



Grouping of optic flow stimuli during binocular rivalry is driven by monocular information



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ABSTRACT

During binocular rivalry, perception alternates between two dissimilar images, presented dichoptically. Although binocular rivalry is thought to result from competition at a local level, neighboring image parts with similar features tend to be perceived together for longer durations than image parts with dissimilar features. This simultaneous dominance of two image parts is called grouping during rivalry. Previous studies have shown that this grouping depends on a shared eye-of-origin to a much larger extent than on image content, irrespective of the complexity of a *static* image. In the current study, we examine whether grouping of *dynamic* optic flow patterns is also primarily driven by monocular (eye-of-origin) information. In addition, we examine whether image parameters, such as optic flow direction, and partial versus full visibility of the optic flow pattern, affect grouping durations during rivalry. The results show that grouping of optic flow is, as is known for static images, primarily affected by its eye-of-origin. Furthermore, global motion can affect grouping durations, but only under specific conditions. Namely, only when the two full optic flow patterns were presented locally. These results suggest that grouping during rivalry is primarily driven by monocular information even for motion stimuli thought to rely on higher-level motion areas.

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1. Introduction

When two images, each presented to a different eye, are sufficiently different, the images will not be fused into a singular percept. Instead, perception alternates between the two images, causing observers to be aware of only one of the two competing images, for most of the time. This phenomenon is known as binocular rivalry and can give insight into the neural correlates of visual awareness. Moreover, since binocular rivalry is a local phenomenon (Blake, O'Shea & Mueller, 1992; Meenes, 1930), the spatial integration of separate image-parts during dominance may reflect part of the mechanisms behind perceptual binding. Binocular rivalry dominance, and the preceding competition, is thought to reflect multiple stages of processing (e.g. Freeman, 2005; Nguyen, Freeman, & Alais, 2003; Wilson, 2003). Especially relevant is the model by Tong, Meng, and Blake (2006) that indicates multiple levels of competition; between monocular channels, between

image-features on a monocular level and between image-representations on a binocular pattern level. However, what determines the relative contributions of each of these eye- and image-based processes remains unresolved.

Dominant percepts containing similar image features such as color (Kovacs, Papathomas, Yang, & Feher, 1996), orientation (Whittle, Bloor, & Pocock, 1968), motion direction (Alais & Blake, 1998) or luminance (Silver & Logothetis, 2004) last longer than percepts with dissimilar features. For example, Diaz-Caneja (1928); translated by Alais, O'Shea, Mesana-Alais & Wilson, 2000) presented images consisting of half a concentric circle pattern, and half a grating and reported that presenting one such image to one eye, and a mirrored version to the other eye, resulted in coherent images (complete circle or grating) for substantial periods of time. These percepts were thus based on the integration of image-features across the eyes. This result fits well with competition between image-features on a monocular level and competition between image-representations on a pattern level. However, these results need to be placed in the context of eye-based integration before any claims on the level of processing can be made. Recently, Stuit, Paffen, van der Smagt, and Verstraten (2011b) examined the relative contributions of eye-based and image-

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based grouping during binocular rivalry. Pairs of gratings with identical or dissimilar orientations were presented to the same eye or to different eyes. The results showed that grouping based on eye-of-origin information generated longer dominance durations than grouping based on image content, indicating that eye-of-origin is a stronger grouping cue than image content. A follow-up study (Stuit, Paffen, van der Smagt, & Verstraten, 2014) showed that image-complexity did not affect the contribution of image content on grouping during rivalry. Specifically, faces are thought to be more complex stimuli than gratings and are processed relatively late in the visual hierarchy, yet the contribution of image-based grouping did not differ between two perceived identical gratings and two combined face-parts. Overall, this shows that grouping of static images during binocular rivalry is biased towards integrating information from the same monocular channel.

The relative contribution of eye-of-origin information and image content on grouping during rivalry might be different for dynamic than for static images. For example, stimulus flicker is an integral part of flicker-and-swap rivalry, which is a variation on the conventional binocular rivalry paradigm that relies on strong image-based grouping and appears to bypass monocular competition (Logothetis, Leopold, & Sheinberg, 1996). Flicker-and-swap rivalry uses dynamic images containing both on-off flicker and an additional transient due to swapping the images between eyes every 333 ms. Observers do not only perceive rapid perceptual alternations, which would be expected if rivalry would be solely eye-based integration (eye-rivalry). Instead, the rapid switch between the eyes often goes unnoticed and observers experience normal rivalry alternations. These relatively slow alternations are thought to reflect competition in higher-level visual areas (stimulus-rivalry). The proportion of eye-rivalry and stimulus-rivalry that are instigated using the flicker-and-swap paradigm alters when the stimulus properties are varied, for instance the temporal layout of stimulation (van Boxtel, Knapen, Erkelens, & van Ee, 2008) or the spatiotemporal properties (Denison & Silver, 2012). In addition, the duration of interocularly grouped percepts increases when the presented stimuli flicker in an on-off regime (Knapen, Paffen, Kanai, & van Ee, 2007), again indicating a shift towards image-based grouping for dynamic stimuli. This raises the question whether the relative contribution of image content on grouping during rivalry also increases for global motion stimuli, since these stimuli are inherently dynamic and are processed by higher-level brain areas.

