Conflict defined by global gestalt can modulate binocular rivalry suppression

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Binocular rivalry suppression is thought to necessarily require local interocular conflict: the presence of incompatible image elements, such as orthogonal contours, in retinally corresponding regions of two monocular displays. Whether suppression can also be driven by conflict at the level of spatially nonlocal surface or object representations is unclear. Here, we kept local contour conflict constant while varying global conflict, defined by the gestalt formed by the two monocular displays. Specifically, each eye was presented with a grid of image elements (crosses or plusses), placed such that the two eyes' individual grid elements did not directly overlap but the grids as a whole did. In a "shared motion" condition, all elements moved in unison, inviting a gestalt made up of all elements across both eyes; in a "different motions" condition, the elements' trajectories differed between eyes, inviting a gestalt of two overlapping surfaces, each associated with one eye. Perceptual disappearances of image elements occurred more readily in the different motions condition, an observation that could not be explained by any between-condition differences in local contour conflict. In a second experiment, we furthermore established that, whereas perceptual disappearances in the shared motion condition tended to involve a single element at a time, in the different motions condition, multiple elements belonging to the same gestalt often disappeared together. These findings indicate that, even though binocular rivalry may critically rely on inhibition due to locally incompatible image elements, this inhibition also depends on the global gestalt to which these elements contribute.

Introduction

A necessary condition for binocular rivalry appears to be the presentation of incompatible visual input to approximately corresponding retinal locations in the two eyes. For instance, Levelt (1965) examined rivalry between a disk shown to one eye and a concentric ring surrounding it in the other eye. While keeping the width of the ring constant, Levelt simultaneously increased the ring's inner radius and outer radius, and thereby the distance between the contours of the two monocular figures. As a result, perceptual suppression diminished, until it disappeared altogether at an inter-contour distance of about 1 degree of visual angle (dva) at the fovea. More recently, Carlson and He (2004) examined binocular rivalry between images comprised of square arrays of large "pixels," with boundaries between pixels overlaid by grid lines that were identical and fusible between the two eyes. Luminance differences between spatially corresponding pixels across the two eyes could elicit rivalry suppression, but only if the differences were such that, locally, one eye viewed edges between the overlaid grid and the pixels that were of opposite contrast polarity to the spatially corresponding edges viewed by the other eye. However, so long as local contrast polarity was matched between the eyes, luminance differences between the two eyes' pixel arrays did not instill rivalry. This was true even if these luminance differences amounted to different global figures (e.g. a pixelated circle shown to one eye, overlapping with a pixelated cross shown to the other). Such evidence

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supports the idea that local interocular contour conflict is critical for rivalry suppression, whereas conflict at a more global, figural level is not; an idea consistent with numerous formal models of binocular rivalry that center on mutual inhibition between oppositely tuned and spatially local feature channels (e.g. Laing & Chow, 2002; Wilson, 2003; Said & Heeger, 2013; Wilson, 2017).

However, global spatial structure does impact the perceptual dynamics of rivalry. For instance, if one presents multiple rivalry stimuli side-by-side, perceptual dominance is not independent across rivalry stimuli, such that there is an above-chance occurrence of simultaneous dominance of local monocular stimuli that together form a coherent global shape (Fukuda & Blake, 1992; Alais & Blake, 1999; Stuit et al., 2011). In fact, even when the local monocular elements of a globally coherent figure are distributed between the two eyes there is a tendency for the observer to perceive the global figure (i.e. for the visual system to piece together matching local elements from both monocular streams; Kovács et al., 1996; Alais et al., 1999; Ngo et al., 2000; Slezak & Shevell, 2018).

It is well established, then, that global image structure affects the synchrony of perceptual dominance across space during binocular rivalry. What is unknown, however, is whether global image structure can also determine whether two monocular displays engage in rivalry to begin with. Specifically, in this study, we asked: is the occurrence of interocular suppression only dependent on whether there is sufficient local feature conflict, as suggested by previous work (Carlson & He, 2004), or does conflict at the level of spatially nonlocal representations also factor into whether interocular suppression occurs? Although this question has been asked in previous studies (Watson et al., 2004; Silver & Logothetis, 2004), the results of those studies can be interpreted in terms of perceptual synchrony across space; an interpretation we aimed to avoid here (see Discussion for further details).

We used image motion to modulate whether two monocular displays contributed to a single, unified gestalt or, alternatively, to two different but spatially overlapping global objects. We did this without changing either the monocular displays themselves, or the degree of interocular conflict in terms of local contours. We then measured the extent to which observers experienced perceptual disappearances of any image elements, thus testing whether the strength of binocular rivalry suppression depends on the degree of compatibility between the two monocular displays, not just at a local level, but also at the level of spatially global object representations.

