Subjective contours and binocular rivalry suppression

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Abstract

Binocular rivalry probably involves distributed neural processes, some responsible for dominance, others for suppression and still others for fluctuations in perception. Focusing on the suppression process, the present study asks whether neural events underlying rivalry suppression take place prior to, or subsequent to those underlying the synthesis of subjective contours. Specifically, we examined whether (i) a subjective contour could prematurely return a suppressed target to dominance and (ii) whether suppression of a Kanizsa-type inducer precludes the formation of a subjective contour. Suppression durations were not abbreviated by the subjective contour, but suppression did prevent the formation of a subjective contour. Evidently suppression precedes the synthesis of subjective contours in the visual processing hierarchy.
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1. Introduction

Vision's seeming effortlessness belies its complexity: visual perception is the culmination of neural activity within multiple, hierarchically organized pathways each comprising stages of processing involving feedforward and feedback connections. Revealing the unique operations of these various stages represents one of the challenges of visual psychophysics, and toward that end a number of clever strategies have been devised. One class of strategies, dubbed "psychoanatomy" by Julesz (1971), seeks to determine whether the neural operations underlying one process provide input for neural operations underlying another process.

Consider, for example, the interaction between visual aftereffects and binocular rivalry. Lehmkuhle and Fox (1974) found that a full-blown motion aftereffect can be generated even when the adaptation pattern is invisible for a substantial portion of the adaptation period owing to binocular rivalry suppression. However, when the adapting pattern is a plaid consisting of two gratings drifting in different directions, rivalry suppression *does* reduce the magnitude of the resulting aftereffect attributable to pattern motion (van der Zwan, Wenderoth, &

Alais, 1993). Taken together, one can reasonably conclude that the neural site at which translational motion is registered precedes the site of rivalry suppression, which in turn precedes the site at which pattern motion is registered.

In this paper, we have employed similar psychoanatomical reasoning to study the interaction between subjective contours and binocular rivalry. We had three motives for pursuing this question. First, there is disagreement in the literature concerning the relative positions of the neural events underlying these two phenomena. On the one hand, rivalry suppression reduces the magnitude of the tilt aftereffect when the adapting and test patterns are subjective contours (van der Zwan & Wenderoth, 1994), implying that the neural events underlying rivalry suppression precede those underlying the synthesis of subjective contours. On the other hand, dichoptically viewed subjective contours can engage in binocular rivalry (Fahle & Palm, 1991; Harris & Gregory, 1973; but see Blake, 1981; Bradley, 1982), implying the opposite. Second, different rules of operation seem to govern dominance phases of rivalry and suppression phases of rivalry (see Blake, 2001, for a discussion of this point). So, for example, variations in the stimulus strength of a rival target primarily affect suppression durations of that target (Fox & Rasche, 1969; Levelt, 1965), whereas variations in global context within which a rival target appears primarily affect

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dominance durations of that target (Sobel & Blake, 2002). Given this dissociation between dominance and suppression, we felt it worthwhile to re-examine the question of subjective contours and rivalry, in particular isolating the effect of subjective contours on suppression and the effect of suppression on the formation of subjective contours. Third, and finally, we now know considerably more about the neural bases of subjective contours (see Nieder, 2002, for a review), and about possible neural concomitants of binocular rivalry suppression (Blake & Logothetis, 2002).

In two complementary experiments, we exploited an aspect of rivalry suppression and an aspect of subjective contours to explore their interrelations.

(1) In the case of rivalry, it is well known that sudden movement of contours suppressed in rivalry will trigger the premature reappearance of those contours (Fox & Check, 1968; Walker & Powell, 1979). This abrupt transition from suppression to dominance can be achieved even if the "motion" is created by successively flashing a bar on either side of a suppressed target, thereby creating an impression of apparent motion over the rival target (Ooi & He, 1999). In our first experiment we tested whether a subjective contour apparently moving across a suppressed target would trigger that target's premature return to dominance.

(2) In the case of subjective contours, a near threshold "probe" line is more easily detected when it is superimposed on an illusory contour of a "Kanizsa" figure created by appropriately arranged sectored discs (Dresp & Bonnet, 1995). Thus in our second experiment we tested whether an illusory contour would boost the detectability of a low-contrast probe even when one of the contour inducers was phenomenally invisible due to rivalry suppression.

