

Effect of binocular rivalry suppression on contrast change detection

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Abstract

In their 2004 study, Watanabe et al. measure the detectability of contrast increment probes during rivalry dominance and suppression by plotting threshold versus contrast (TvC) functions, finding significant elevation of detection thresholds during suppression. But what about contrast decrements, a probe that actually makes the target image harder to see? Here I review the literature on binocular rivalry and probe studies and measure the effect of two new probe types on detection thresholds. Results show that contrast decrement probes produce a very different pattern of detection thresholds than their increment counterparts. Extrapolating from these results, I also theorize on the effect of suppression on the underlying contrast response function (CRF).

1. Introduction

As human beings, we like to think that, in general, our senses do not deceive us. We like to think that our perceptual experiences mirror the actual world surrounding us, especially in the case of vision, the sense we most depend on. It is no wonder, then, that the phenomenon of multistable perception has interested and continues to interest so many perceptual scientists today. The idea that one's visual perception can change so markedly in the face of a completely invariant stimulus is downright unsettling. Different types of multistable phenomena include form ambiguity, monocular rivalry, and binocular rivalry, but the term is generally defined by the presence of stochastic alternations between two or more perceptual experiences in the face of an unchanging stimulus. Perhaps the most intriguing and scientifically valuable of the three is binocular rivalry. When different images are mapped onto the corresponding retinal space in each eye, the brain lapses into a state of perceptual alternation where the observer sees one image as visible for a few seconds, then the other. The non-dominant image is rendered completely invisible. These switches continue for as long as the observer looks at the stimuli. This confusion the brain experiences is caused by its inability to resolve which image occupies the particular area of three-dimensional space they both appear in. Binocular rivalry differentiates itself from other types of multistable perception in its mode of presentation (a different image is shown to each eye as opposed to monocular rivalry, where two images are shown to one or both eyes) and the degree to which the non-dominant stimulus is suppressed. Indeed, the suppressed image seems to be completely erased from visual awareness, though there is recent evidence that some information from the suppressed stimulus can reach dorsal brain areas (Fang and He, 2005) and structures in the limbic system (Pasley et al., 2004). Given binocular rivalry's strong perceptual fluctuations and robust suppression of a clearly visible stimulus, vision scientists have

for many years considered its study worthy as a pathway to unlocking the neural concomitants of visual awareness itself.

1.1 General Characteristics of Binocular Rivalry

Assuming sufficient exposure time, binocular rivalry is instigated whenever the brain receives signals from both eyes indicating that two different images are occupying the same visual space. Though it is true that normal stereo vision provides different images to each eye, in a typical environment these inconsistencies are minor and result in coherent depth perception. But when the images presented to each eye differ sufficiently in any of a wide variety of color, form, or motion properties, rivalry occurs and perception begins to alternate. Most vision scientists agree that the characteristics of rivalry can be separated into spatial and temporal characteristic categories, though I will also address characteristics of suppression.

1.1.1 Spatial Characteristics

Binocular rivalry is not unique to the fovea; it can occur for images mapped anywhere on the retina so long as the images are exposed to the same area in each eye and are magnified for increasing retinal eccentricity (and thus decreasing visual acuity). In cases where the stimuli are of sufficiently small size, the entirety of both images will rival as wholes, meaning that viewers will typically see an entire image as dominant before it gives way to the suppressed image, which is then seen in its entirety as well. However, when the rivalry targets are relatively large (where “large” depends on retinal eccentricity), the viewer observes the rivalrous alternations as occurring in multiple discrete “zones” throughout the image (Meenes, 1930). This phenomenon results in portions of each image achieving dominance in different parts of the target space and is thus dubbed “patchwork” or “piecemeal” rivalry. Non-foveated targets require larger target sizes to produce patchwork rivalry (Blake et al., 1992) and, in general, larger targets will reveal more

of these zones. Many believe that patchwork rivalry is strong evidence that rivalry occurs not strictly between the eyes as historical convention states, but rather between corresponding local zones in each eye (Blake, 2001).

Furthermore, there are several reasons to believe these rivalry zones are not independent of one another. Blake et al. (1992) found that in larger targets, complete dominance of a particular image occurs more often than one should expect based on the independent dominance probabilities of the zones alone. Similarly, collections of separate smaller rivalry targets achieve unified dominance at a higher than chance rate (Alais and Blake, 1999; Whittle et al., 1968). Finally, the nature of dominance transitions in rivalry targets suggests a certain degree of inter-zone interaction as well, considering that the suppressed image often attains dominance in a coherent “wave” that begins at one or more points and sweeps across the previously dominant image, erasing it from awareness (Wilson et al., 2001). From this evidence, many have theorized that the dominance state of a particular zone influences and is influenced by the state of adjacent zones.

1.1.2 Temporal Characteristics

The experience of binocular rivalry given dichoptic stimulation is not instantaneous. According to Blake et al. (1991), achievement of normal binocular rivalry requires at least several hundred milliseconds of exposure, though participants were able to distinguish dichoptic from dioptic stimuli at an above chance rate for exposure times as low as 80 ms. Once instigated, the normal time course for dominance alterations fits a gamma distribution (Fox and Herrmann, 1967), though average dominance durations can range from half a second to nearly ten seconds depending on the observer. Typically, older rivalry viewers experience longer average dominance durations (Jalavisto, 1964), but these values vary between individuals of the

same age quite a bit as well. It is especially interesting to note that rivalry viewers are unable to bring a particular stimulus to dominance on demand simply by exerting their will (Blake, 1988), though Helmholtz (1925) and Ooi and He (1999) note that attention can prolong dominance of a particular stimulus somewhat. The influence of attention appears to merely bias rivalry in favor of the attended stimulus, evidenced by the fact that most people cannot hold an image in dominance indefinitely. One particularly interesting study, however, reported that Tibetan monks with extensive training in meditation were able to hold a particular stimulus in dominance for surprising amounts of time (Carter et al., 2005).

Despite its seeming invulnerability to viewer control, binocular rivalry is remarkably susceptible to various other altering and disrupting forces. Transient stimulation is one such force. Even completely suppressed stimuli can immediately be brought to dominance by transient stimulation such as physical motion in front of the suppressed eye (Grindley and Townsend, 1965), abrupt contrast changes (Blake and Fox, 1974a), introduction of stimulus motion (Fox and Check, 1968), or sudden flickering of the images (O'Shea and Crassini, 1984). In fact, this property of rivalry makes it useful as an experimental paradigm whereby an investigator can mask a presented image with extreme effectiveness by presenting it in rivalry with a moving image (Pasley et al., 2004). Investigators may also alter the normal time course of rivalry with a large variety of non-transient stimulus manipulations, evidence for which is well-documented throughout the literature. Differences in contrast, color, luminance, spatial frequency, semantic content, size, motion, and emotional affect between the competing images can bias rivalry's fluctuations in favor of a particular stimulus. Levelt (1965) discovered that in these cases, the stronger stimulus (higher contrast, brighter, more contours, more compelling motion, etc.) does not manifest itself in longer dominance durations, but instead in more *frequent*

dominance periods caused by shorter periods of suppression . Levelt also notes that this means two rivalrous high contrast gratings will induce more rapid alternations than otherwise identical low contrast gratings.