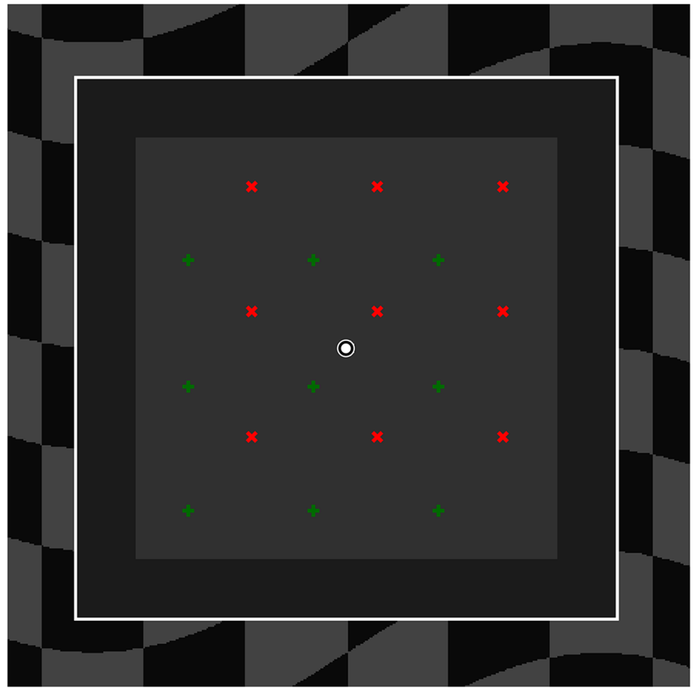

Figure 1. Schematic depiction of our stimulus. This figure illustrates the joint stimulus formed by both monocular images combined; the actual monocular image viewed by a given eye contained only a subset of the elements shown here, depending on condition (see Figure 2).

Experiment 1

Methods

Stimulus

The basic design for the stimulus is illustrated in Figure 1, which shows a compound of both eyes' images together. In all conditions, the stimulus consisted of nine green crosses (70.5 cd/m^2 using only the monitor's green channel; line length and width 0.45 dva and 0.15 dva, respectively) and nine red plusses (same luminance using only the red channel; same size) presented on a gray background (35.2 cd/m^2) with a black (2.9 cd/m^2) and white (335.5 cd/m^2) bullseye marking fixation in the screen center (outer radius 0.29 dva), and framed by a fusion pattern (inner diameter of the dark frame: 15.1 dva). The green crosses formed a three-by-three square grid and the red plusses formed a second grid of the same kind. The interelement distance within each grid was 4.5 dva unless otherwise noted. The grid of crosses and the grid of plusses were offset to the left and to the right relative to the screen center, respectively (by one fourth the interelement distance). The grids were also displaced in opposite directions vertically (by the same amount), but those directions alternated from trial to trial. Accordingly, and as shown in the figure, the grids overlapped substantially but individual grid elements were spaced apart, both within and across grids. As a result, observers did not always experience perceptual suppression of grid elements: frequently all 18 were visible simultaneously.

Our main objective was to vary the degree to which the two types of grid elements would contribute to a single gestalt – corresponding to a surface made up of two types of marks – or alternatively, to two separate perceptual objects – a surface covered with green crosses overlapping with a surface with red plusses. For that reason, all elements translated along a circular trajectory with a radius that was much smaller than the distance between grid elements (radius of 0.23 dva; 2 revolutions per second) and this motion could either be in phase for all elements or, in a different condition, in opposite phases between crosses and plusses (so that the crosses' leftmost position coincided with the plusses' rightmost position, etc.). Consistent with the Gestalt principle of grouping by common fate, the former type of motion gave rise to the subjective impression that all elements belonged together regardless of color and shape, whereas the latter type gave the impression that the green crosses belonged to one object whereas the red plusses belonged to a different but spatially overlapping object. Our two main conditions, then, were as follows:

1. Shared motion. In this condition, one eye viewed only crosses and the other viewed only plusses, and all these elements moved in phase.
2. Different motion. In this condition, one eye viewed only crosses and the other viewed only plusses, and crosses moved in counterphase relative to the plusses.

We included a number of additional conditions to gain a more complete understanding, in particular of any interactions between Gestalt-level factors and factors related to eye-of-origin (see Figure 2 for an overview of all conditions).

1. Different motion; monocular. In this condition, the crosses and plusses moved in counterphase, but all elements were shown to only one eye. The other eye viewed only a gray background. This substantially reduced interocular feature conflict, although one eye's display was still in conflict with the other eye's blank screen.
2. Different motion; binocular. In this condition, the crosses and plusses moved in counterphase, but all elements were shown to both eyes. This removed any interocular conflict, leaving only potential conflict at the level of surface representations.
3. Different motion; split. In this condition, the crosses and plusses moved in counterphase and the display was dichoptic, but the two types of elements were distributed between the eyes, so that each perceptual object (surface) corresponded to monocular elements coming from two different eyes. In particular, counting all elements of a given kind in the English reading direction, one eye viewed all odd-numbered elements and the other viewed all even-numbered ones.

