-eye percepts at the two difference color saturations. (Table) The magnitude of the changes overall are less pronounced as that in single-eye percepts especially for the first five subjects as can be seen in (B) and by comparing corresponding numbers in the table: values in the table are computed in the same way as in Fig. 3.



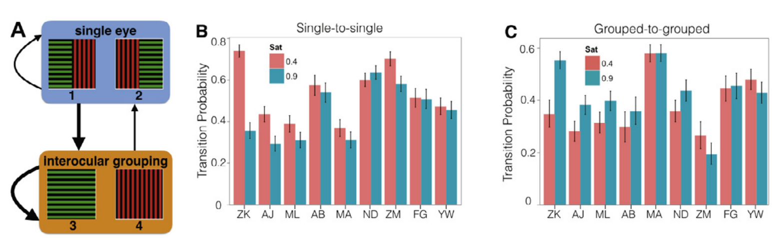
ID	diff.	95%CI	prob.
ZK	0.32	(0.25, 0.39)	0.999
AJ	0.08	(0.02, 0.14)	0.996
ML	0.07	(0.00, 0.13)	0.975
AB	0.06	(-0.01, 0.14)	0.948
MA	0.03	(-0.03, 0.08)	0.829
ND	-0.01	(-0.09, 0.06)	0.351
ZM	0.04	(-0.03, 0.10)	0.873
FG	0.01	(-0.05, 0.07)	0.630
YW	0.02	(-0.05, 0.08)	0.700

Fig. 8. Frequency of visits to grouped percepts out of all visits. The mean increases for eight out of nine subjects when color saturation is increased from 0.4 to 0.9. The five subjects who experienced an increase in grouped percept predominance, also showed an increase in the frequency grouped percept visits.

"trapping", as it suggests a subject's perception is trapped in a subset of all possible percepts (Suzuki & Grabowecky, 2002).

4. Discussion

Multistable perceptual phenomena have long been used to probe the mechanisms underlying visual processing (Leopold & Logothetis, 1999). While binocular rivalry is used most frequently (Blake & Logothetis, 2002), different insights can be obtained with stimuli that are integrated to produce interocularly grouped percepts (Kovacs et al., 1996; Suzuki & Grabowecky, 2002). These experiments are particularly informative when guided by Levelt's Propositions, originally developed in the case of binocular rivalry



single-to-single				grouped-to-grouped			
ID	diff.	95% CI	D-prob.	ID	diff.	95% CI	prob.
ZK	-0.37	(-0.42, -0.32)	0.999	ZK	0.19	(0.12, 0.25)	0.999
AJ	-0.14	(-0.19, -0.09)	0.999	AJ	0.09	(0.04, 0.15)	0.999
ML	-0.08	(-0.13, -0.03)	0.998	ML	0.08	(0.03, 0.13)	0.999
AB	-0.04	(-0.10, 0.03)	0.868	AB	0.06	(-0.01, 0.13)	0.941
MA	-0.06	(-0.12, -0.01)	0.985	MA	0.01	(-0.04, 0.05)	0.640
ND	0.03	(-0.01, 0.08)	0.087	ND	0.08	(0.02, 0.13)	0.996
ZM	-0.12	(-0.17, -0.07)	0.999	ZM	-0.06	(-0.12, 0.00)	0.032
FG	-0.01	(-0.08, 0.05)	0.645	FG	0.02	(-0.05, 0.08)	0.712
YW	-0.02	(-0.08, 0.04)	0.774	YW	-0.04	(-0.10, 0.02)	0.089

Fig. 9. (A) Diagram showing the case where single-to-single percept transitions are less likely than grouped-to-grouped transitions, represented by the thickness of transition arrows. (B,C) The probability of transitions from (B) single-to-single percepts, and (C) grouped-to-grouped percepts. The probability of a single-to-single transition tends to decrease with color saturation whereas the grouped-to-grouped transition probability tends to increase in the cohort of subjects whose grouped predominance increased. The table gives the posterior probability of a decreases in single-to-single transition, and an increase in grouped-to-grouped transitions given the data.

(Brascamp et al., 2015; Levelt, 1965). Here we used this approach to identify how color saturation influences the dynamics of perceptual multistability involving interocular grouping.