The current theory on dominance/suppression transitions in binocular rivalry is based on neural adaptation. Most vision scientists believe that excitatory action potentials from the currently dominant stimulus begin to wane over time, steadily giving way to action potentials from the suppressed stimulus until it eventually fades from consciousness and is replaced by the previously invisible image (Mueller, 1990; Sugie, 1982). This model is supported by evidence from dominance recovery period studies (Blake et al., 1990).

1.1.3 Traits of Rivalry Suppression

Particularly interesting among vision scientists is the nature of suppression during binocular rivalry. Paradoxically, a suppressed image falls completely outside visual awareness, but many types of transient stimulation are able to cancel suppression and force a target into dominance, as described above. At the same time, many groups have reported that the suppressed target suffers increased detection thresholds for these types of stimulation (Wales and Fox, 1970; Fukuda, 1981; Smith et al., 1982). Non-transient changes in the suppressed stimulus are even more difficult, often impossible, to detect. Even large changes in the suppressed stimulus can escape detection, as long as the changes are introduced in a way that minimizes abrupt transients (Blake and Fox, 1974a; Blake et al., 1998). This loss in visual sensitivity accompanying rivalry suppression is observed physiologically as well; the pupillary light reflex is depressed in the suppressed eye compared to the dominant one (Lorber et al., 1965).

Despite suppression's effect on visual sensitivity, some aspects of normal visual behavior are preserved, nearly completely unperturbed by rivalry suppression. Specifically, many types

of visual adaptation can co-exist with normal rivalry with only a handful of exceptions (Blake and Fox, 1974b; O'Shea and Crassini, 1981; Wade and Wenderfoth, 1978). This evidence together with results from the above sensitivity loss studies illustrates some of the difficulty investigators face in their attempts to pinpoint various aspects of rivalry within specific neural areas comprising the visual pathway.

1.2 Probe Studies

Though there is presently no overarching model of rivalry with widespread support that can account for all of its demonstrated characteristics, it is generally assumed that rivalry involves neural inhibition of signals associated with a particular stimulus (Blake & Logothetis, 2002). One of the unique hallmarks of binocular rivalry, this inhibitory mechanism is currently a very popular topic of study among perceptual scientists and appears to be one of the most promising avenues to gaining insight into the neural workings of binocular rivalry. One particularly successful way scientists study inhibition is by presenting stimulus “probes” to a monocular rival image during its dominance or suppression phases (Fox, 1963). For example, investigators might introduce motion, color, form, or contrast changes in a suppressed target and monitor whether or not the subject noticed the probe. Alternatively, the subjects might be required to make a particular judgment on the probe or report if it prematurely terminated suppression. From this technique we know that particular types of probes are more likely to break suppression than others, as reviewed above. The thresholds of detection for these probes are easily calculable and have been shown to be consistently elevated for probes shown during suppression versus probes shown in dominance (Wales and Fox, 1970), though the degree of threshold elevation does vary depending on both the suppressed image type and the probe type (Alais and Melcher, 2007). Furthermore, Wales and Fox also demonstrated that detection

thresholds for probes shown during dominance are identical to probes shown in monocular viewing conditions. Additionally, the level of suppression seems to remain uniform independent of the contrast of the suppressor (Blake & Camisa, 1979) and irrespective of how long it has been suppressed (Fox & Check, 1972; Norman et al., 2000).

Clearly the probe technique can be quite revealing about the depth of suppression experienced during binocular rivalry. However, Watanabe et al. (2004) noted that nearly all probe studies use probes that are superimposed onto one of the two target images. Instead of using one of these traditional superimposed probes that aren't part of the stimulus itself, these investigators studied the depth of suppression by implementing a probe that briefly altered the contrast of one of the stimuli during binocular rivalry. Probes in this experiment were 500ms "pulses" where the contrast of either the upper or lower half of the stimulus was increased and then decreased according to a Gaussian time profile (Figure 1). The subjects' task was to report whether the probe was presented in the top or bottom half of the stimulus image. Using this method, the investigators mapped threshold versus contrast (TvC) functions on a log-log scale that described the effect of pedestal contrast (contrast of the to-be-probed stimulus) on probe detection thresholds (Figure 2). As expected, they found that detection thresholds for probes shown during suppression were modestly but significantly elevated (about 0.3 log units) compared to probes shown during dominance or monocular viewing. However, they also found that the slope of the TvC functions was identical for probes shown during suppression and dominance. This finding implies that the contrast gain control mechanism (whereby the same absolute contrast increment becomes more difficult to detect as the pedestal contrast is increased) operates without regard to pedestal visibility. To put it in other words, it appears that rivalry suppression operates "after" the gain control mechanism in the visual process.

In summary, the investigators found that the contrast increments were more difficult to detect during rivalry suppression versus dominance, but only by a relatively small amount. This confirms previous work conducted concerning rivalry probes and makes sense considering that increasing the contrast of a stimulus during rivalry increases its effective strength and makes it less difficult to see. According to Levelt (1965), this strength increase manifests itself in a decrease in the amount of time the strengthened stimulus is suppressed. However, perceptual scientists have not yet tested the detectability of a rivalry probe that makes the image *more* difficult to see. Watanabe et al. measured the effect of contrast increment probes, but what about contrast decrements? What sort of TvC functions would such a probe produce? A study similar to that of Watanabe et al. using contrast decrements as probes could reveal new information about the effect of rivalry suppression on contrast change detection. Are contrast decrement probes more difficult to detect than increment probes or are they equally detectable? Could they even be easier to detect than contrast increments? On one hand, any stimulus change during rivalry should increase the salience of the pedestal image and therefore make probe detection easier. On the other hand, decreasing the contrast of part of the pedestal image should make it more difficult to detect overall simply because lower contrasts are inherently harder to perceive than higher contrasts. Furthermore, it is possible that there is an asymmetry in the suppression of contrast increments versus contrast decrements. An investigation similar to that of Watanabe et al. but with modified probes should reveal more.