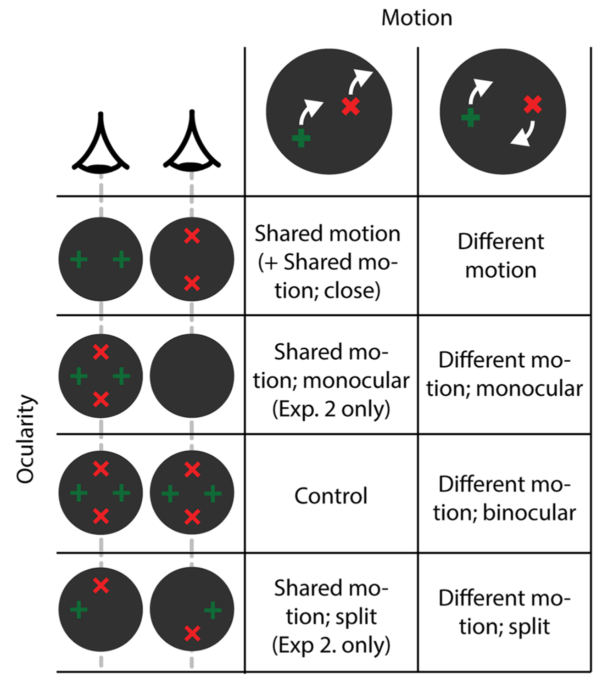

Figure 2. Overview of the experiment conditions. Conditions differed with regard to the factor's motion and ocularity. The former refers to whether crosses moved in unison with plusses or, alternatively, out of phase with them. The latter refers to the way in which crosses and plusses were distributed between the two eyes.

We also included a condition to account for the fact that in the various different motion conditions the distance between elements of different kinds varied over time due to the asynchronous motion trajectories. As a result, across time a given cross element and its closest plus neighbor reached a minimum distance that was smaller than their distance in the shared motion condition, potentially giving rise to more conflict at the level of local contours. In particular, even though the spacing between the centers of the elements' circular motion was identical between all conditions (4.5 dva between elements of a given kind; 3.2 dva diagonally between elements of different kinds), the shortest distance over time between a given cross element and the closest plus element was smaller in the different motion conditions than in the shared motion condition by twice the radius of the rotary motion (i.e. by

0.45 dva). The following condition was included to account for this fact.

1. Shared motion; close. This condition was identical to the shared motion condition except that the distance between neighboring elements of different kinds was equal to their minimal distance in the different motion conditions, rather than to their average distance.

A final condition was included as a control to weed out observers who did not perform the task at an acceptable level (see below for task details): in this condition, all elements were moving in unison and shown to both eyes simultaneously, thus minimizing any tendency for perceptual disappearances. One element was removed from the screen on some of the condition's trials (randomly chosen), and observers' performance was evaluated based on the assumption that those physical disappearances were the only occasions that any elements were seen to disappear in this condition. We will refer to this condition as the control condition, although, for consistency with the other conditions, it might also be thought of as shared motion; binocular.

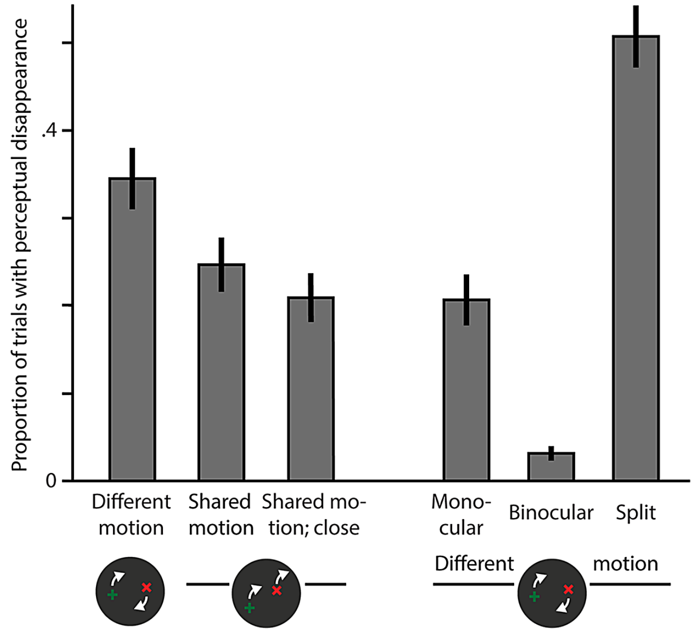

Figure 3. Main result of Experiment 1. The conditions of Experiment 1 (x-axis) differed with regard to the proportion of trials (y-axis) in which the perceptual disappearance of at least one image element (cross or plus) was reported (see text for details).

Observers and task

One hundred six undergraduate students from Michigan State University participated for course credit (30 men and 76 women; 94 indicated their age category as 18–20 years old; 12 indicated they were 21–25 years old). They viewed the stimulus shown on two computer screens through a mirror stereoscope while seated in a darkened room and resting their heads on a chin and forehead rest, as described in Qian and Brascamp (2017). They completed one block of this task as part of a larger, three-session experiment that included several other psychophysical tasks unrelated to the present study. This task consisted of fixating the central bullseye for trials that lasted 8 seconds each, and pressing and holding down the spacebar whenever any of the 18 grid elements was / were perceived to be missing.

After receiving verbal instructions, the observers completed one practice trial of each condition, in random order. After this, the observers were presented with an on-screen text saying that the practice trials had ended, followed by nine repetitions of each condition, randomly interleaved (63 trials total, or about 8 minutes). After each trial, observers could press the spacebar to continue to the next trial, and every eight trials an on-screen text reminded them to keep their eyes on the fixation mark. Assignment of the monocular displays to the left and right eye was determined randomly on each trial (for conditions with a dichoptic or monocular stimulus), as was the rotation direction of the image elements (clockwise or counterclockwise; always the same for all elements during a given trial). On those trials of the control condition where a stimulus element physically disappeared (5 out of 9 trials total; randomly selected), this element was chosen randomly and the moment of disappearance was drawn from a uniform distribution ranging between 2 and 6 seconds into the trial. Once an element had physically disappeared, it remained gone for the remainder of the trial.