2. Experiment 1: does a moving subjective contour break suppression?

In the first experiment observers dichoptically viewed two displays, each containing one target in the center of the display that was incompatible with the target at the same location in the other eye's display. Additionally, one display contained two horizontal arrays of discs, with one of the rows positioned above and the other below the rival target. Observers indicated that a particular rival target was visible by pressing a key, thereby initiating one of the four animation sequences depicted in Fig. 1. In some trials notches were progressively removed and replaced in the discs, as if a rectangular bar the same color as the background were sweeping across the display. Will a subjective contour sweeping across a suppressed target trigger that target's return to domi-
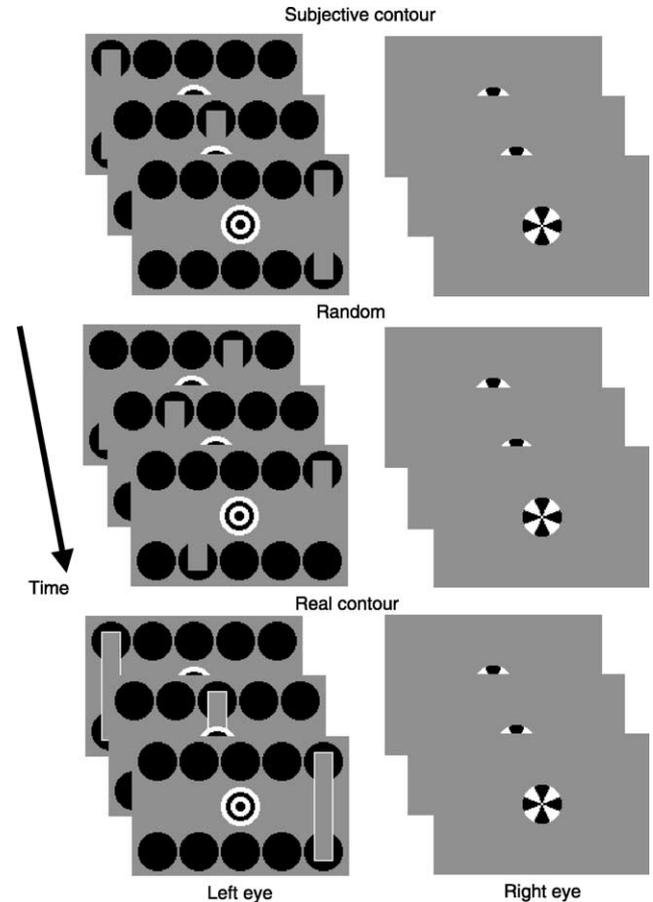

Fig. 1. Left- and right-eye displays for three conditions in Experiment 1. Depicted here are displays from the suppression condition; i.e., the two rows of discs surround the item that is suppressed at the onset of the trial, as indicated by the observer's keypress.

nance? If so, is that triggering effect attributable to the moving subjective contour per se, or to the transients associated with the appearance of the notches on the discs?

If the triggering effect is due primarily to the transients associated with the appearance of the notches, then the effect should be more acute when the discs are closer to the target than when they are farther away. Thus we varied the separation of the discs and included a comparison condition in which the notches appeared on the discs in a spatially random manner. When the notches appeared randomly they did not convey the impression of a moving subjective contour, so in this condition any premature return to dominance would be attributable solely to the transients associated with the appearance of the notches on the discs, *not* the motion of a subjective contour. As well as the random condition, there were two other comparison conditions: (a) a bar defined by a thin line swept across the display, or (b) no changes whatsoever occurred within the display. Given the experimental and control conditions, we were able to ask: Is the effectiveness of the subjective contour

more like that of a real contour, or like that of random, unstructured flicker?

2.1. Methods

2.1.1. Observers

Both authors and three other experienced but naïve psychophysical observers (one female, two male) served as observers in this experiment. All have normal or corrected-to-normal vision.

2.1.2. Apparatus and stimuli

Stimuli were generated by an Apple Macintosh G4 computer and presented on a NEC MultiSync 21″ monitor (85 Hz frame rate, 1024 × 768 resolution); the screen luminance provided the only light in the otherwise dark room. A mirror stereoscope presented displays to each eye separately, at a viewing distance of 89 cm. All stimuli were presented against a medium-gray (18.2 cd/m^2) background.