There is also the secondary issue of the probes used in the Watanabe et al. study. The probe used is likely an improvement over previous probe types that are simply superimposed over one of the two stimuli, but it might also have undiscovered limitations. As discussed above, the probe consists of a contrast “pulse,” which is generally referred to by the scientific

community as an increment but is actually composed of both a contrast increment and decrement. Since the increment is always followed by the decrement in the Gaussian pulse, we cannot be certain that the effects measured by Watanabe et al. and others before them are due to the increment alone. It might be useful to test the strength of suppression using a new probe that separates increments and decrements more effectively and compare the TvC functions for the traditional pulse probe and this modified probe.

In order to address these issues, I investigated the threshold versus contrast functions for probes consisting of separate contrast increments and contrast decrements.

2. Method

This experiment was intended to be a replication and extension of the Watanabe et al. (2004) study with some stimulus modifications. Thus, the method, apparatus, and procedure adhered very closely to the original study as described in its publication in *Vision Research*.

2.1 Participants and Apparatus

Most of the participants were naïve to the purpose of the investigation and had normal or corrected-to-normal acuity, color, and depth perception. For the main experiment, data were collected from four adult males with ages ranging from 22 to 33. The stimuli were displayed in a dark room on a gamma-corrected CRT monitor of identical dimensions and refresh rate to that used by Watanabe et al. (19.2° x 25.6°, at 75 Hz). The software used was the original code used in the Watanabe et al. study modified to allow for separate increment-only and decrement-only probes. Participants viewed the stimuli dichoptically using a haploscope and responded using a normal computer keyboard.

2.2 Procedure

Procedure closely followed that outlined by Watanabe et al. in *Vision Research* and illustrated in Figure 1. Upon instigation of a trial, a radial checkerboard pattern (1.5 ° in size) and a horizontal sine-wave grating (1.5 ° in size, 6.7 cycles/deg) were presented against a gray background (29 cd/m²). They were positioned so that subjects could view them dichoptically through a haploscope, and a border surrounded each stimulus in order to promote stable binocular alignment. The horizontal grating pattern acted as the probe pedestal across all conditions and subjects. Its contrast was selected from five values (10%, 15%, 22.5%, 33.8%, and 50.6%). The contrast of the competing radial checkerboard pattern was 40%. The horizontal grating pedestal was presented to a predetermined eye in each subject, randomized for each subject for the duration of the experiment.

The subjects were instructed to fixate on the center of the rivalry target for the duration of each block. Subjects indicated by keypress when the pedestal achieved the necessary rivalry state. Half of the blocks measured thresholds for probes presented during dominance and half measured thresholds for probes presented during suppression. The probe followed this initial keypress by 250 ms and was designed based on results from pilot work (see Figure 7 for pilot method and results). The objective of the pilot study was to determine whether to use the contrast pulse probes used by Watanabe et al. or a new “pure” probe type consisting only of a contrast increment or decrement. To illustrate the nature of this new probe type, during a “pure” increment probe trial the grating contrast was increased in either the top or bottom half of the image over a 250ms Gaussian window. However, instead of immediately returning to the baseline pedestal contrast as the pulse type used by Watanabe et al. did, the probe contrast remained at the altered level for 340 ms, after which the stimuli were removed from the screen. The pure decrement probe trials followed an identical time course, excepting that the decrement

probe caused a decrease in contrast in either the top or bottom half of the pedestal. Following pilot results, I decided to use these new pure increments and decrements for the main experiment. After the stimuli were removed from the screen, the subject was instructed to indicate by appropriate keypress whether the probe appeared in either the top or bottom half of the grating image. Subjects were able to abort a trial by keypress both before and after the appearance of the probe and were instructed to avoid instigating a probe during dominance transitions. Subjects were also instructed to abort trials in which the dominance state of the pedestal image changed in the interval between initial keypress and trial instantiation. Once the subject responded to or aborted the trial, another trial began.

Each block of trials presented one of the probe types (increments or decrements) throughout and used a staircase method to determine an empirical detection threshold. The probe increment or decrement amplitude was initially be set to 50% of the pedestal contrast at the start of each staircase. Once the subject responded correctly to three consecutive trials, the subsequent trial reduced its increment or decrement amplitude by 30%. If the subject made an incorrect response, the subsequent trial increased its increment or decrement amplitude by 30%. Once the subject achieved four reversals in a given staircase, the magnitude of the contrast changes dropped to 15% in order to more accurately estimate the empirical threshold. The staircase terminated once the subject achieved 12 staircase reversals. The threshold measured by this procedure represents the smallest contrast change in the pedestal image that the subject could detect and locate with an accuracy of 81%.

Given the nature of the staircase procedure, the number of trials in a given block varied, but block durations ranged from 5 to 15 minutes, considerably less time than Watanabe et al. reported (>20 minutes). Since the subjects were able to control the instigation of probes, they

were able to rest between trials if they desired and data were collected from subjects for no more than one hour at a time. Each subject completed three staircases in each of the dominance and suppression conditions with the five pedestal contrasts and two probe types, generating 60 detection thresholds total from 60 blocks across 20 unique condition combinations. Subjects were given substantial practice time in all cases before data collection began.

3. Results

The data collected across all four subjects were qualitatively similar. Averaged and single subject results from all conditions and pedestal contrasts are shown in Figures 3 and 4.

Mapped TvC functions conformed to the large body of literature showing that contrast increment thresholds are proportional to pedestal contrast for the higher range of contrasts used here. Normally a facilitation effect, commonly referred to as the “dipper” portion of the curve, is observed at near- and sub-threshold pedestal contrast values, but I did not test subjects at these values because they do not produce rivalry alternations. An example of a typical full TvC curve for contrast increment probes seen in the literature is shown in Figure 5. The TvC curves produced here exhibited significant positive linear slopes in all four conditions and a one-way ANOVA confirmed the significant positive effect of pedestal contrast on detection thresholds ($F = 38.935, p < .001$). Slopes of the TvC functions for each subject varied from .15 to .75, but most fell between .35 and .65, consistent with results found by Watanabe et al. Slopes for contrast increments did not differ significantly between dominance and suppression, replicating the results of Watanabe et al. However, slopes for contrast decrements were found to differ significantly between dominance and suppression ($F = 7.387, p = .035$), a departure from the conclusion drawn by Watanabe et al. that pedestal visibility has no effect on contrast gain control.

As expected, functions found during suppression demonstrated larger y-intercepts than those found during dominance, resulting in the same vertical shift that Watanabe et al. showed. Functions differed in vertical position by about .5 to .6 log units (though one subject showed a stable 1 log unit difference), a slightly more sizable effect than that demonstrated in Watanabe et al., where a steady .3 to .4 log unit difference was reported. An ANOVA confirmed this main effect of dominance state on detection thresholds across increment and decrement conditions ($F = 563.252, p < .001$).