Results

Twelve observers (11.3%) responded inaccurately on more than one of the nine trials of the control condition (see Methods). Inaccurate here is defined as either not pressing the spacebar on a trial where a grid element physically disappeared, or pressing the spacebar on a trial where no element physically disappeared. After removing those observers, we analyzed the data of the remaining 94 observers.

Figure 3 shows the average proportion of trials during which any disappearance was reported separately for each condition (except the control condition). This proportion differed between conditions (repeated-measures ANOVA with condition as its factor; $F(4,372) = 75.6$, $P < 0.0001$). Our main comparison was between the shared motion condition and the different motion condition: in both cases, each eye viewed only one type of grid elements (potentially eliciting binocular rivalry) but, in the former condition, all elements moved in unison (promoting a unified Gestalt) whereas, in the latter condition, element motion differed between the crosses and the plusses (promoting the impression of two separate but overlapping grids). The proportion of trials during which any disappearance was reported was significantly higher in the different motion condition (0.35) than in the shared motion condition (0.25; two-tailed paired *t*-test, $t(93) = 5.1$; $P < 0.0001$). This difference was not due to the fact that over time the shortest distance between crosses and plusses was smaller in the different motion condition (see Methods) because it still existed when comparing the different motion condition to the shared motion; close condition, wherein elements were more closely spaced to control for that fact (proportion = 0.21; two-tailed paired *t*-test, $t(93) = 6.4$; $P < 0001$). Indeed, the proportion of disappearance trials in the shared motion; close condition (0.21) was similar to, and even slightly smaller than, that in the shared motion condition (0.25; two-tailed paired *t*-test, $t(93) = 2.1$; $P = 0.035$).

The above result suggests that conflict at the level of a spatially global surface representation influences binocular rivalry suppression. At the same time, in the absence of local interocular conflict, the mere presence of such spatially global conflict (i.e. of two different and overlapping perceptual objects) causes only modest perceptual suppression. In particular, the proportion of disappearance trials was relatively low (0.21) if there was global conflict but all grid elements were shown to the same eye (the different motion; monocular condition), and the proportion was negligible (0.03) when there was global conflict but all grid elements were shown to both eyes (the different motion; binocular condition).

Interestingly, a high proportion of disappearances was also observed when the crosses and plusses, in addition to moving out of phase relative to each other, were each distributed between the two eyes (different motion; split condition). This proportion (0.51) was even significantly higher than in the different motion condition (two-tailed paired *t*-test, $t(93) = 5.0$; $P < 0.0001$). This suggests that, even though both local interocular conflict and global object-level conflict contribute to perceptual suppression in this experiment, there is no need for each object to be associated with a particular eye in terms of its constituent elements.

Figure 4 shows a different perspective on the data from this same experiment, only for our two main conditions: shared motion and different motion. As a function of time within the trials, this figure displays the proportion of trials where any disappearance had been reported prior to that time. This perspective shows that observers typically started off a trial perceiving all 18 grid elements, and that elements started becoming

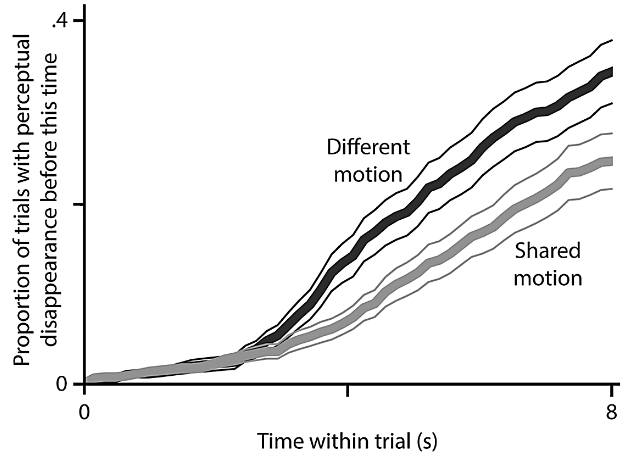

Figure 4. Experiment 1: The within-trial moment at which the first perceptual disappearance was reported in two critical conditions. In both conditions, perceptual disappearances tended to first occur after several seconds of viewing the stimulus. Disappearances were more common in the different motion condition than in the same motion condition, consistent with the data shown in Figure 3.

perceptually suppressed after a few seconds. The vertical ordering of the two conditions in this plot shows the same pattern as Figure 3, with the curve for different motion running higher than the curve for the same motion condition.

Experiment 2

The results of Experiment 1 suggest that conflict at the level of object representations – not just at the level of local features – can contribute to perceptual suppression during binocular rivalry: perceptual disappearances occurred more readily in the different motion condition that promoted an impression of two separate surfaces, than in the shared motion condition that invited a single Gestalt involving both crosses and plusses. To further evaluate this idea of a surface-based contribution to perceptual suppression in the different motion condition, in a second experiment, we investigated whether particular combinations of grid elements tended to become perceptually suppressed. In particular, rivalry suppression that is rooted in spatially local mechanisms might mostly involve perceptual disappearances of single grid elements at a time. Rivalry suppression rooted in surface-based mechanisms, in turn, might more often involve simultaneous perceptual disappearances of multiple grid elements that contribute to the same perceptual surface.