Global motion stimuli such as expanding, contracting and rotating motion patterns (e.g. optic flow patterns) are not dissimilar until higher-level visual motion areas such as the medial superior temporal area (MST; Duffy & Wurtz, 1991; Lagae, Maes, Raiguel, Xiao, & Orban, 1994; Saito et al., 1986; Smith, Wall, Williams, & Singh, 2006) and the ventral intraparietal area (VIP; Schaafsma & Duysens, 1996). However, the parameters of such motion signals can still influence binocular rivalry dominance. Specifically, expanding flow generates longer dominance durations than contracting optic flow during binocular rivalry (Malek, Mendoza-Halliday, & Martinez-Trujillo, 2012; Parker & Alais, 2007). Likewise, expanding optic flow is detected earlier than contracting optic flow during breaking continuous flash suppression (b-CFS; Holten, Donker, Verstraten, & van der Smagt, 2015). These results suggest that the different content of these dynamic stimuli may result in different contributions of image-based integration.

In the current study, we present radial optic flow stimuli in a binocular rivalry grouping paradigm. This paradigm has previously been used by Stuit et al. (2011b, 2014), to dissociate high-level, image-based contributions from low-level, eye-based contributions to grouping, as well as a possible synergy between them. If only low-level visual areas are involved in grouping of motion

stimuli during rivalry, this would be manifested by the occurrence of primarily eye-based grouping. Conversely, if only high-level visual areas are involved, we should primarily observe grouping to be based on image-content. If both low-level and high-level visual areas are involved, a synergy between eye-based and image-based grouping should become apparent (see Fig. 1 for a graphical depiction of these possible outcomes). Moreover, since the areas thought to be responsible for processing complex motion signals are known to have large receptive fields and to be position-invariant (Duffy & Wurtz, 1991), we will also vary the spatial scale across which integration need to occur. In Experiment 1, we present a full, complete, radial optic flow pattern in a single aperture with the focus of expansion in the center of that aperture (see Fig. 2). In Experiment 2, we present both a part of the upper and lower half of an optic flow pattern (i.e. partial optic flow) in an upper and lower aperture. When both partial flow image parts are dominant during rivalry, the percept can be interpreted holistically as a single optic flow pattern. How the image parts of the optic flow pattern are presented to observers might affect the duration of grouping based on a shared image content.

2. Methods

2.1. Observers

Ten observers (8 females, 2 males; age 18–32 years, mean age: 23.5 years) participated in Experiment 1 (full local optic flow patterns) and eleven observers (10 females, 1 male, age 18–32 years, mean age: 22.7 years) participated in Experiment 2 (partial optic flow patterns). Eight of the above observers participated in both experiments. All observers had normal or corrected-to-normal visual acuity and were naïve to the purpose of the study. However, one of the observers that participated in both experiments was removed from the analyses, due to a lack of perceptual alternations during several conditions. The experiment involved healthy human participants, and did not utilize any invasive techniques, substance administration or psychological manipulations. Therefore, compliant with Dutch law, this study only required, and received approval from our internal faculty ethics board (Faculty's Advisory Committee under the Medical Research Human Subjects Act, WMO Advisory Committee) at Utrecht University. Written informed consent was obtained from all observers. The experiment was conducted according to the principles expressed in the Declaration of Helsinki. By signing the informed consent, observers indicated to have read and agreed with both the rules regarding participation and proper (laboratory) behavior, and the researchers' commitments and privacy policy. Observers were also informed that they could stop participating in the experiment at any time and that all data would be analyzed anonymously.

2.2. Stimuli & apparatus

Stimuli were generated on a MacPro and presented on a linearized 20" LaCie Electron Blue IV CRT monitor (refresh rate 100 Hz, resolution 1024 × 768 pixels). Observers viewed the stimuli through a mirror-stereoscope that was mounted on a chin-rest. The viewing distance was 57 cm. Stimuli were presented on a gray background (23.2 cd/m²). To facilitate binocular fusion a white (47 cd/m²) frame (diameter of line 0.5°) surrounded the stimuli (Fig. 2). To provide additional help with fusion, a smaller black frame (diameter of line 0.15°) was presented on top of the white frame. The outer edges of the frames were placed on ~3.4° (white) and ~3.1° (black) from the fixation dot (diameter 0.22°). Two vertically aligned half-images in circular apertures (diameter 2.0°) were presented to each eye. The center of each aperture was posi-