A significant issue under examination in this experiment concerns the detectability and suppression of the novel contrast decrement probe used in my study. While pilot data suggested that decrements would be easier to see during dominance (see Figure 7 for pilot method and results), I found no main effect of probe type in the dominance condition ($F = .894, p = .346$). However, a main effect of probe type was found in the suppression condition ($F = 8.245, p = .005$), where detection thresholds for contrast decrement probes were significantly elevated. An additional ANOVA revealed that this interaction between the probe type and dominance state was significant ($F = 11.730, p = .001$).

4. Discussion

4.1 Pure Increments and Decrements

Overall the novel pure increment and decrement probes used here behaved very similarly to the pulse probes used by Watanabe et al. and others. The separation of the conventional pulse probe into its increment and decrement components did not radically alter subjects' ability to perceive the novel probes during dominance or suppression, evidenced by subject report and the qualitative and quantitative similarity between the TvC functions found here and in Watanabe et al. Despite the lack of surprising data from pure increments and decrements in the main

experiment, it is interesting to note that pure increments and decrements produced significantly lower detection thresholds than their pulse counterparts in the pilot experiment ($F = 39.300$, $p < .001$), where the two were directly compared during nonrivalrous viewing within four subjects. One might argue that this result was found due to the time course of the pure increments and decrements (Figure 1). The pure probes remain at their altered level for 340 ms after onset; perhaps subjects were explicitly comparing the top and bottom half of the target image instead of trying to detect changes. However, a control experiment found that this was not the case. A target image's post-probe exposure time (designated as α) has no significant effect on detection thresholds ($F = .046$, $p = .836$ for 2 subjects at 2 α levels; $F = .257$, $p = .854$ for 1 subject at 4 α levels).

If subjects are not benefitting from explicit comparison of the top and bottom target image halves, then how is this result explained? It is possible that the conventionally used pulse contrast increment probes suffer from some level of inhibition or interference between their component increments and decrements. If true, this suggests that what previous pulse probe studies have been measuring (detection thresholds for an interaction/interference between the two halves of a pulse probe) is not actually what they have been purporting to measure (detection thresholds for a pure increase in contrast). This issue is further complicated by the fact that there appears to be an asymmetry in the detection of pure contrast increments and decrements.

4.2 Contrast Decrements in Dominance

This experiment also introduced another novel probe type – contrast decrements. Despite the lack of precedence for this kind of probe, one that actually decreases the overall visibility of the pedestal image, knowledge of the underlying contrast response function could inform

hypotheses about how detection thresholds for contrast decrements might compare to those for traditional contrast increments.

It is possible, through measuring behavioral or physiological responses to various contrast values and changes in contrast, to generate a function for a given observer that describes the relationship between the contrast of a given stimulus and the response that stimulus generates in contrast-sensitive neurons. This function is referred to as the underlying contrast response function (or CRF) and though it can vary depending on stimulus conditions and the observer it is characterized by a signature sigmoid shape. Given this model, widely accepted in the literature, we can see that for the pedestal contrast values used in this experiment (10%-50%) a contrast decrement of discrete magnitude x_{-1} should produce a larger change in neuronal response than a contrast increment of the same magnitude, x_1 , making it easier to detect. Of course, this prediction only applies to pedestal contrast values beyond the CRF's inflection point (i in the figure). For pedestal contrast values less than i , we should expect contrast increments to be more easily detectable than identical decrements. While this model is useful for hypothesizing about contrast changes during normal binocular viewing, it is important to note that it has not been tested or adapted for binocular rivalry. However, here I attempt to infer from subjects' TvC functions the effect of rivalry dominance and suppression on the underlying CRF.

Given the shape of the CRF and the relatively high pedestal contrast values used here, I hypothesized that contrast decrements would produce lower detection thresholds than increments during dominance. However, main experiment results showed no significant difference between the two ($F = .894, p = .346$). This null result was surprising considering that pilot experiment results revealed that detection thresholds were significantly lower for decrements than for increments ($F = 7.111, p = .008$). The fact that the two experiments shared only one subject may

be able to account for the different pattern of results; a closer look at subject level data will reveal more. Despite the lack of a significant effect for data averaged across all subjects, two of the four subjects do show decrement thresholds significantly lower than increment thresholds in the main experiment (paired t-test: $t = 2.865$, $p = .006$ for subject MK; $t = 4.386$, $p = .001$ for subject SL; see Figure 4). Additionally, the one subject (subject SL) common to both the main experiment and the pilot demonstrated lower detection thresholds for pure decrements in both experiments. This subject level data suggests that individual differences can account for the different pattern of results in the main and pilot experiments. Aside from the subject pools, the primary difference between the two experiments was the viewing conditions: in the pilot the target stimulus was viewed binocularly without a competing stimulus while in the main experiment the target stimulus was viewed monocularly during the dominance phases of rivalry. Results found by Wales and Fox in their 1970 study show that for changes in contrast, the dominance phases of rivalry are equivalent to normal nonrivalrous viewing, so I find it unlikely that viewing condition played a significant role in the differing results between the pilot and main experiment.

4.3 Contrast Decrements in Suppression

Examining the literature on rivalry discloses that the use of contrast decrements to probe rivalry suppression is without precedent, so once again my hypotheses were based on the shape of the underlying contrast response function. In other studies measuring the effect of suppression on stimuli of varying contrasts, it is generally concluded that suppression of an image is equivalent to “turning down” its effective contrast (Blake et al., 2006). With this in mind, we can treat any given pedestal as if it were a pedestal with lower contrast. Given the strength of rivalry suppression we might also assume that this “adjustment” of pedestal contrast

values due to suppression will push a pedestal's perceived contrast to the left of the inflection point i of the CRF into its vertically accelerating portion. If this is indeed the case then we would predict that contrast decrements should be more difficult to detect than contrast increments. Alternatively and somewhat more informally, we could make the same prediction based on the fact that presenting a contrast decrement to a suppressed stimulus is essentially making an invisible image even less visible by decreasing its overall contrast.

As stated in the results section, an ANOVA did reveal a significant elevation of detection thresholds for contrast decrement probes compared to increment probes in the suppression condition ($F = 8.245, p = .005$). One potential explanation for these results is outlined in the hypothesis above. A potential avenue for further investigation into this explanation was to attempt to actually map a subject's underlying CRF in suppression from their TvC function data using the Naka-Rushton function:

$$r = \frac{c^p}{c^q + z}$$

Here r is neuronal response, c is the contrast of the pedestal image, p and q control the slope of the CRF, and z is a constant. The technique is more fully described elsewhere (Boynton et al., 1999; Bex et al., 2007), but it involves cycling through all the permutations of these variables until a CRF is found that produces the best TvC fit to the observed data. Since the pedestal values I use in the main experiment are all relatively high and do not fall in the dipper portion of the traditional TvC curve, this required some additional data collection at threshold and near-threshold pedestal contrasts so a CRF could be generated from the full range of pedestal contrast values.