Each eye's display contained a frame 7.22° wide × 6.40° tall and 1.16° thick, containing a checkerboard pattern of small black and white squares. The frame promoted stable binocular alignment. In the center of one display was a radial grating (the "pinwheel"), and in the center of the other display was a set of concentric circles (the "bullseye"); each rival target was 0.873° in diameter and had a contrast of 0.50. Also contained in one of the displays were two horizontal rows of five black discs, one above and one below the central rival target. This "gauntlet" was located at the same position as uniform gray field in the other eye's display, and all observers reported that it was continuously visible. Each of the discs was the same size as the rival targets and separated horizontally from adjacent discs by 0.0582°. There were four levels of vertical spread between the rows of discs, with either 0.146°, 0.291°, 0.437°, or 0.582° intervening between the closest edges of the rival target and the disc immediately above or below that target.

Observers viewed this static display until the pinwheel became exclusively dominant, at which point they pressed a key, initiating one of four animation sequences. In the subjective-contour condition, a notch was removed from the bottom of a disc in the upper row and from the top of a disc in the lower row; the notches initially appeared in either the two rightmost discs or in the two leftmost discs. Each notch was 0.233° wide × 0.669° tall, and together the two notched discs created the clear impression of a narrow rectangular bar positioned in front of, and thereby occluding the discs. After 110 ms the two notched discs were replaced by intact discs and the next two discs in the gauntlet (either those just to the left of the rightmost discs or those to the right of the leftmost discs) were notched. This sequence continued until the notches proceeded all the way through

the rows to the discs on the opposite side of the gauntlet, creating the impression of a narrow bar sliding across the display. After 550 ms the notches disappeared and the display returned to its original form. In the real-contour condition the notches were deployed just as in the subjective-contour condition, but the borders of the moving bar were delineated by a thin (2 pixels) white line. In the third frame of the animation, when the position of the bar coincided with the central rival target, the borders of the bar were occluded by the rival target; i.e., the bar appeared to pass behind the rival target and the target itself remained completely unchanged. In the random condition notches initially appeared in a randomly selected disc in the upper row and a randomly selected disc in the lower row. Every 110 ms the notches in each row moved to a randomly selected disc that had not previously been selected; after 550 ms the display reverted to its initial state just as in the two conditions described above. In the final, no-motion condition, the display simply remained unchanged until the observer released the key.

2.1.3. Procedure

At the beginning of the session observers carefully adjusted the mirrors of the stereoscope to achieve stable binocular alignment. Observers began each trial by viewing a display and waiting for the pinwheel to become dominant, at which time they pressed the space bar and held it until the bullseye became dominant; the duration of the keypress was taken to represent the duration of the exclusive visibility of the pinwheel. After the observer released the space bar, all items in the display except for the alignment frame were erased; the press of another key revealed the items for the following trial. Along with the four display conditions described above, the other independent variables were the eye to which the pinwheel was presented (left eye or right eye), the eye to which the gauntlet was presented (left or right), the direction of motion of the bar (leftward or rightward), and the spread between the two rows of the gauntlet (4 values of angular separation). Observers ran 5 blocks of 128 trials, with each block containing every combination of the independent variables presented in random order. Because the gauntlet surrounded the dominant target in half the trials and the suppressed target in the other half, the keypress duration indicated the effect of each animation sequence on both the dominance durations *and* the suppression durations relative to that of the other sequences.

2.2. Results and discussion

The pattern of results from all the observers were quite similar, but the rivalry alternation rate, as reflected in the dominance and suppression durations, varied across individuals. Thus each observer's data were

normalized by dividing each duration by that observer's mean duration on "no-motion" trials.