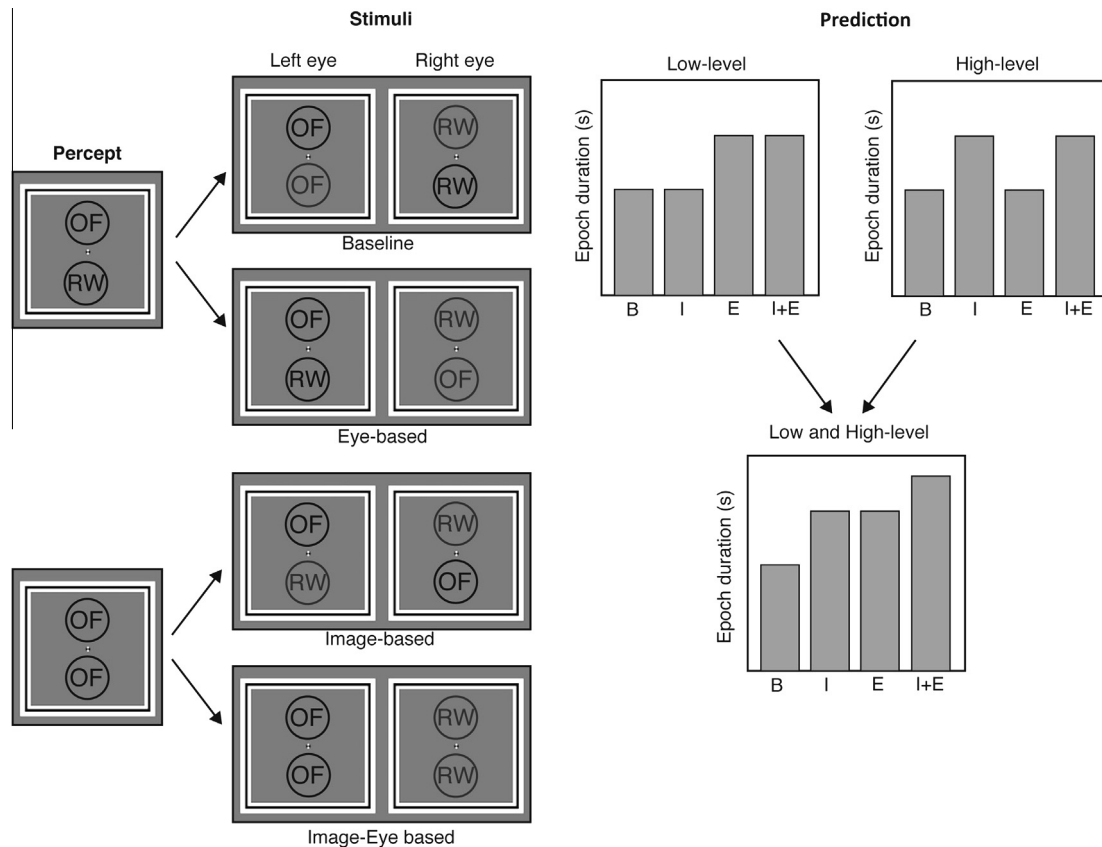


Fig. 1. Examples of percepts that could be perceived during the experiment and the corresponding stimuli causing these percepts. Observers perceive two half-images (one upper and one lower) that can either contain optic flow (OF) or random walk motion (RW). The type of grouping (baseline (B), eye-based (E), image-based (I), image-eye (I + E) based) depends on whether the perceived half-images are presented to the same or different eyes. For instance, when two optic flow patterns are perceived, grouping is image-based when the optic flow patterns are presented to different eyes, and image-eye based when the optic flow patterns are presented to the same eye. The half-images that are suppressed are faded for illustration purposes only. We predict that grouping based on eye-of-origin and grouping based on both eye-of-origin and image content generate the longest epoch durations when only low-level visual areas are involved. When only high-level visual areas are involved, we predict that grouping based on image content and grouping based on both eye-of-origin and image content generate the longest epoch durations. If grouping during rivalry involves both lower and higher-level visual areas, we predict that image content and eye-of-origin induce equal epoch durations but that both grouping cues act additively and induce the longest epoch durations.

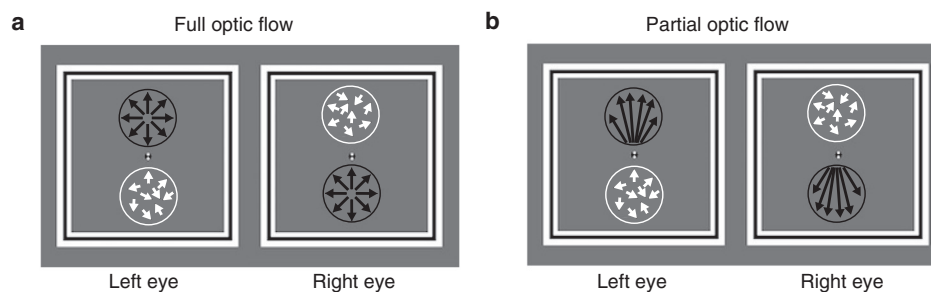


Fig. 2. Schematic representation of the stimuli used in the experiments. Two apertures containing half-images were presented in the left eye and two in the right eye. For each eye, an aperture was presented above and below the fixation dot. Two apertures contained optic flow and the other two contained random walk motion. Note that the aperture boundaries were not visible to observers. Two apertures contained moving bright (white) dots and the other moving dark (black) dots, represented by arrows indicating their motion direction. In the depicted stimulus condition, the upper left aperture and the lower right aperture contain expanding optic flow. The other apertures contain random walk motion. a) In experiment 1, each aperture contained either random walk motion or a full expanding or contracting optic flow pattern with the focus of expansion in the center of the aperture. b) In experiment 2, the apertures either contained random walk motion or expanding or contracting optic flow parts that could be interpreted holistically as a single optic flow pattern.

tioned at about 1.5° above or below the fixation dot. The half-images contained a radial optic flow pattern that was expanding or contracting and, presented to the other eye, random walk motion (Fig. 2). We decided not to present expanding and contracting optic flow simultaneously, since mutual interactions may occur between these two motion directions when they are presented at the same time. Given our specific interest in grouping during

rivalry of dynamic coherent images features, we tried to avoid these interactions as much as possible. We therefore presented optic flow simultaneously with random walk motion since this motion is incoherent. If mutual interactions between optic flow and random walk motion occur, we assume that they will be comparable for expanding and contracting optic flow. All apertures contained 100 randomly placed dots (diameter 0.1°) with an

unlimited lifetime. The dot density was approximately 29 dots/deg². A dot was replaced at a random position within the aperture when it moved beyond the border of the stimulus aperture.