To test this, Experiment 2 included an opportunity for observers to report what kind of combinations of grid elements appeared to be missing (see Methods). In addition, Experiment 2 was designed to shed light on an unexpected pattern of results observed in Experiment 1: although we set out to examine the effects of our motion manipulation, Experiment 1 showed that the dependent variable has similar sensitivity to the manipulation of distributing grid elements of a given kind (i.e. crosses or plusses) between the two eyes (in the different motion; split condition). For that reason, Experiment 2 included more conditions than Experiment 1 to allow us to examine the roles of our various manipulations and their interactions in a factorial design.

Methods

The stimulus and experimental setup were identical to those of Experiment 1.

Observers and task

Twelve members of the Brascamp laboratory at Michigan State University participated: 11 students and the PI (7 men and 5 women; average age 22 years old). They all had experience as observers in psychophysics experiments and all but two (the first 2 authors) were naïve to the purpose of the experiment.

Observers participated in one session consisting of two separate blocks. During the first block, they completed the same task as the observers of Experiment 1, except that there were more stimulus conditions (see below for details). During the second block, they completed a new variant of the task. Here, each trial lasted a maximum of 8 seconds but was terminated immediately if at any time the observer pressed the spacebar indicating a grid element had become perceptually suppressed. As soon as that happened, the stimulus display was replaced by a prompt asking for a three-alternative forced-choice response: had they pressed the spacebar because a single grid element had disappeared, because multiple grid elements of the same kind had disappeared, or because multiple grid elements including both kinds had disappeared?

The stimulus conditions included those of Experiment 1 and two additional ones (see also Figure 2):

1. Shared motion; monocular. In this condition, the crosses and plusses moved in phase, but all elements were shown to only one eye. The other eye viewed a gray background.
2. Shared motion; split. In this condition, the crosses and plusses moved in phase and the display was dichoptic, but the two types of elements were distributed between the eyes in the same way as in the different motion; split condition.

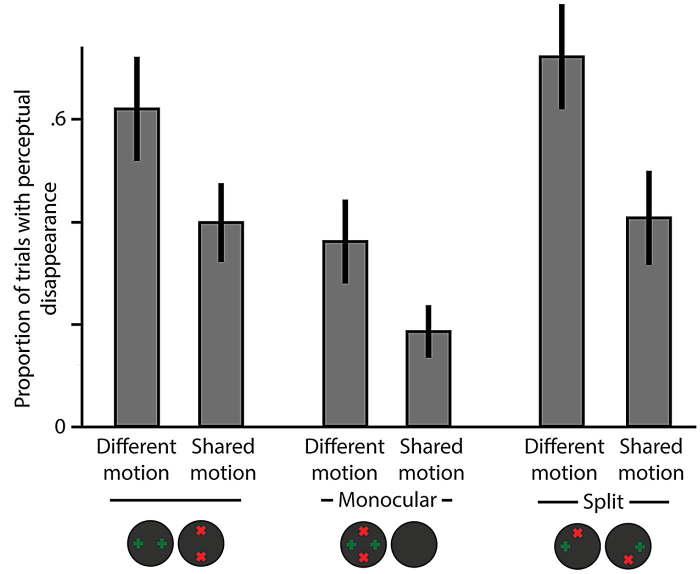

Figure 5. Result of the first block of Experiment 2. This block forms a replication of Experiment 1 (Figure 3) but with a more complete set of stimulus conditions. As in Experiment 1, conditions were found to differ with regard to the proportion of trials in which the perceptual disappearance of at least one image element (cross or plus) was reported.

Results

For each observer, Experiment 2 included one block that copied the report method of Experiment 1 (but that had two additional stimulus conditions; see Methods), and we report results of that experiment block first. None of the observers made an error reporting disappearances on more than one of the 9 control trials, so all 12 observers were included in the final analysis. As in Experiment 1, we found that the proportion of trials in which a perceptual disappearance occurred was indistinguishable between the shared motion condition (proportion = 0.40) and the shared motion; close condition (proportion = 0.38; two-tailed paired *t*-test; $t(11) = 0.41$; $P = 0.69$), confirming that any differences in this measure between the shared motion condition and the different motion condition are unrelated to the slight difference in inter-element distance between those conditions (see Experiment 1). We also verified that disappearances again occurred very infrequently in the different motion; binocular condition, which had no interocular conflict (proportion of trials: 0.07), confirming that interocular conflict is a major contributor to perceptual suppression in our study.