Fig. 2A plots the normalized mean keypress durations across all observers from trials in which the gauntlet surrounded the pinwheel (dominant target) and Fig. 2B plots the keypress durations from trials in which the gauntlet surrounded the bullseye (suppressed target). These data are collapsed across the eye to which the pinwheel was displayed and direction of motion of the bar since neither "eye" nor "direction" affected these durations. As can be seen in Fig. 2A, there was little difference in durations between any of the display conditions when the animation sequence occurred in the same eye's display as the dominant target. This finding is consistent with earlier work showing little if any effect of transients on the dynamics of dominance durations (Sobel & Blake, 2002; Walker & Powell, 1979). Suppression durations, however, *did* vary systematically across conditions, as can be seen in Fig. 2B. When the moving bar was defined by a real contour, suppression

durations were brief relative to those in the other conditions, regardless of the magnitude of the spread between the gauntlet rows. Apparent motion of real contours through the zone of suppression was effective at returning the previously suppressed target to dominance (as in Ooi & He, 1999). In contrast, when the display remained unchanged after the keypress, suppression durations were relatively long. As expected, transients associated with randomly appearing notches broke suppression more effectively when the discs were closer to the target; i.e., in the random condition, suppression durations increased along with the separation between the gauntlet rows.

The chief aim of this experiment was to determine whether subjective contours per se prematurely terminated suppression. In the subjective-contour condition the suppression durations increased with gauntlet width just as in the random condition. From this fact we conclude that any curtailment of suppression durations in the subjective-contour condition was due to the transients appearing on the inducers, i.e., the presence of a moving subjective contour did not itself tend to prematurely terminate suppression.

One interpretation of these results is that the neural events underlying suppression occur at a site prior to the site underlying the neural synthesis of subjective contours. Another possibility is that these two processes rely upon neural events occurring at the noninteracting neural sites (e.g., in separate, parallel pathways). To distinguish between these two possibilities, we performed a second experiment in which the roles of rivalry suppression and subjective contours were swapped. In the second experiment we asked whether suppression interferes with the formation of subjective contours.
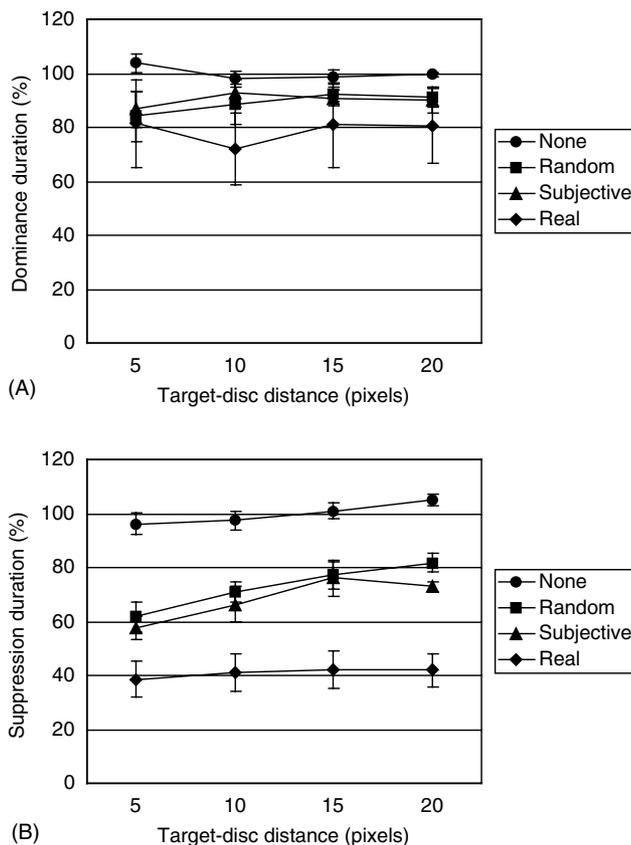

Fig. 2. Results from the dominance and suppression trials of Experiment 1 averaged across all five observers. Each data point represents the length of time that an item remained in the same rivalry state as it had been at the onset of the trial, i.e., the time that an initially dominant item remained dominant, or that an initially suppressed item remained suppressed. Because each duration was normalized by dividing by the mean duration from the "no-motion" condition, durations are expressed as a percentage of the normalizing divisor.