In Experiment 1, two of the four half-images contained a full radial (expanding or contracting) optic flow pattern, with the focus of expansion positioned at the center of the aperture (Fig. 2a). An annulus (diameter of 0.5°) containing background luminance was presented at the center of the optic flow half-image to prevent the dots from occluding each other at the focus of expansion. The optic flow pattern contained a quadratic speed gradient that simulated observer movement through a circular tunnel. We used a quadratic speed gradient since differences in detection duration were observed during b-CFS between an expanding and contracting optic flow stimulus containing this speed gradient (Holten et al., 2015). The dot speed increased from the inner edge of the annulus (0.086°/s) towards the outer edge of the aperture (1.49°/s). The other two half-images contained random walk motion.

Random walk motion contained dots moving in a random direction and for each frame each dot had a 20 percent chance to obtain a new motion direction. Each dot comprising the random walk motion pattern contained a constant speed that was randomly selected from the speed range of the radial optic flow pattern. Therefore, some dots of the random walk pattern translated faster than other dots. Two of the four half-images consisted of bright (white) dots and the other two contained dark (black) dots. Both the top and the bottom half-images always had opposite polarities between the eyes. The distribution of the motion signals across the four half-images was counterbalanced with the contrast polarity of the dots across conditions.

Experiment 2 was similar to experiment 1. However, the focus of expansion of the optic flow pattern was not at the center of the aperture but was positioned at the fixation dot (Fig. 2b). Consequently, only the upper or lower part of a radial optic flow pattern was presented per half-image. Partial upper optic flow parts were always presented in an upper aperture and partial lower optic flow parts were presented in an aperture below the fixation dot. As in Experiment 1, two half-images consisted of random walk motion and the other two consisted of optic flow (Fig. 2b).

2.3. Procedure

Both experiments were divided into two sessions that contained the same conditions, although in a new random order. The sessions of each experiment were conducted on separate days. Observers participating in both experiments thus performed four sessions in total (two per experiment, four separate days). Before the start of each session, observers were presented with the fixation dot and stimulus-surrounding frames, presented to both the left and right eye, and adjusted the horizontal separation between the two half images. Once fusion was obtained, observers could practice the experiment until they indicated they understood the task. For the actual experiments, observers were instructed to fixate on the fixation dot while performing a 3-alternative-forced-choice tracking task. They indicated via a key press the *contrast-polarity* of the dots in the two apertures they perceived (bright, dark or mixed). The contrast-polarity task was chosen to prevent observers from paying attention to the type of motion of the stimulus (optic flow, random walk) they perceived. Observers had to continuously press one of three response keys. The left arrow indicated that both perceived apertures contained bright dots, the up arrow indicated that one of the apertures contained bright dots and the other dark dots, and the right arrow was pressed when the dots of both perceived apertures were dark. In case of a mixed percept where bright and dark dots within a single aperture were perceived, observers were instructed to make a forced-choice which polarity was perceived most. In total, 32 conditions

(4 motion-type configurations, 4 contrast-polarity configurations, 2 motion directions) were used in the experiments. Each of the 32 conditions was presented once per session. Hence, one session contained 32 trials, each lasting 1 min, and in each trial one of the 32 conditions was presented. After a trial was finished, the fixation dot and the rectangles facilitating binocular fusion were presented on the screen and observers could start a new trial by pressing the spacebar. This allowed observers to take a short break between trials. One session lasted about 35 min.

2.4. Analysis

Classification of the different epochs was based on the analysis of Stuit et al. (2011b); Epoch durations for each perceptual outcome (32 possible perceptual outcomes in total) were determined based on the percept and the presentation conditions (within- or between-eyes). There were 16 perceptual outcomes per motion direction (expanding, contracting); that is, the percept could be based on integration of information in the same eye or different eyes (2 possibilities), the perceived half images could both consist of optic flow, both random walk motion or a combination of random walk and optic flow (3 possibilities), the perceived half-images could both consist of bright dots, both dark dots or a combination of the two polarities (3 possibilities). Together, these possibilities ($2 \times 3 \times 3$) would result in 18 possible perceptual outcomes per motion direction. However, the design did not enable us to distinguish four of the possible perceptual outcomes. For these four perceptual outcomes we could determine that the perceived half-images were presented to the same or different eyes, that one of the apertures contained bright dots and the other dark dots and that two similar motion-types (either optic flow or random walk) were perceived, but not whether observers perceived two optic flow or two random walk patterns. We therefore aggregated these four perceptual outcomes into two perceptual outcomes, resulting in the above-mentioned 16 perceptual outcomes per motion direction. Note that the inability to dissociate these perceptual outcomes stems directly from the chosen task ('What is the contrast polarity of the perceived dots?'). Any other task would require attention towards motion direction. Since it is known that the focus of expansion attracts attention (Wang, Fukuchi, Koch, & Tsuchiya, 2012), the orientation and direction of motion influence suppression durations during continuous flash suppression (Hong, 2015) and attention has known effects on binocular rivalry dominance durations, we opted to have observers attend polarity instead.