At the time of this writing two subjects had collected enough additional data to produce CRFs for dominance and suppression (Figure 6). Though the data for the near-threshold pedestal

contrasts do not show the desired dip in the TvC curve for subject MK, typical-looking sigmoidal CRFs were produced for dominance in both subjects. The CRFs generated from the suppression data support aspects of the hypothesis outlined above, though they do not likely account for the original finding that decrements are easier to detect than increments in suppression. The horizontal asymptotes, representing response saturation, are depressed in both cases compared to the dominance CRFs and the entire functions appear to be shifted downwards and to the right. The CRFs also shows some indication that the inflection point has moved rightward as a consequence of this shift. However, in these subjects the portion of the CRF that corresponds to the main experiment pedestal values remains to the right of any observable inflection point, predicting decrements as more easily detectable, something the main experiment data clearly do not support. It is important to note that I very tentatively present and interpret these TvC to CRF findings, as they incorporate data from only two subjects and the Naka-Rushton function did not always produce a very good fit to the data.

In summary, this finding that contrast decrements are harder to detect than increments in suppression, while intuitive, does not fit into the existing contrast response function model of contrast change detection. Given the results, it is possible that the observers here were employing a strategy for detecting changes in a suppressed stimulus different from the strategy they employed while detecting changes during dominance or nonrivalrous viewing. A different strategy could involve different neural mechanisms and would thus explain why the results found here for contrast decrements during suppression do not fit into our current understanding of contrast change detection. If this is the case, then further investigation is needed to determine the neural processes at work when subjects attempt to detect changes in suppressed stimuli.

In fact, it is notable that subjects were able to detect decrements during suppression at all given that the probe introduces a change in the pedestal that decreases its overall visibility. Contrast increments are detected due to a summation of their onset and contrast energy, but in decrements these two components are opposed. In other words, a contrast increment is detected because of the contrast energy it introduces to the pedestal, but a contrast decrement must be detected in spite of the contrast energy it removes. In the present experiment, the transient energy introduced by the change in the pedestal (i.e., the decrement probe onset) outweighed the contrast energy it removed from the pedestal. The opposition between probe nature and probe onset introduced by the novel contrast decrement probe used here represents one possible direction for further investigation.

Finally, the fact that observers can see decrements presented to a suppressed stimulus implies that the effective contrast of that suppressed stimulus is not zero, as early studies of rivalry suggested. Control experiments in studies of binocular rivalry have often involved a rivalry “mimic” condition in which observers binocularly view a realistic recreation of a typical rivalry exposure duration, in which two target images alternate in visibility as if they were truly rivaling. The use of such a condition to mimic binocular rivalry implies an assumption that a suppressed image during rivalry is completely unprocessed by the visual system. However, results shown here demonstrate that there *is* a neural representation of the suppressed stimulus somewhere in the brain and it *is* being processed at least at a rudimentary level. This assertion agrees with studies demonstrating that subjects can get an aftereffect from suppressed images (Blake et al., 2006) or even make sophisticated judgments on them (Pasley et al., 2004). The results shown in these previous studies and further confirmed here demonstrate that a suppressed stimulus is by no means equivalent to the physical absence of that stimulus.

5. References

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6. Figure Captions

Figure 1 – Contrast probe time profiles and example pulse increment probe. Both pure and pulse increments and decrements were used in the pilot study; results showed pure and pulse probes were detected similarly enough to warrant use of pure increments and decrements to map TvC functions in the main experiment. Thus, the main experiment used pure increments and decrements exclusively. In the main experiment, the horizontal grating target seen here rivaled with a radial checkerboard grating of 40% contrast.

Figure 2 – Threshold versus contrast (TvC) results found by Watanabe et al. in their 2004 *Vision Research* publication. The investigators found a significant .3 to .4 log unit elevation of thresholds found during suppression versus during dominance. They also noted the parallel slopes for dominance and suppression TvC functions, concluding that this was evidence that the contrast gain control mechanism operates regardless of pedestal visibility.

Figure 3 – TvC functions for all four test conditions averaged across all subjects. All best fit lines are significant ($p_{\text{dominc}} < .001$, $p_{\text{domdec}} = .014$, $p_{\text{supinc}} = .004$, $p_{\text{supdec}} = .003$). Error bars show standard error. Primary axes show logs of actual % contrast; alternate axes show unmodified % contrast (“real” contrast). Detection thresholds are significantly elevated for decrements compared to increments in suppression ($F = 8.245$, $p = .005$), but not in dominance ($F = .894$, $p = .346$).

Figure 4 – TvC functions for individual subjects. Subjects MK and SL show decrements as more easily detectable than increments in dominance ($t = 2.865$, $p = .006$ for subject MK; $t = 4.386$, p

= .001 for subject SL), but no significant effect was found averaging across all four subjects (see Figure 3). Results during dominance for subjects SH and JK are inconclusive.

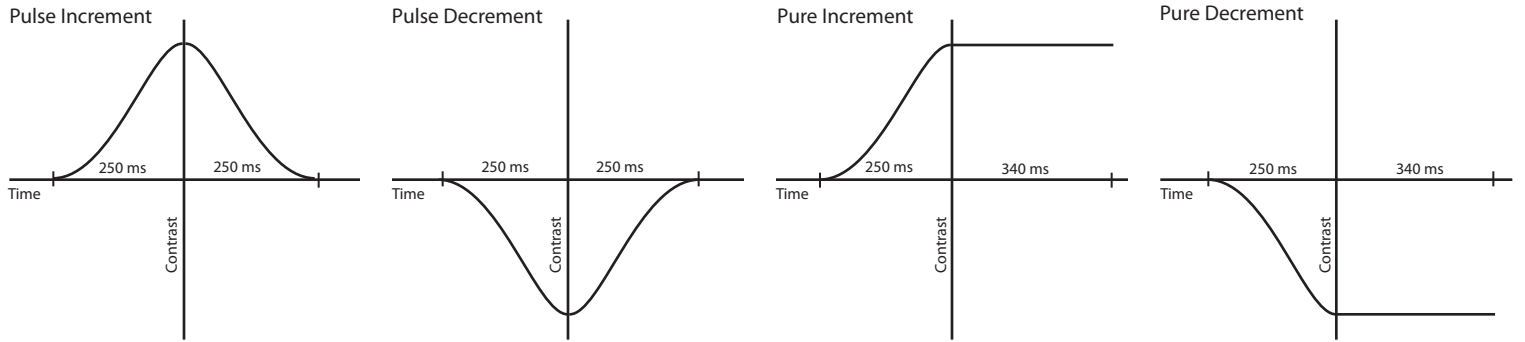
Figure 5 – Sample TvC functions from Legge and Foley’s 1980 *Journal of the Optical Society of America* publication. Shown here is the characteristic “dipper” portion of the curve representing a facilitation effect on increment detection thresholds at near-threshold pedestal contrast values. The contrast values used in the present study, however, fall in the steady upward sloping section of the traditional TvC, so we should not expect to see any dipper activity in results found here.