Leaving out the shared motion; close condition and the different motion; binocular condition, then, Figure 5 shows the results of the six conditions that together form a factorial design with two factors: motion (different or shared between crosses and pluses) and ocularity (crosses and plusses each confined to a different eye, each distributed across eyes, or all shown to the same eye). A two-factor repeated measures ANOVA showed a significant effect of motion (F(1,11) = 22.0; $P = 0.0007$) as well as ocularity (F(2,22) = 10.2; $P = 0.0007$) but no interaction (F(2,22) = 1.6; $P = 0.22$). Pairwise comparisons showed that disappearances were more frequent for each different motion condition than for its shared motion counterpart (two-tailed paired *t*-test; different motion vs. shared motion: t(11) = 3.7; $P = 0.003$; different motion; split vs. shared motion; split: t(11) = 3.9; $P = 0.002$; different motion; monocular vs. shared motion; monocular: t(11) = 2.8; $P = 0.02$). The main effect of ocularity was due to a relatively low frequency of disappearances in the monocular conditions as compared with the dichoptic conditions (two-tailed paired *t*-test; different motion vs. different motion; monocular: t(11) = 3.5; $P = 0.005$; shared motion vs. shared motion; monocular: t(11) = 4.4; $P = 0.001$). These results closely resemble the results of Experiment 1, and reinforce its conclusion that global surface-level conflict (the motion factor) and local interocular feature conflict (the ocularity factor) both contribute to perceptual suppression.

The only point at which the results of the Experiments 1 and 2 diverge is with regard to the split conditions: in contrast to Experiment 1, we now find no increase of perceptual suppression when distributing grid elements of a given kind (i.e. crosses or plusses) between the two eyes as opposed to segregating them by eye (two-tailed paired *t*-test; different motion vs. different motion; split: t(11) = 1.2; $P = 0.26$; shared motion vs. shared motion; split: t(11) = 0.13; $P = 0.90$). This could be a matter of statistical power because the numerical trend is in the same direction as it was in Experiment 1, with numerically more disappearances in the split conditions.

During the second block of Experiment 2, as soon as any display element was reported to perceptually disappear, this terminated the trial and observers then reported whether the disappearance involved only a single grid element, multiple grid elements of the same kind (i.e. either crosses or plusses), or multiple grid elements including both kinds. To reiterate our hypothesis: if surface-level mechanisms contribute to perceptual suppression in the different motion conditions (which invite a perceptual organization in which a surface made of plusses overlaps with one made of crosses), then perceptual disappearances in those conditions might specifically involve simultaneous disappearance of multiple grid elements of the same kind. In the shared motion conditions, on the other hand, a dominant contribution of local, feature-based conflict might lead specifically to disappearances of single grid elements at a time.

Figure 6 shows the results for the same six conditions as shown in Figure 5. For each condition, the plot displays the proportions of trials where each of the three response options was selected (one grid element, multiple elements of a single kind, or multiple elements including both kinds). Some observers reported no disappearances at all for some conditions, so the relative proportions of the three kinds of disappearances were not always defined (see caption of Figure 6 for details). This means that our design contained missing cells, and we centered our statistical testing around linear mixed-effects models instead of repeated measures ANOVAs. Specifically, we implemented random intercept models with observer as the random effect (using *R*'s *lmer* function from the *lme4* package; Bates et al., 2015) and tested for significance by performing likelihood ratio tests between full and reduced models (using *lme4*'s ANOVA function).

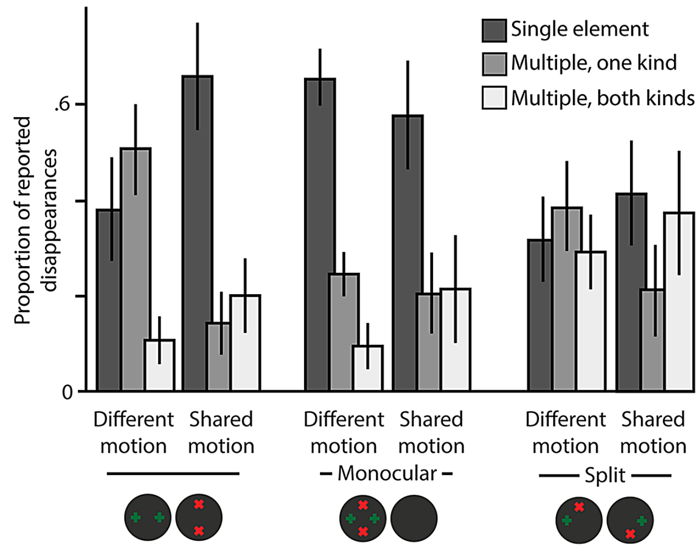

Figure 6. Result of the second block of Experiment 2. Here, reporting a perceptual disappearance terminated the trial, prompting the observer to report what disappeared: a single element (darkest shade), multiple elements of a single kind (intermediate shade) or multiple elements including both kinds (lightest shade). The relative contributions of the three kinds of disappearances differ between conditions (see text for details). Note that each bar here summarizes data only from those observers who reported any disappearances at all in the associated condition, because otherwise the relative contributions of the three report options are not defined for that observer and condition. Across the bars the number of observers included ranges between 8 and 11 (out of 12 observers included in the experiment), with an average of 9.3. The proportions displayed here are relative to the numbers of trials where a perceptual disappearance occurred to begin with; not relative to the overall trial numbers.

A model with factors motion (two levels) and ocularity (three levels), and as its dependent variable the proportion of trials where only a single element disappeared (darkest bars in Figure 6), showed a significant effect of ocularity ($\chi^2(2) = 6.3$; $P = 0.04$)

but none of motion ($\chi^2(1) = 2.6$; $P = 0.11$), nor a significant interaction ($\chi^2(2) = 3.5$; $P = 0.17$). The effect of ocularity was mainly due to the fact that single-element disappearances were more common if all 18 grid elements were shown to the same eye (in the monocular conditions) than if elements of a given type were distributed between eyes (in the split conditions). In particular, limiting the levels of the ocularity factor to only monocular and split yields a significant effect of ocularity ($\chi^2(1) = 8.1$; $P = 0.005$), but limiting it to either of the other pairs does not.