Epoch durations reflect the duration of simultaneous dominance of two images and increased epoch durations reflect increased percept stability. For each perceptual outcome, the epoch durations of both sessions were aggregated before analysis. To correct for individual differences in epoch durations, the epoch durations of each perceptual outcome were normalized using the observer's median epoch duration of all epochs of all perceptual outcomes. The perceptual outcomes were divided in four groups based on which percept was perceived in a certain presentation condition. Note, that from each presentation condition, two perceptual outcomes were derived. Thus, within a single trial, grouping durations for two different perceptual outcome groups were recorded (see Fig. 1). Specifically, when a random walk pattern and an optic flow pattern were presented to each eye and these patterns were both perceived, the percept was based on a shared eye-of-origin only (see also Fig. 1). From the same presentation condition, perceptual outcomes that either contained two optic flow patterns or two random walk patterns were only based on a shared motion-type. When two optic flow or two random walk patterns were presented to each eye, and observers reported perceiving one optic flow pattern and one random walk pattern, the

percepts did not reflect any eye-of origin or motion-type based grouping. The epoch durations belonging to this perceptual outcome group are called baseline. However, when observers perceived two optic flow patterns or two random walk patterns in this presentation condition, the percept was based on both a shared eye-of-origin and a shared motion-type. For each observer, the normalized median epoch duration was calculated per grouping cue (shared eye-of-origin, shared motion-type, baseline, both shared eye-of-origin and motion-type). The average normalized median epoch duration of each grouping cue was calculated across observers.

2.5. Statistics

To examine the effect of each grouping cue on the epoch duration, separate repeated measures analyses of variance (ANOVA) were performed for each experiment. If the assumption of sphericity was violated, the number of the degrees of freedom was adjusted using the Greenhouse-Geisser method. Partial eta squared (η_p^2) was used to report effect sizes of main and interaction effects. Pairwise comparisons with a Bonferroni correction were used to compare main effects and to examine significant differences between conditions. First, the epoch durations were analyzed using a $2 \times 2 \times 2$ repeated measures ANOVA with the factors motion-type (the perceived apertures contained similar (i.e. two optic flow or two random walk patterns) or different (i.e. one optic flow and one random walk) motion patterns), eye-of-origin (the perceived apertures were presented to the same or to different eyes) and contrast polarity (the perceived apertures contained the same or opposite contrast polarities). Based on the initial results, the data of the full optic flow patterns was subsequently analyzed using a 2×2 ANOVA.

3. Results

The average median normalized epoch duration across observers, represented for each grouping cue, is shown in Fig. 3 for the full optic flow patterns (Fig. 3a) and the optic flow patterns that were partially presented within an aperture (Fig. 3b). Separate repeated measures analyses of variance (ANOVA) were performed for full optic flow patterns and partial optic flow patterns. We first performed a $2 \times 2 \times 2$ repeated measures ANOVA with the factors motion-type, eye-of-origin and contrast polarity. We used contrast polarity as a factor to determine whether besides motion-type, the contrast polarity of the dots of the half-images also acts as an image cue and if it affected motion-type-based grouping durations.

3.1. Results Experiment 1: Full optic flow patterns

For the full optic flow patterns, the results showed a main effect of motion-type based grouping ($F(1,8) = 25.69, p = 0.001, \eta_p^2 = 0.76$) on the dominance epoch duration, indicating that epoch durations increased when similar motion-signals were perceived compared with dissimilar motion-signals. A main effect of eye-of-origin ($F(1,8) = 52.90, p < 0.001, \eta_p^2 = 0.87$) was also observed. Longer epoch durations were observed when the perceived half-images were presented to the same eye rather than to different eyes. Whether the perceived dots had the same or opposite contrast polarities did not affect the epoch durations, since no main effect of contrast polarity was observed ($F(1,8) = 4.93, p = 0.057, \eta_p^2 = 0.38$). However, the results do show an interaction between eye-of-origin and contrast polarity ($F(1,8) = 14.43, p = 0.005, \eta_p^2 = 0.64$). Further examination of this interaction revealed that the effect of a shared eye-of-origin on the epoch duration decreased when both perceived half-images contained dots with

a similar contrast polarity compared to a dissimilar polarity. No interactions were observed between eye-of-origin and motion-type based grouping ($F(1,8) = 3.22, p = 0.111, \eta_p^2 = 0.29$), or between eye-of-origin, motion-type based grouping and contrast polarity ($F(1,8) = 2.53, p = 0.150, \eta_p^2 = 0.24$). Importantly, no interaction between motion-type based grouping and contrast polarity was apparent ($F(1,8) = 0.67, p = 0.437, \eta_p^2 = 0.08$), indicating grouping by contrast polarity did not affect the grouping based on the type of motion-signals that were perceived.