3. Experiment 2: does suppression of an inducer prevent the formation of subjective contours?

Imagine an array of three sectored discs that together create the impression of three, connected subjective contours forming an illusory triangle. Let one of those sectored, inducing discs be presented to one eye only, with the corresponding region of the other eye receiving a dissimilar shape that engages the inducing disc in binocular rivalry. The monocularly viewed inducing disc, in other words, will be intermittently suppressed from visual awareness. Will suppression of that disc preclude it's participation in the formation of the subjective contours that the disc normally supports? Based on appearances alone, the answer appears to be "yes" in that the illusory figure disappears when the disc is suppressed. However, it is conceivable that the suppressed disc *does* remain effective and that the component illusory contours *are* synthesized, only to be lost to visibility at a subsequent stage of neural processing where rivalry

suppression is engaged. What is needed, therefore, is a more definitive test of the effect of suppression on the formation of subjective contours. Toward that end, we exploited the fact that a briefly presented, low-contrast line segment is more easily detected when aligned with the subjective contour indicated by inducing shapes than when the inducing shapes are not presented (Dresp & Bonnet, 1995). The subjective contour, in other words, gives a "subthreshold" boost to the contrast of a real line superimposed on the illusory one. Now, if the neural events underlying synthesis of subjective contours are unperturbed by binocular rivalry suppression, the contours formed by the inducers should boost the detectability of a line probe even when one of those inducers is phenomenally invisible. This is the rationale motivating our second experiment.

For this experiment we made two pairs of rival displays, one called the "configural" display and the other the "nonconfigural" display (see Fig. 3). In the configural display, one eye viewed an upright equilateral Kanizsa triangle formed by notched discs ("pacmen"), and the other eye viewed a display in which the upper pacman was replaced by a complete disc. From pilot work leading up to Experiment 2, we determined for each observer the luminance contrast required for a briefly presented probe lying along one of the two diagonal legs of the Kanizsa triangle to be detected approximately 80% of the time. Using this threshold contrast value, we then measured the detectability of probes when presented among displays containing three pacmen and when presented among displays containing two pacmen and a disc. Results from this phase of the
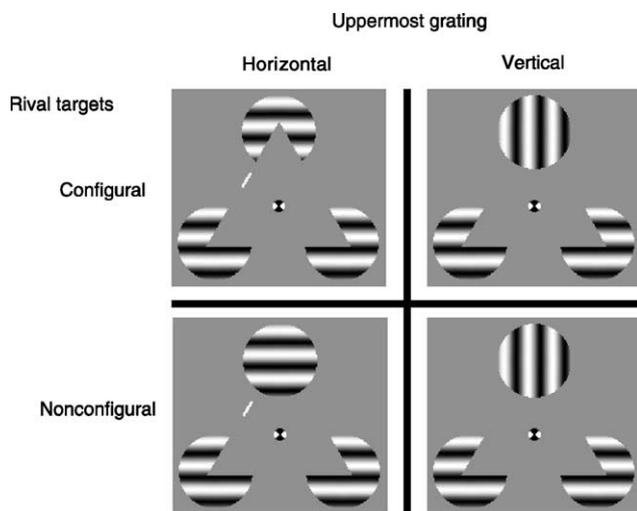

Fig. 3. Displays for Experiment 2. We dichoptically presented the two upper displays in configural trials, the two lower displays in nonconfigural trials. When observers pressed a key indicating that either the horizontal or vertical grating was visible in the shape at the top of the display, a line segment probe appeared briefly in the display containing the horizontal grating.

pilot work confirmed that the findings of Dresp and Bonnet (1995) extended to our displays, in that detection rates were higher for probes presented amid configural displays than for probes presented amid nonconfigural displays.

In the critical experiment the display containing the intact disc was presented to one eye and the display containing the pacman was presented to the other eye. In half of the trials observers pressed a key when the pacman was visible ("dominance" condition), and in the other half of the trials observers pressed a key when the disc was visible ("suppression" condition); although the inducer was physically present on all trials, it was phenomenally present only on the dominance trials. Will phenomenal invisibility prevent the inducer from boosting the detectability of the probe just as if it had been physically removed? If so, then the probe should be easier to detect on trials when the pacman is visible compared to trials when it is invisible. Of course, it is possible that the probe is more difficult to detect not because the pacman is suppressed but because suppression has spread to neighboring regions of the display (Kaufman, 1963), including the region where the probe was presented. To evaluate the contribution of spreading suppression, we constructed the nonconfigural displays depicted in Fig. 3. If probe detection with these displays is equivalent to that with the configural displays, we would be unable to draw any conclusions about the consequence of suppression of the inducing pacman per se. However, if the detectability of the probe is boosted more under the configural condition than under the nonconfigural condition, we can safely conclude that it is the phenomenal absence of the subjective contour that is impairing detection, not just a general spreading of suppression from one region of the display to another.