Figure 6 – Full TvC functions and CRFs for two subjects. The TvC functions here incorporate data from all five pedestal contrast values used in the main experiment as well as additional data from three near-threshold contrast values, but only subject SL showed the characteristic “dipper” section of the curve. Since contrast decrements are impossible to detect at threshold and sub-threshold pedestal contrasts, TvC curves here were plotted based on detection thresholds for increments only. CRFs were generated based on the Naka-Rushton function described in the Discussion section.

Figure 7 – TvC functions for both pulse and pure probe increment and decrement probes in the pilot study averaged across all four subjects (only one common subject between pilot and main). Pilot procedure and method were identical to that used in the main experiment except that target images and probes were viewed in normal nonrivalrous conditions and both pure and pulse probes were used.

Figure 1.

Contrast probe time profiles



Sample probe - pulse increment

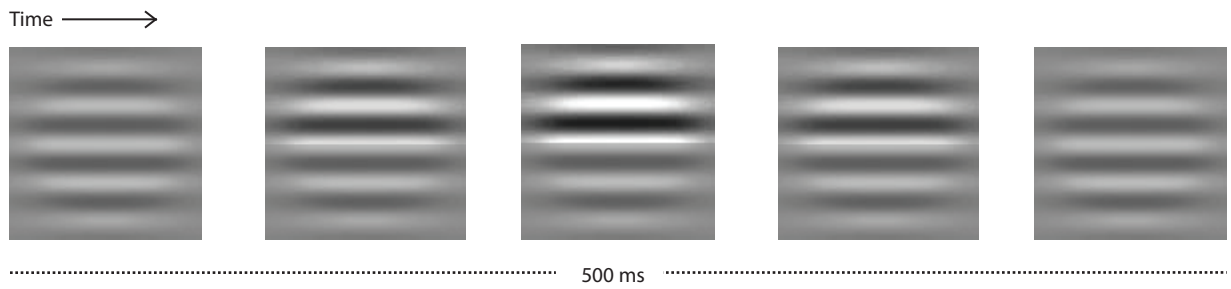


Figure 2.

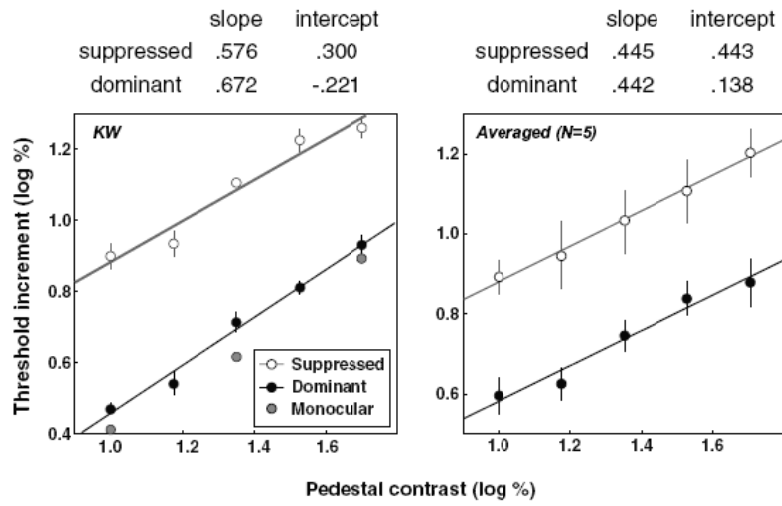


Figure 3.