Since the results showed no main effect of contrast polarity on the epoch duration, nor an interaction between polarity and the perceived motion-type, we excluded contrast polarity as a factor and analyzed the data using a 2×2 ANOVA with the factors motion-type and eye-of-origin. Not surprisingly, main effects of motion-type based grouping ($F(1,8) = 21.26, p = 0.002, \eta_p^2 = 0.73$) and eye-of-origin ($F(1,8) = 61.30, p < 0.001, \eta_p^2 = 0.89$) were again observed. Furthermore, the results showed an interaction between motion-type based grouping and eye-of-origin ($F(1,8) = 8.94, p = 0.017, \eta_p^2 = 0.53$). The origin of this interaction can be seen in Fig. 3a, from which it is immediately apparent that the grouping-effect of similar motion-type only exists when the apertures containing the same motion-type are presented to the same eye. Consequently, motion-type based grouping is absent when the apertures containing a similar motion-type were presented to different eyes. This was the case for both random walk ($t(8) = 1.25, p = 0.245$) and optic flow patterns ($t(8) = 0.17, p = 0.872$), indicating that the absence of motion-type based grouping was not influenced by the perceived motion-type.

3.2. Results Experiment 2: Partial optic flow patterns

For the partial optic flow patterns, a main effect of eye-of-origin ($F(1,9) = 25.92, p = 0.001, \eta_p^2 = 0.74$) on the epoch duration was observed, indicating that the epoch durations increased when the perceived images were presented to the same eye than to different eyes. The contrast polarity of the dots also influenced the epoch duration ($F(1,9) = 10.07, p = 0.011, \eta_p^2 = 0.53$), since half-images containing the same contrast polarity were perceived for longer durations than half-images with opposite contrast polarities. No main effect of motion-type based grouping ($F(1,9) = 0.37, p = 0.556, \eta_p^2 = 0.04$) on the epoch duration was observed, nor were interactions between motion-type based grouping and eye-of-origin ($F(1,9) = 0.48, p = 0.507, \eta_p^2 = 0.05$), motion-type based grouping and contrast polarity ($F(1,9) = 2.74, p = 0.132, \eta_p^2 = 0.23$), eye-of-origin and contrast polarity ($F(1,9) = 2.19, p = 0.173, \eta_p^2 = 0.20$) or motion-type based grouping, eye-of-origin and contrast polarity ($F(1,9) = 0.02, p = 0.883, \eta_p^2 = 0.003$) apparent. These results indicate that perceiving identical motion types did not affect dominance durations for partial optic flow patterns. This was the case for both random walk and optic flow motion, since no difference between the dominance durations of these motion-types was observed ($t(9) = -0.71, p = 0.497$) when both apertures were presented to different eyes. This indicates that the absence of motion-type based grouping did not depend on whether optic flow or random walk patterns were perceived. Since the dynamic image-feature, motion-type, did not affect dominance durations, the data for partial optic flow patterns was not further analyzed.

3.3. Effect of motion-direction

A shared motion-type affected dominance durations only when the two motion patterns were presented to the same eye (full optic flow patterns). We therefore used a 2 (direction) $\times 2$ (motion-type) repeated measures ANOVA to test if within-eye grouping durations of motion signals were larger for optic flow compared to random walk (Fig. 4).