3.1. Methods

3.1.1. Observers

The authors and two of the naïve observers from the first experiment served in this experiment.

3.1.2. Apparatus and stimuli

The apparatus used in this experiment was the same as in the previous experiment. In the pair of configural displays, both eyes' displays contained a frame 3.72° wide × 3.49° tall and 0.291° thick, consisting of alternating black and white checks. In the center of each frame was a circular fixation mark with a diameter of 0.349°, in which the upper and lower quadrants were black and the left and right quadrants were white. The frame and fixation mark, both of which remained visible throughout the experiment, served to ensure stable binocular alignment. In either the right or left eye's display appeared three "pacmen", or circular discs with wedges colored the same gray as the background

(18.2 cd/m^2)—these three pacmen created the vivid impression of an upright equilateral Kanizsa triangle for which each leg was 2.04° long. Each pacman had a diameter of 1.05°, was centered on a point 1.05° from the center of the fixation mark, and contained a horizontal sinusoidal grating with a frequency of 2.87 cpd and a contrast of 0.95. The other eye's display also included the lower two pacmen, but the upper pacman was replaced by an intact disc containing a vertical sinusoidal grating, itself 2.87 cpd in spatial frequency and with a contrast of 0.95. In the nonconfigural displays the notch from the upper pacman was replaced, thereby forming an intact disc containing a horizontal grating. To enhance the conspicuity of the subjective triangle, we set the gratings in motion; each grating oscillated smoothly back and forth at 1 Hz in a direction orthogonal to the orientation of the gratings' bars.

At the press of a key a low-contrast line segment appeared monocularly in the display containing the three pacmen (or for the nonconfigural condition, the display with three horizontal gratings), positioned on either the left or right leg of the subjective triangle. To avoid abrupt transients the luminance of the probe was increased and then decreased gradually over a 500 ms duration. The line segment probe was a quarter of the length of the gap between the two inducing pacmen, with its lowest point coinciding with a point halfway along the gap. After the offset of the line segment probe, the display remained unchanged for another 500 ms, after which all items but the frames and fixation marks were erased. With the press of another key the displays for the next trial would appear.

3.1.3. Procedure

At the onset of each trial observers dichoptically viewed either the configural or nonconfigural pair of displays in Fig. 3 and pressed a key when either the horizontal grating or the vertical grating was dominant. Trials were blocked so that each observer ran four different blocks of trials (2 pairs of displays × 2 dominance conditions), with 200 trials per block. The eye to which the horizontal gratings were presented and the order of blocks were counterbalanced across observers. The keypress initiated the brief presentation of a line segment probe along either the left or right leg of the Kanizsa triangle, in the same display as the one with horizontal gratings in the top position of the triangle. After the display elements were removed, observers made a forced choice between the two positions in which the probe could have appeared, guessing if necessary; error feedback was not provided.

3.2. Results and discussion

The percentage of correct responses in each of the four blocks is presented in Fig. 4. Because results from
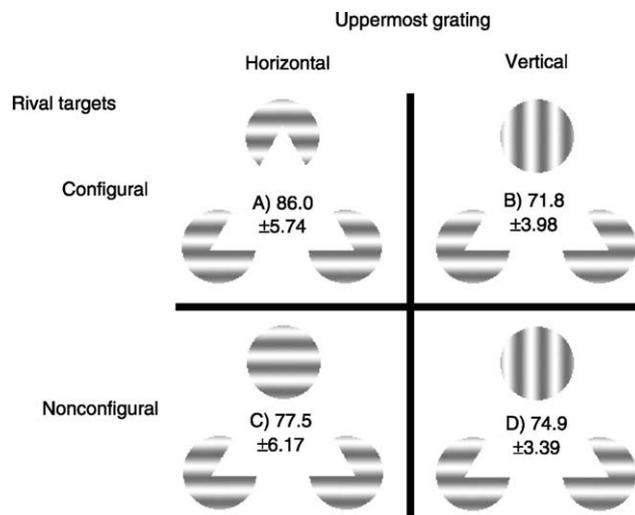