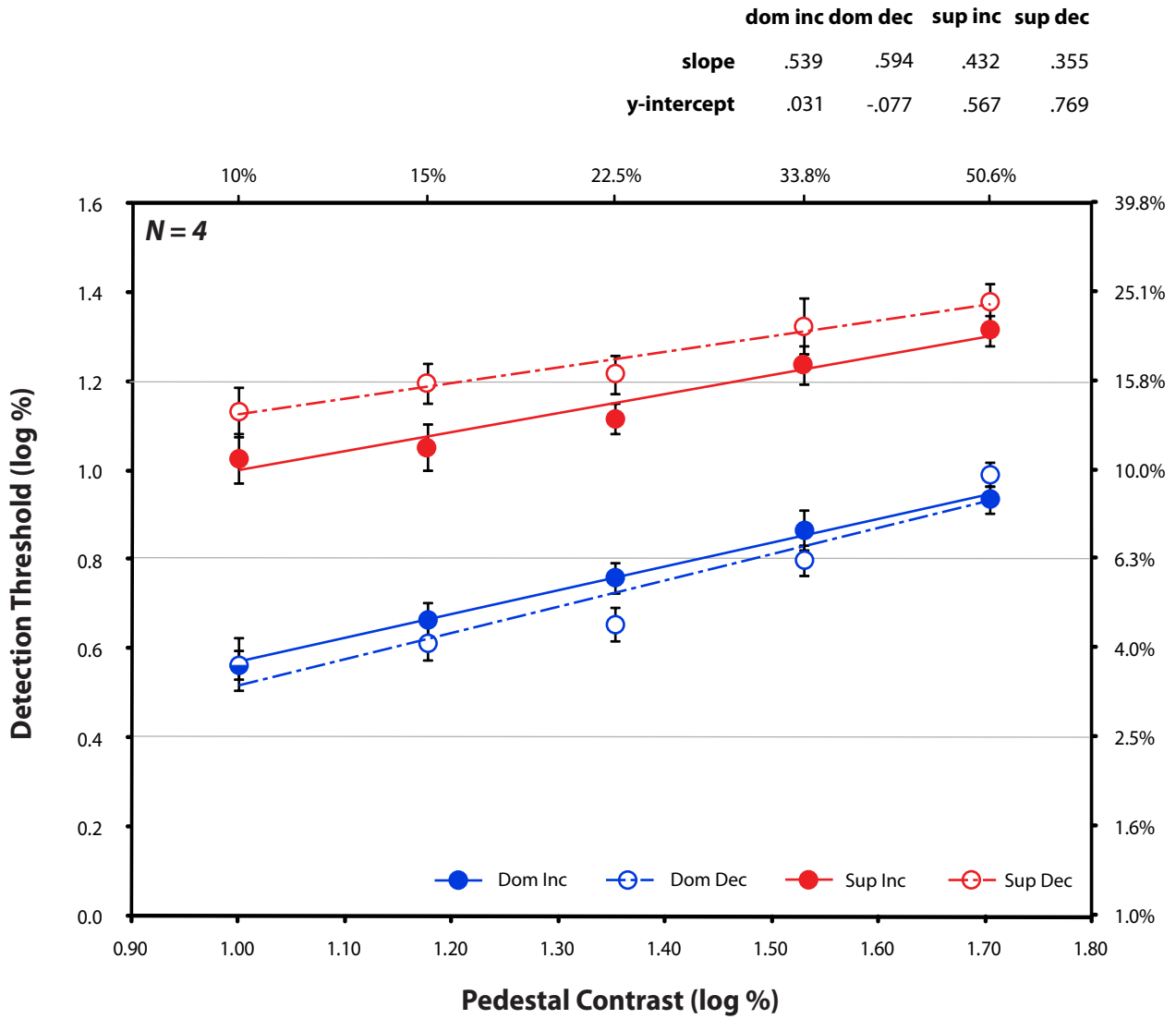


Figure 4.

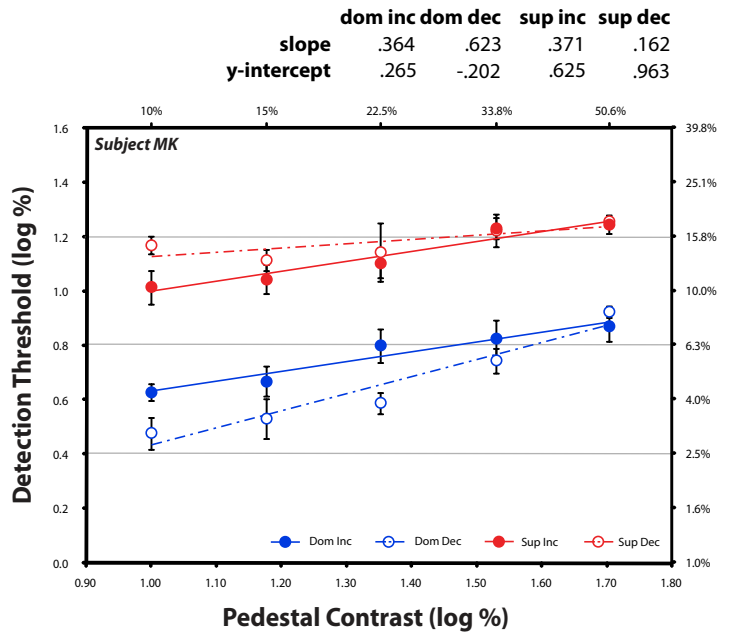
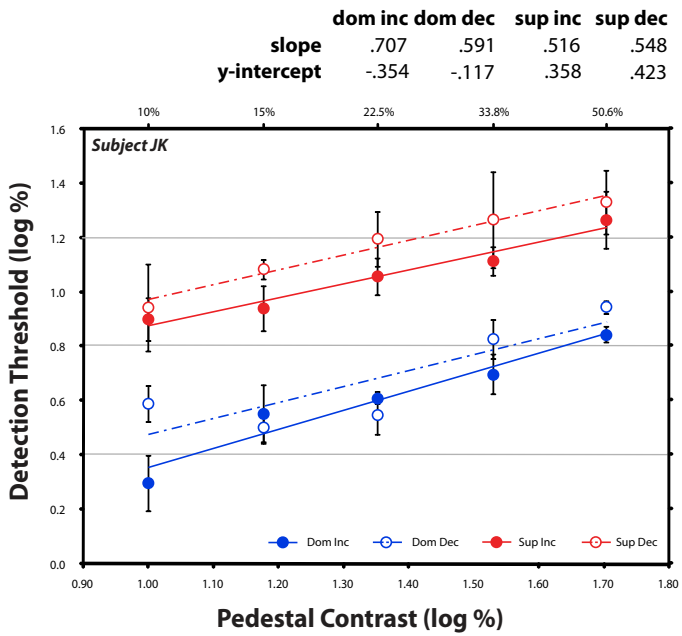
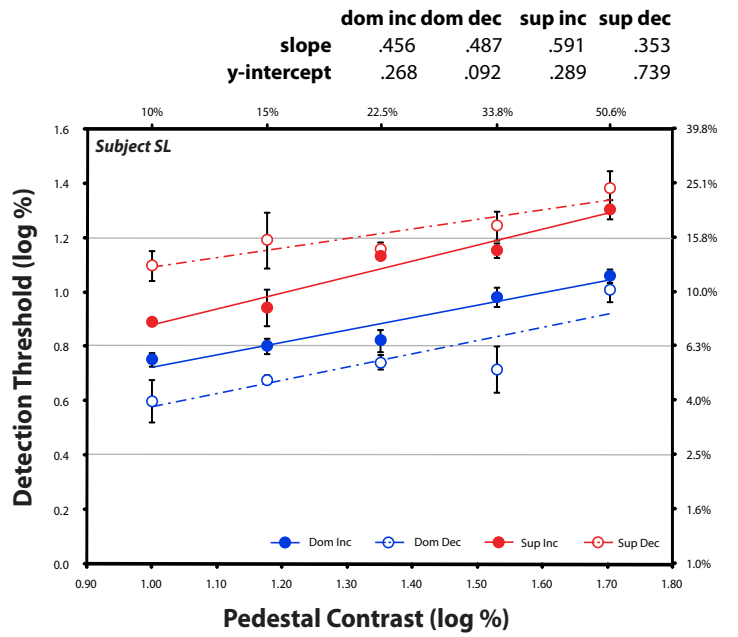
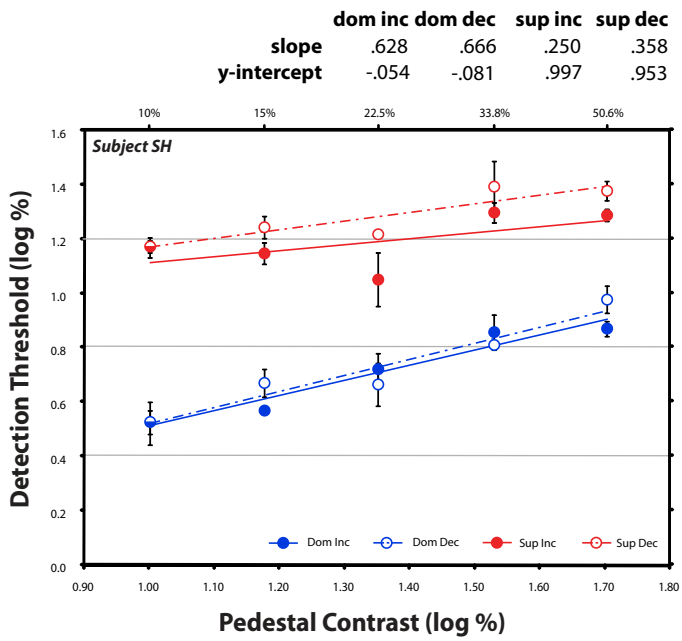


Figure 5.