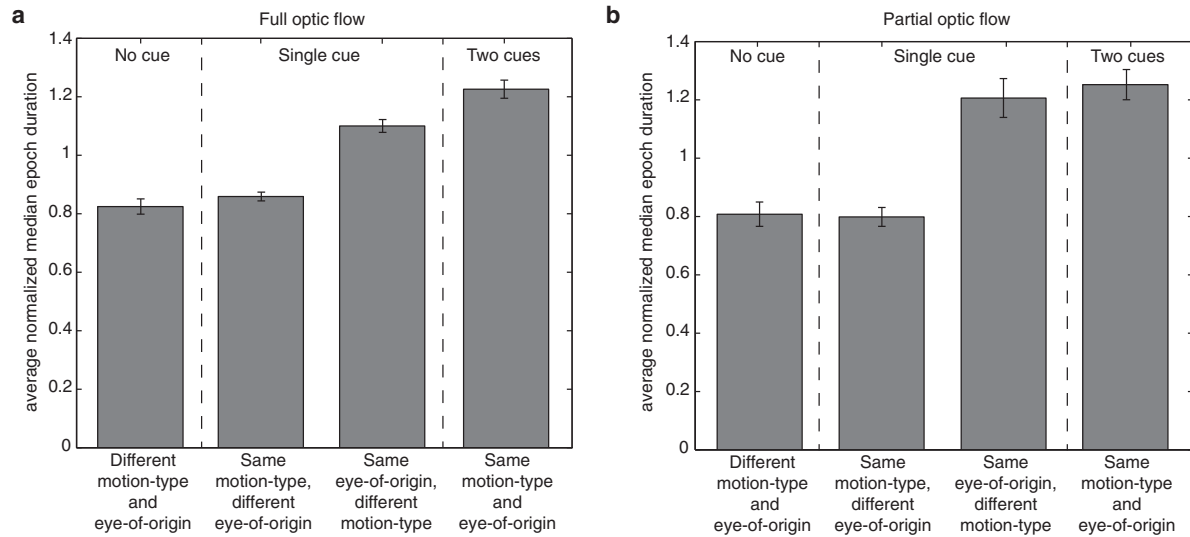


Fig. 3. The median normalized epoch duration, averaged across observers (y-axis), for each grouping cue (x-axis). Epoch durations of optic flow (both expanding and contracting) and random walk are collapsed. Error bars indicate the ± 1 SEM. a) Results for Experiment 1 where full, localized optic flow patterns were presented within an aperture. Perceiving two optic flow patterns or two random walk patterns that were presented to different eyes (2nd bar: same motion-type, different eye-of-origin) did not lead to longer dominance durations compared to perceiving one optic flow pattern and one random walk pattern when these patterns were presented to different eyes (1st bar: different motion-type and eye-of-origin). However, perceiving one optic flow pattern and one random walk pattern increased dominance durations when both patterns were presented to the same eye (3rd bar: same eye-of-origin, different motion-type). Perceiving two optic flow or two random walk patterns did increase dominance durations even more when they were presented to the same eye (4th bar: same motion-type and eye-of-origin). b) Results for Experiment 2 where optic flow stimuli were partially presented and only became apparent when both signals are perceived together. Here, perceiving two optic flow or two random walk patterns did not affect dominance durations at all.

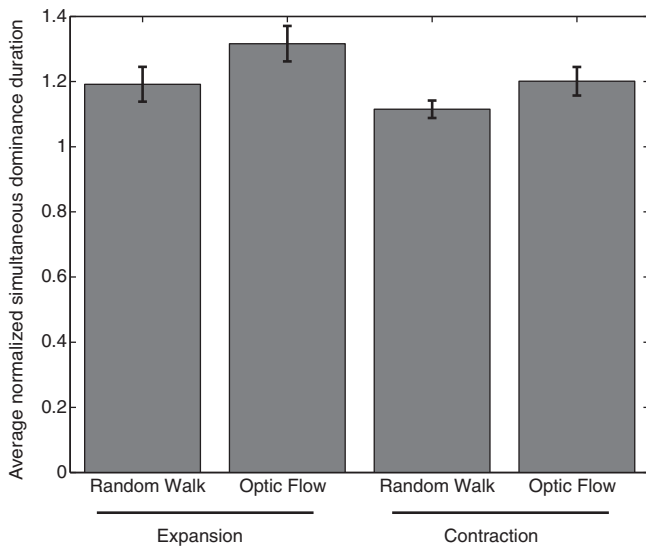


Fig. 4. Normalized epoch duration, averaged across observers, for within-eye grouping of optic flow or random walk patterns. On the y-axis are the averaged normalized epoch durations for simultaneous dominance and on the x-axis are the perceived motion percepts (either two optic flow or random walk patterns) per motion direction (expansion versus contraction). Errors indicate ± 1 SEM. Results indicate optic flow half-images are perceived together for longer durations and that, although there is a small bias for longer expansion durations, the relative effects for expansion and contraction do not differ significantly.

Results show a main effect for direction. Specifically, percept durations were longer for conditions containing expanding optic flow compared to conditions containing contracting optic flow ($F(1,8) = 10.23$, $p = 0.013$, $\eta_p^2 = 0.56$). A main effect for motion-type was also observed ($F(1,8) = 31.49$, $p = 0.001$, $\eta_p^2 = 0.80$), indicating that optic flow was perceived for longer durations compared to random walk. Importantly, no interaction between direction and motion-type was found ($F(1,8) = 0.72$, $p = 0.420$, $\eta_p^2 = 0.08$). This shows that dominance durations for expanding optic flow did *not*

differ from random walk more than the durations of contracting optic flow differed from random walk.

4. General discussion

In the current study, we investigated the integration of dynamic image features during binocular rivalry dominance. We employed optic flow motion in the context of binocular rivalry grouping not only because it is a dynamic signal, but also because previous studies have actually shown the direction of flow to affect dominance durations (Malek et al., 2012; Parker & Alais, 2007). These differences in dominance duration suggest that integration across space into a single dominant image may also differ for different optic flow directions.

Our results show that grouping based on shared monocular information has the largest effects on dominance durations and results in longer epochs than grouping based on shared motion-parameters. This indicates that a shared eye-of-origin is more important for image integration than perceiving two similar motion patterns (either optic flow or random walk). Our results imply that, as has been shown for static images with different levels of complexity (Stuit et al., 2011b, 2014), grouping of motion information is mostly affected by its eye-of-origin. We therefore suggest that integration of optic flow during rivalry stimuli is primarily driven by and/or achieved in monocular stages of information processing. In terms of the model of Tong et al. (2006), this means that the early monocular interactions dictate the formation of a dominant percept during rivalry. The importance and potency of eye-based spatial integration on the formation of a dominant percept has now been shown for a variety of image-types. In fact, this has been shown for stimuli that were thought to be processed either early or late in the visual hierarchy, as well as for static and dynamic images. Hence, the dominant percept during rivalry is always dependent on the spatial integration of monocular (eye-of-origin) information.