Fig. 4. Results from Experiment 3. Each cell corresponds to one of the four display conditions depicted in Fig. 3, and contains the percentage of correct answers in a two-alternative forced choice, averaged across four observers, ±one standard error.

the four observers were comparable, the values represent the means across observers. Comparing the performance when the horizontal grating was dominant across display type (cell A > cell C) reveals that the inducer boosted the detectability of the probe, replicating the results from the pilot work as well as from Dresp and Bonnet (1995). More importantly in the context of the present study, the probe was more easily detected when the pacman was visible than when it was physically presented but phenomenally invisible (cell A > cell B). As mentioned above, if this effect is due primarily to the suppression of the probe, then the probe should have been more easily detected when in the same display as the dominant eye, regardless of the particular shape of the dominant target. However, while there remained a difference between dominant and suppressed eye for the nonconfigural displays (cell C > cell D), the difference between dominance and suppression was greatly reduced from what it had been for the configural displays. Thus, while the probe may have been somewhat affected by spread of suppression, we conclude that the lion's share of the effect with this pair of displays was attributable to the phenomenal state of the inducer itself.

To bolster this conclusion, one of the authors (RB) repeated this experiment with the probes now positioned farther from the inducer. Specifically, the uppermost point of the line segment probe now coincided with what had previously been the bottommost point. Under these conditions the probe was unaffected in the nonconfigural display but was still facilitated in the configural display (albeit by an amount slightly less than that found when the probe was nearer the middle of the subjective contour). We remain confident, therefore, that rivalry suppression interferes with the synthesis of subjective contours.

4. General discussion

Taken together, the results from these two experiments provide converging evidence that the site of the neural events underlying binocular rivalry suppression precedes the site at which subjective contours are explicitly represented in visual cortex: suppression is unaffected by a moving subjective contour whereas the formation of a subjective contour is impaired as indexed by the contour's failure to enhance probe detection. How do these findings and the associated conclusion square with other results on rivalry and subjective contours?

Turning first to subjective contours, the widely cited study by von der Heydt, Peterhans, and Baumgartner (1984) implicated visual area V2 as the cortical site where subjective contours are explicitly represented, with no evidence that V1 neurons were responsive to these stimuli (for corroborating evidence, see Bakin, Nakayama, & Gilbert, 2000). Several later papers, however, presented evidence that at least a fraction of V1 cells, too, respond to illusory contours (Grosof, Shapley, & Hawken, 1993; Sheth, Sharma, Rao, & Sur, 1996). These seemingly contradictory findings may depend on the specifics of the stimulus conditions creating subjective contours: fracture lines in abutting, phase shifted lines activate some neurons in V1 whereas illusory bars defined by implied occlusion do not. Based on optical imaging and dynamical analysis of the evolution of neural activity, several research teams have concluded that subjective contours are first explicitly represented in V2 (Ramsden, Hung, & Roe, 2001), with these signals then propagating back to V1 (Lee & Nguyen, 2001). Brain imaging and evoked potential studies in humans also point to extrastriate cortical areas—not V1—as primary sites at which subjective contours are neurally formed (Mendola, Dale, Fischl, Liu, & Tootell, 1999; Murray et al., 2002).

What, then, can be said about the neural site of binocular rivalry suppression? Focusing on V1 as a region of interest, several brain imaging studies have observed fluctuations in V1 BOLD signals correlated with dominance and suppression phases of binocular rivalry (Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001). These findings imply that at least some of the neural events underlying rivalry transpire at the very earliest stages of cortical processing. Yet the single-cell recording work by Logothetis and colleagues has disclosed modulations in neural responses in just a fraction of V1 neurons of alert, behaving monkeys experiencing binocular rivalry; only at higher visual areas, such as inferotemporal cortex, are wholesale modulations in neural activity observed during rivalry (e.g., Leopold & Logothetis, 1996; Sheinberg & Logothetis, 1997). It will be interesting to see how these seemingly conflicting results—human brain imaging and monkey single cell

recordings—are resolved. In the mean time, the psychophysical evidence reported here points to a relatively early site of suppression.

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