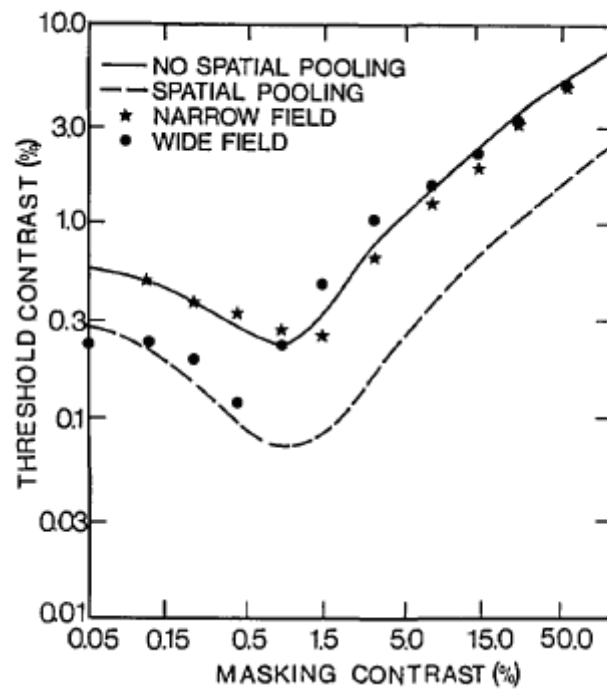
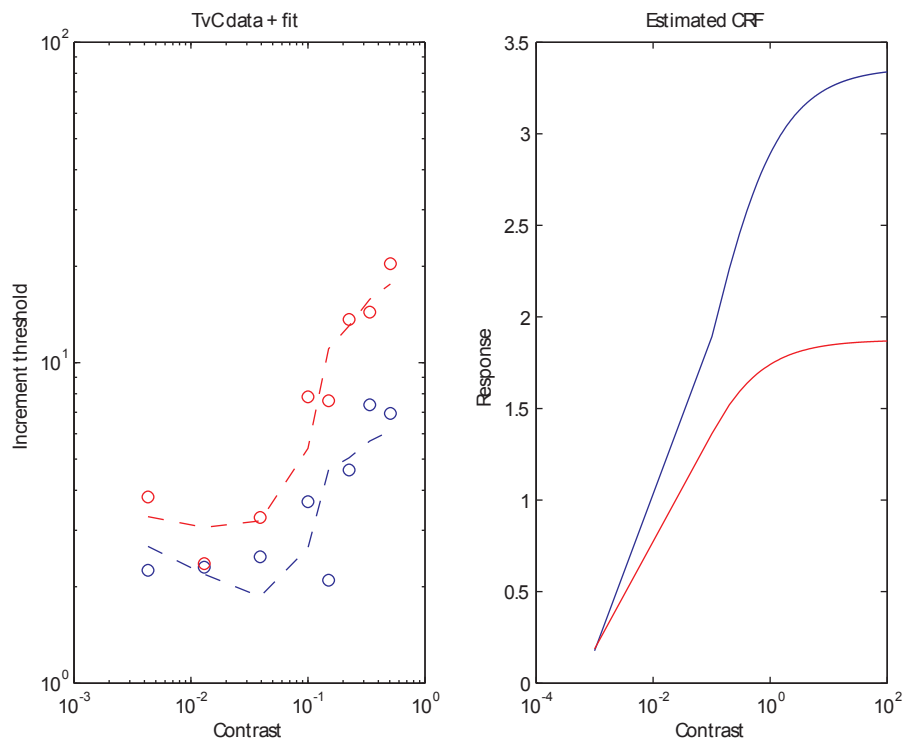
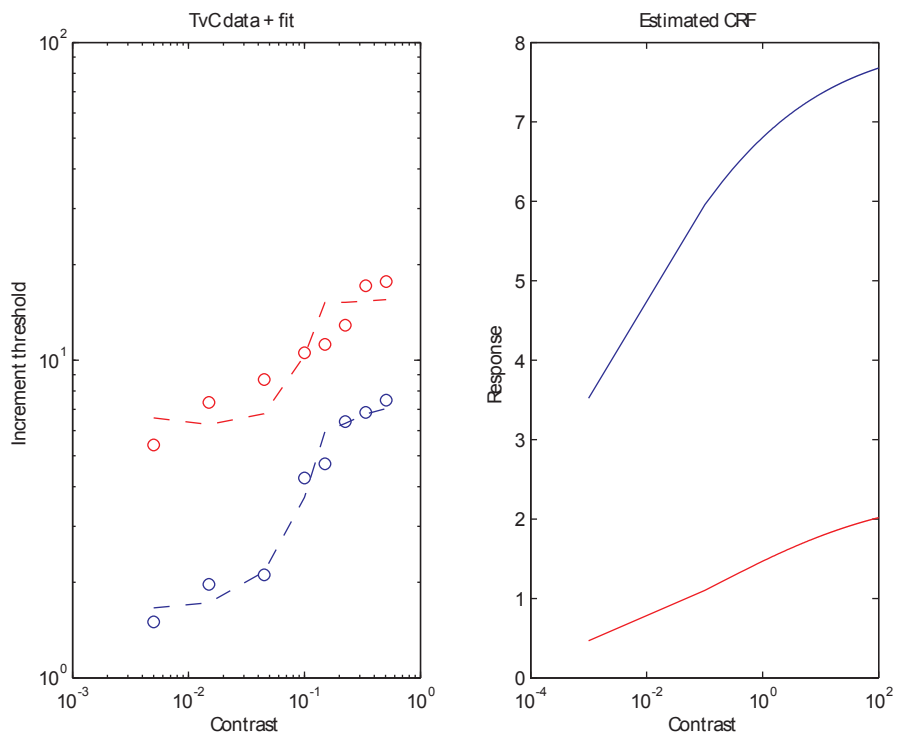


Figure 6.



Subject SL



Subject MK

Figure 7.