Examining the proportions of trials where multiple elements of the same kind disappeared simultaneously (intermediate-shaded bars in Figure 6), the full model with factors motion (two levels) and ocularity (three levels) showed a significant effect of motion ($\chi^2(1) = 9.4$; $P = 0.002$) but none of ocularity ($\chi^2(2) = 2.3$; $P = 0.32$), nor a significant interaction ($\chi^2(2) = 5.2$; $P = 0.07$). The effect of motion primarily reflects the fact that trials where multiple elements of the same kind disappeared simultaneously were quite common (the majority, in fact) in the different motion condition but not in the shared motion condition. In particular, a single-factor model that compares the different motion and shared motion conditions yield a significant difference ($\chi^2(1) = 11.8$; $P = 0.0006$). Such a difference is not observed when comparing either the two monocular conditions ($\chi^2(1) = 0.21$; $P = 0.65$) or the two split conditions ($\chi^2(1) = 1.8$; $P = 0.18$), even though the numerical trends for those conditions are in the same direction. These findings are consistent with our hypothesis that surface-based mechanisms play a role in perceptual suppression when the crosses move out of sync with the plusses, leading multiple elements that contribute to the same surface to perceptually disappear at the same time.

Examining the proportions of trials where multiple elements of different kinds disappeared simultaneously (lightest-shaded bars in Figure 6), the full model with factors motion and ocularity showed no significant effects (motion: $\chi^2(1) = 1.2$; $P = 0.26$; ocularity: $\chi^2(2) = 5.1$; $P = 0.08$; interaction: $\chi^2(2) = 0.01$; $P = 0.99$), even though there is a numerical trend across all ocularity conditions for the shared motion conditions to have a higher proportion of this type of disappearances than the different motion conditions.

Discussion

In this study, we investigated whether conflict between two monocular displays at the level of spatially nonlocal surface or object representations can contribute to instigating interocular suppression. The results of Experiment 1 indicate that nonlocal conflict, indeed, promotes perceptual disappearances beyond what can be explained by local feature conflict. Experiment 2 provides additional evidence for the involvement of spatially nonlocal representations by demonstrating that conditions with more global surface conflict (the different motion conditions) tend to give rise to simultaneous perceptual disappearances of multiple elements that jointly contribute to the same surface, as opposed to disappearances of either single local elements or multiple elements that contribute to different surfaces.

Several existing studies have examined the impact of global image structure on binocular rivalry, and we are aware of two studies that are particularly relevant here. Like our work, both those studies involved dichoptic displays in which individual display elements did not occupy corresponding locations in the two eyes yet, in which the global figures formed by those elements did overlap between the two eyes. One of the studies investigated rivalry between two biological motion displays made up of dots (i.e. point-light walkers; Watson et al., 2004); the other used interocularly offset dot grids quite similar to ours (Silver & Logothetis, 2004). Both studies included stimulus manipulations to modulate perceptual grouping, e.g. presenting a point-light walker upright versus upside-down (Watson et al., 2004), or constructing a monocular dot grid entirely out of identical dots versus intermixing various kinds of dots within a grid (Silver & Logothetis, 2004). We believe that there are two relevant differences that distinguish between these studies and ours. First, we did not manipulate the monocular displays themselves in an attempt to modulate the degree of perceptual grouping within each display. Instead, we manipulated the relation between the two monocular displays – the images either moved in unison for both eyes (shared motion) or differently for each eye (different motion) – in an attempt to modulate whether perceptual grouping extended across the two monocular displays. The second difference with our study is more important. Our main dependent variable indexes whether perceptual disappearances occurred or not: it quantifies the prevalence of trials involving perceptual disappearances relative to ones involving uninterrupted visibility of all display elements (Figures 3 through 5). In contrast, the dependent variable in both existing studies indexes whether a single coherent figure was perceived exclusively (i.e. a single point-light walker or a single dot grid), as opposed to elements of both figures being visible at the same time. In other words, whereas we investigated whether all elements of both grids were perceived or not, the existing work investigated whether the elements of one figure were perceived exclusively or not. The overall finding of both existing studies was that manipulations that promote perceptual grouping within a monocular display (e.g. presenting a monocular point-light walker upright; using only one kind of dots to construct a dot grid) increase the prevalence of such perceptual exclusivity. What the results do not reveal, however, is whether this is because those manipulations increase synchrony in perceptual dominance between different image regions (without synchrony there is no perceptual exclusivity), or because those manipulations increase the prevalence of perceptual disappearances (without disappearances there is no perceptual exclusivity either). Existing work on factors that promote rivalry coherence across space (Fukuda & Blake, 1992; Alais & Blake, 1999; Stuit et al., 2011) renders it plausible that changes in the degree of spatial synchrony contributed to the results reported by Watson et al. (2004) and Silver and Logothetis (2004), and our present findings suggest that changes in the prevalence of perceptual disappearances may have contributed as well. Based on the reported results, however, the two potential contributions cannot be distinguished.