Interestingly, in our study only percepts of monocular, locally presented full optic flow patterns presented to the same eye affected grouped dominance durations more than random walk patterns. When the optic flow signal required integration over a larger extent of visual space, grouped binocular rivalry dominance did not differ between optic flow and random walk stimuli. In contrast to previous findings by Silver and Logothetis (2004), the results for the full optic flow patterns show longer periods of exclusive dominance for optic flow motion compared to random walk motion. The differences between their and our findings can most likely be attributed to differences in stimuli that result in interocular conflict. While in our study all half-images contained motion, Silver and Logothetis (2004) used one static and one dynamic half image. This makes a direct comparison of results difficult since the relative feature content of the competing images has profound effects on the degree of suppression as well as the dynamics of binocular rivalry (Alais & Melcher, 2007; Alais & Parker, 2006; O'Shea & Crassini, 1981; Stuit, Cass, Paffen, & Alais, 2009; Stuit, Paffen, van der Smagt, & Verstraten, 2011a; Vergeer & van Lier, 2010). Taken together, this suggests that the findings by Silver and Logothetis (2004) and our findings are not mutually exclusive and illustrate the importance of the relative feature content of the two half-images during binocular rivalry grouping.

The data of the current experiment only showed an effect of motion-type based grouping on dominance durations when the two motion patterns were presented locally. This suggests integration between or within relatively small receptive fields, which is difficult to reconcile with higher-level motion processing. However, if spatially localized low-level processes would exclusively drive grouping during rivalry, one would not expect any effect of motion-direction on dominance durations at all. Especially not for the direction of a complex motion stimulus such as optic flow. A possibility is that this effect is caused by processing in higher-level visual motion areas that are tuned to expanding compared to contracting optic flow (Duffy & Wurtz, 1991; Saito et al., 1986; Schaafsma & Duysens, 1996). The position invariance of MST cells may be responsible for the finding that dominance durations of two perceived random walk or optic flow patterns were only affected for locally presented motion patterns. Specifically, MST cells maintain their responses when the position of optic flow signals is changed within their receptive field (Graziano & Andersen, 1994). For our experiment, this suggests the spatial separation between the two half-images may have been irrelevant for higher-level motion processing when full flow patterns are presented. For the partial optic flow patterns, the signal may simply have been too degraded to be registered as optic flow. Instead, the signal could have evoked responses as if opposite translational motion signals were presented. Opposite translational motion signals would not be expected to result in long grouping durations (Alais & Blake, 1998).

One finding that we do want to note is the interaction of contrast-polarity and eye-of-origin and, importantly, the lack of such an effect with motion coherence. Although not the main focus of this study, this pattern of results suggests a new insight into integration during rivalry dominance. Specifically, the two image-features contrast-polarity and motion coherence did not affect each other. In other words, the effect on grouped dominance duration of a particular image-feature was not altered by the presence of an unrelated image-feature. This suggests image-feature grouping cues may add up (into longer dominance durations) but do not lead to either synergistic effects nor do they interfere with each other. Vergeer and van Lier (2010) also showed additive effects of grouping different feature types during rivalry. They showed that a suppressed image became dominant sooner when it was flanked by visible images with a shared color and/or a shared orientation. Their results indicated an additive effect when

both the colors and orientations of the flankers were identical to the suppressed image. Furthermore, Knäpen, Kanai, Brascamp, van Boxtel, and van Ee (2007) showed that multiple grouping cues independently affect dominance durations during rivalry. Specifically, they used a flicker and swap paradigm to show that eye-of-origin, color and stereo-depth information additively and independently influenced rivalry durations.

The results of our study also show that contrast-polarity did affect eye-based dominance durations. In fact, eye-based grouping was weaker when two identical polarities were perceived. This suggests image-based grouping can interfere with eye-based grouping. Although requiring formal testing, this may explain the potency of flicker-and-swap rivalry where perception appears to alternate between coherent images even though the coherent images are rapidly swapped between the eyes (Logothetis et al., 1996). In this paradigm, many image-cues to grouping are present simultaneously (e.g. color, flicker, orientation, contrast).

In summary, previous studies have shown the potency of multiple static image-features to affect spatial integration into a coherent percept during binocular rivalry dominance. In depth investigation of the contributors and level of processing underlying these effects have shown that a shared source, eye-of-origin, for these image features is very important. Without a shared eye-of-origin, image-based grouping effects tend to drop to baseline levels. Dynamic image-features are also known to affect rivalry dominance of coherent images. For example, dominance durations are longer for temporally correlated contrast modulations compared to uncorrelated modulations (Alais & Blake, 1999). Moreover, increasing the motion coherence of a pattern presented to one eye above the fixed motion coherence level of a pattern presented to the other eye increases the dominance duration of the pattern with the increased motion coherence (Platonov & Goossens, 2013). Likewise, it is known that increasing the motion coherence decreases the suppression duration of optic flow stimuli during a breaking continuous flash suppression paradigm (Holten et al., 2015; Kaunitz, Fracasso, Lingnau, & Melcher, 2013). Although coherent, optic flow motion is thought to be processed much later in the visual hierarchy compared to simple static features such as orientation and color, these dynamic features show similar dependencies on the eye-of-origin of the competing image-features. Taken together, these results suggest that it is the monocular information that is integrated first. Note that image-features, whether dynamic or static do influence this process. This fits well with the ocular dominance columns in early visual cortex that code for image features while simultaneously having a strong eye-preference (De Valois, Yund, & Hepler, 1982; Hubel & Wiesel, 1962, 1974). Since we here show a difference based on complex forms of motion, one wonders if eye-of origin information may be present at higher levels motion processing.

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