Related work We showed that multiple cues (color and collinearity) affect interocular grouping. The major goal of our study was to extend and test Levelt's Propositions for multistable percepts that include interocular grouping. Levelt's Propositions make predictions about how the resulting percepts change when the stimulus changes. We found that a change in color saturation impacted the dominance of integrated images in accordance with a generalization of Levelt's Propositions. A number of previous studies provided related results: Alais and Blake (1999) studied the impact of orientation on the predominance of grouped stimuli when percept halves originated from the same eye. Stuit, Paffen, van der Smagt, and Verstraten (2011) and Stuit, Paffen, van der Smagt, and Verstraten (2014) explored how the orientation of complementary image halves impacted interocular grouping. While they identified orientation as a cue for interocular grouping, the increase in predominance was not analyzed in detail. Zhaoping (2008) showed that the eye-of-origin plays an important role in attracting attention, and hence saliency, in a search display. These results imply that the eye-of-origin could influence rivalry, which is consistent with the work of Stuit et al. (2014), who found that eye-of-origin dictates image-based rivalry, and with our results. We showed that single-eye percepts overall demonstrate stronger dominance than grouped percepts (interocular grouping) especially when the color saturation is low. A priori, we do not know how the effective contrast stemming from the eye-of-origin compares to the contrast between the two halves of the image. However, this is not critical in our study, since our main focus is not on which percept dominates at a fixed level of stimulus, but rather how percepts change when we change the stimulus (saturation). The focus on how percepts change when the stimulus changes is at the heart of Levelt's Propositions. Zhaoping and Meng (2011) showed that binocular stimuli can be arranged so that interocular grouping occurs with surfaces being perceived as "transparent." In this case, binocularly overlapping red/green regions are perceived as transparent red and green surfaces rather than exclusively red or green (rivalry) or yellow (binocular fusion). While the authors stated that this outcome was "insensitive to the choices of surface colors," no data were presented on how the percepts change as a function of changes in color parameters, such as saturation.

Color, among other features, has also been shown to facilitate object detection (Nothdurft, 1993). Our results are more closely related to the work of Kim and Blake (2004) and Kovacs et al. (1996). Kovacs et al. (1996) showed that color promotes interocular grouping: they obtained evidence for stable and relatively long percepts of same color elements (all-red or all-green). The abstract by Kim and Blake (2004) reported that color promotes interocular grouping. However, neither study examined the underlying causes of these effects or how they extend to Levelt's Propositions to multistable perceptual rivalry involving interocular grouping.

Color saturation facilitates grouping of complementary image halves We demonstrated that increasing the color saturation of ambiguous visual inputs can increase the predominance of grouped percepts. This is consistent with the Gestalt law of similarity (Kohler, 1947; Wertheimer, 1938; Wertheimer, 1923; Wagemans et al., 2012). While this effect tended to be strongest for the grouped red percept, we did find evidence that the grouped green percept became more salient than in the low color saturation condition. The neural mechanisms underlying collinear facilitation for chromatic and achromatic contours appear to be different (Beaudot & Mullen, 2003; Huang, Mullen, & Hess, 2007), suggesting that multiple channels in the visual system affect the grouping of image halves.

Inter-subject variability We only observed an appreciable increase in grouped percept predominance in five out of nine subjects (Fig. 3). One possible reason is that subjects differed in their sensitivity to color saturation (Kaiser & Boynton, 1996). Although no subjects reported problems with distinguishing colors, they may have responded differently if the change in color saturation was larger, or if we used different colors. For example, the wide array of sensitivities to contrast across human subjects is reflected in the range of mean dominance time durations in binocular rivalry (Bossink, Stalmeier, & de Weert, 1993; Brascamp, Van, Noest, Jacobs, & van den Berg, 2006; van Ee, 2009). Also, the relationship between color saturation and percept predominance is likely nonlinear (Stalmeier & de Weert, 1988). The color saturation values we used may have fallen in the flat portion of the function that describes the relation between color saturation and predominance for the four unaffected subjects.

As mentioned previously, Stalmeier and de Weert, 1988 found significant inter-subject variability even when isoluminance points were calibrated individually for each subject. The effect of chromatic signal strength on binocular rivalry depended both on the calibration criterion (flicker photometry versus MDB) and the direction along which colors were sampled in the color space. (Stalmeier & de Weert, 1988) also showed significant inter-subject variability both in the absolute effectiveness of achromatic contrast and its relative effectiveness with respect to chromatic contrast (Stalmeier & de Weert, 1988). Inter-subject variability has been reported in relatively low-level tasks (e.g. Halpern, Andrews, & Purves, 1999), as well as in multistable perception (Kleinschmidt, Sterzer, & Rees, 2012), which was interpreted to include both low-level and high-level factors. Hence, for future studies, we suggest the use of multiple levels of the percept-strength variable in order to characterize more completely the performance of each subject individually. In addition, it would help us identify the relative contributions of color saturation and luminance to percept strength, since red and green have different luminance at a fixed saturation (See Methods). This would provide a test for the generality of our conclusions, and would help identify stronger instances of grouping for the grouped green percept. Increasing the number of subjects would allow us to better characterize inter-subject variability, but would likely not make it disappear.