It may deserve mention that, although our findings indicate that nonlocal conflict can boost interocular suppression, they do not argue against the notion that local interocular feature conflict is necessary, too (Carlson & He, 2004). On the contrary, we observed negligible perceptual suppression in the condition that eliminated local interocular feature conflict while maximizing nonlocal surface conflict (i.e. in the different motion, binocular condition). This provides further evidence that local interocular conflict is critical. The fact that grid elements in our study did not occupy precisely corresponding locations across the two eyes is not inconsistent with this conclusion as long as one allows for a certain spatial extent across which a local element can interact with local elements in the other eye; a notion supported by findings such as those by Levelt (1965; see Introduction section).

We were somewhat surprised by the result of our split conditions, in which the stimulus was dichoptic but each eye viewed a proportion of both kinds of grid elements (i.e. some of the crosses as well as some of the plusses). In the different motion, split condition, therefore, the elements contributing to a given surface were split between both eyes rather than contained to one eye. Our results show that this does not reduce perceptual disappearances – if anything, this configuration produced more disappearances than the one in which the elements of each surface were shown to a different eye (in Experiment 2, this increase was not significant). The fact that disappearances were not reduced in the different motion, split condition indicates that, even though perceptual suppression in our experiments is boosted, both by local interocular interactions between image elements and by global interactions between the surfaces made up of those elements, the relevant surface representations are not, themselves, associated with a particular eye of origin. In other words, the surface-based conflict that is relevant here does not seem to be a type of interocular conflict. It is, therefore, conceivable that the underlying mechanism also contributes to other perceptual suppression phenomena that involve no dichoptic stimulation, such as motion-induced blindness (Bonneh et al., 2001; Graf et al., 2002), and conceivably to other cases of ambiguity in surface perception, such as bistable depth ordering (Mamassian & Wallace, 2010). Similarly, the surface-based interactions identified here would form a natural candidate for the noninterocular interactions thought to be involved in so-called flicker and swap rivalry or stimulus rivalry (Logothetis et al., 1996; Wilson, 2003; although see Brascamp et al., 2013).

We have no ready explanation for the finding in Experiment 1 (but not in Experiment 2) that disappearances were, in fact, more frequent in the different motion, split condition relative to the different motion condition in which each surface was tied to elements shown to only a single eye. One clue as to what underlies this high rate of disappearances comes from the second block of Experiment 2 (Figure 6). The results of that block show that the different motion; split condition has a relatively large amount of simultaneous disappearances of elements of both kinds, as compared with the different motion condition. This suggests that any excess of disappearances in the different motion; split condition relative to the different motion condition does not come from mechanisms that act at the level of competing surfaces. We offer two suggestions as to what factors might be at play instead. First, because all elements in a given eye moved in unison in the different motion condition but not in the different motion, split condition, we speculate that the different motion condition might have elicited small, nonconjugate pursuit eye movements, effectively reducing the amount of retinal motion and thereby potentially reducing the motion cue that promotes a perceptual organization involving two overlapping surfaces. If this is true, then that effect would act against, rather than explain, the difference in perceptual suppression between the different motion conditions and the shared motion conditions that is our primary interest here. A second factor that could conceivably play a role here is within-eye contrast normalization. Specifically, in the competition that underlies binocular rivalry, some interactions occur between the eyes' representations, but others, such as within-eye contrast normalization, occur within each monocular representation (Baker et al., 2007; Moradi & Heeger, 2009). Given that the different motion; split condition differs from the different motion condition in terms of the individual monocular images (not in terms of the integrated display across both eyes), it is possible that the strength of a monocular interaction, such as contrast normalization, differs between conditions, potentially explaining the increased incidence of disappearances in the different motion; split condition.

Another perhaps surprising aspect of our results is that we observed many more disappearances in the different motion; monocular condition than in the different motion; binocular condition (e.g. Figure 3). Whereas, in the latter condition, both eyes received congruent stimulation, in the former condition, one of the eyes was presented with a blank screen. The blank screen plausibly amounts to an extremely weak stimulus and, accordingly, one might not have expected the monocular configuration to induce substantially more perceptual disappearances than the binocular configuration. We suspect that the process at work in the different motion; monocular condition is related to what Levelt (1965) termed spurious rivalry. Although Levelt observed a foveal monocular stimulus to rarely disappear perceptually, he observed such disappearances to be more common for peripheral monocular stimuli. Levelt argued that these disappearances were related to Troxler fading; hence the term spurious rivalry. More recently, Leng and Loop (1994) similarly observed that monocular contours failed to permanently suppress a blank screen shown to the other eye. We suspect that our results are related to those previous observations, especially because our stimuli were large enough to extend beyond the fovea.

In conclusion, we have provided evidence that spatially global, object- or surface-level conflict can increase the strength of perceptual suppression during binocular rivalry. Although the role of global configuration in rivalry is well-documented, the existing evidence is consistent with this role being restricted to modulating the coherence of rivalry dominance across space, and has left undisputed the notion that only local feature conflict can elicit rivalry suppression. Our results qualify this notion by showing that perceptual suppression itself is boosted by conflict defined by global Gestalt.

Keywords: binocular rivalry, perceptual organization, gestalt grouping

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