Extending Levelt's Propositions to interocular grouping Interocular grouping has been reported with different sets of patchwork images (Kovacs et al., 1996; Suzuki & Grabowecky, 2002). However, earlier studies did not quantify specific ways in which a stimulus parameter could affect the predominance of grouped images. We have shown that color saturation used as a grouping cue differentially controls the strength of single-eye and grouped percepts, and increasing color saturation can increase grouped percept predominance. As this effect was strongest for the all red percept, it suggests that color saturation, and particularly saturation of the color red, may act as a stimulus strength parameter for grouped percepts.

In agreement with Proposition II, the predominance of single-eye percepts was higher at low color saturations, and their dominance durations decreased in the higher color saturation condition, while the overall dominance duration of grouped percepts did not change much. Proposition III then follows from Proposition II. Finally, since we could not determine whether we equally increased the strength of both single-eye and grouped percepts, it is unclear whether our results are consistent with Levelt Proposition IV. Color saturation may affect monocular and binocular integration in different ways (Sincich & Horton, 2005). Stimulus parameter changes obeying Proposition IV would have to keep predominance fixed, while decreasing mean dominance durations.

Studies of interocular grouping in perceptual multistability have a long history (Diaz-Caneja, 1928). We focused on split single-eye images for simplicity, but we anticipate that our findings extend to the patchwork images of Kovacs et al. (1996). The simple grating-based inputs we used were more similar to the geometric images of Suzuki and Grabowecky (2002). We expect that our findings extend to achromatic images as long as a parameter can be identified that affects grouped percept predominance. For example, we could use achromatic textures as a cue to group complementary stimulus halves. In general, we suggest that our findings apply to any stimulus feature that promotes grouping along the lines of Gestalt laws of grouping.

Neural mechanisms of perceptual multistability. Our observations support the prevailing theory that perceptual multistability is significantly percept-based and involves higher visual and object-recognition areas (Leopold & Logothetis, 1999). Since the first systematic study of binocular rivalry (Wheatstone, 1838), much work has been devoted to identifying its underlying neural mechanisms: Mutual inhibition allows for the selection of one percept among many (Haynes, Deichmann, & Rees, 2005; Lee, Blake, & Heeger, 2005; Lumer, 1998; Tong et al., 1998; Meng, Remus, & Tong, 2005; Moutoussis, Keliris, Kourtzi, & Logothetis, 2005; Seely & Chow, 2011; Tong, 2001; Wunderlich, Scheneider, & Kastner, 2005), adaptation can lead to switching between percepts (Brascamp et al., 2006; Kim, Grabowecky, & Suzuki, 2006;van Ee, 2009), and neuronal noise accounts for the irregularity of perceptual dominance intervals (Brascamp et al., 2006; Lankheet, 2006; Moreno-Bote et al., 2007; Shpiro, Morento-Bote, Rubin, & Rinzel, 2009). However, a number of issues remain unresolved. Activity predictive of a subject's dominant percept has been recorded in lateral geniculate nucleus (LGN) (Haynes & Rees, 2005), primary visual cortex (V1) (Lee & Blake, 2002; Polonsky et al., 2000), and higher visual areas (e.g., V2, V4, MT, IT) (Logothetis & Schall, 1989; Leopold & Logothetis, 1996; Sheinberg & Logothetis, 1997). Thus, rivalry likely results from interactions between networks at several levels of the visual system (Dayan, 1998; Freeman, 2005; Wilson, 2003).

Collinear facilitation involves both recurrent connectivity in V1 as well as feedback connections from higher visual areas like V2 (Angelucci et al., 2002; Gilbert & Sigman, 2007), reenforcing the notion that perceptual rivalry engages a distributed neural architecture. However, a coherent theory that relates image features to dominance statistics during perceptual switching is lacking. It is unclear how neurons that are associated to each subpopulation may interact due to grouping factors such as collinearity and color.

Conclusion Our work supports the general notion that perceptual multistability is a distributed process that engages several layers of the visual system. Interocular grouping requires integration in higher visual areas (Leopold & Logothetis, 1996), but orientation processing and competition occurs earlier in the visual stream (Angelucci et al., 2002; Gilbert & Sigman, 2007). Furthermore, the fact that color saturation can modulate the statistics of perceptual multistability provides a stimulus parameter that can be varied in visual inputs to probe the neural mechanisms of visual integration and competition.

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