

The spatial extent of lateral interactions in flicker perception

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Abstract

We investigated the influence of the relative phase of a temporally modulated annulus on the perceived flicker strength of a center stimulus having the same temporal modulation. These measurements were performed in two subjects at two temporal frequencies and with different outer diameters of the annulus. The perceived flicker strength was strongly modulated by the phase difference between center and surround stimulus. This modulation depended on the size of the annulus. In the absence of an annulus the perceived flicker strength was not modulated. The modulation initially increased with increasing annulus size and reached a plateau. The space constant of the function describing the modulation as a function of annulus size was about 0.5° and is similar to the sizes of receptive field surrounds of subcortical cells. This finding is in favor of the hypothesis that the physiological basis of the perceived flicker strength in the center stimulus is present already at a subcortical level.

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1. Introduction

The perceived flicker strength (PFS) of a temporal modulation in a central stimulus is influenced by the relative phase of a modulation of the same temporal frequency in a surrounding stimulus. A demonstration of this effect can be found at the following web-site: <http://journalofvision.org/4/7/10/> (Kremers, Kozyrev, Silveira, & Kilavik, 2004a). The response amplitude of cells in the lateral geniculate nucleus (LGN) to a similar stimulus, in which the central stimulus matches the receptive field (RF) center

and the surround stimulus covers the RF surround, shows a very similar dependency on the relative phase between the center and surround stimulus. This resemblance led to the hypothesis that the physiological basis of the PFS in the center stimulus lies in the interactions between RF center and surround of subcortical neurons (LGN- or retinal ganglion cells) (Kremers et al., 2004a). The link between single LGN cell recordings and psychophysical data was further strengthened because it was possible to explain the psychophysical data on the basis of a cortical peak to trough detector, the output of which is proportional to the difference between the maximal and the minimal responses in an array of responding LGN cells (Kremers & Kozyrev, 2003). The output of such a cortical peak to trough detector depends on the relative phase between center and surround stimuli in a very similar manner as the psychophysical data (Kozyrev, Silveira and Kremers, submitted for publication). The above-mentioned hypothesis predicts that the spatial extent of the lateral interaction should correspond to the size of the RF surround of

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subcortical neurons (Croner & Kaplan, 1995) and therefore be limited to about half a degree around the center stimulus. On the other hand, if the modulation of the PFS originates in horizontal connections or in feedback mechanisms present in the visual cortex, the spatial extent of the spatial interactions would be much larger [$>2^\circ$; (Angelucci et al., 2002; Sceniak, Ringach, Hawken, & Shapley, 1999)]. In the present paper, we describe the results of psychophysical measurements in which the spatial extent of the lateral interaction is measured by changing the size of the surround stimulus. We have previously shown that similar results could be obtained when the diameter of the center stimulus was 1° or 0.4° . The data clearly suggest a subcortical origin of the lateral interactions.

2. Methods

2.1. Participants

Two naive male subjects (DK, 26 years and DC, 34 years) volunteered to participate in the study. The purpose of the study was explained and a written consent was obtained. The experiments were performed in accordance with the tenets of the Declaration of Helsinki and approved by the ethics committee of the University of Tübingen.

2.2. Apparatus

The subjects sat in a chair and rested their head on a chin rest. Stimuli were displayed on a monitor at 114 cm distance from the eye. The subjects were asked to focus the stimuli monocularly through a 3 mm diameter artificial pupil. A reference and a test stimulus were presented alternately on a BARCO monitor (CCID 7751 MKII) controlled by a VSG 2/2 graphic card (Cambridge Research System).

2.3. Stimuli

The *reference stimulus* consisted of a circular center and an annulus. The diameter of the center stimulus was 1.02° . The outer diameter of the annulus was variable and could have the following values: 1.02° (i.e. no annulus present), 1.224° , 1.428° , 1.632° , 2.65° , 5.1° , 7.14° , and 10.2° . A black 3 arc min gap between center stimulus and annulus enabled the subjects to identify the two stimuli at all conditions. Without the gap, the center and surround stimuli could not be distinguished at 0° phase difference. A comparison of results of measurements with and without the gap, performed in a pilot experiment, indicated that the gap had minor influence on the psychophysical data. In both center and surround (annulus) a sinusoidal temporal luminance modulation was presented. The center and surround stimuli had identical mean luminance (66 cd/m^2), chromaticity (20, 40, and 6 cd/m^2 mean luminance of the red, green, and blue phosphors, respectively, resulting in a white with (0.33 and 0.32) CIE, 1964, large field coordinates), Michelson contrast (50%) and temporal frequency (either 4 or 8 Hz). The temporal phase between the center and the annulus was varied between -180° and $+180^\circ$ in 30° steps. Additional measurements were performed at center-surround phase differences of -15° and $+15^\circ$. By definition, negative phase differences indicate that the surround stimulus lags the center stimulus, whereas positive phase differences indicate a phase lead of the surround stimulus.

The *test stimulus* had the same size, temporal frequency, time averaged luminance, and time averaged chromaticity as the center of the reference stimulus. No surround stimulus was present. The contrast of the test stimulus was changed depending on the responses of the subjects until the PFS in the test stimulus matched the PFS in the center of the reference stimulus.

2.4. Experimental procedure

A two alternative forced choice method with a PEST procedure (Taylor and Creelman, 1967) was used for the matching procedure. The procedure was described previously (Kremers et al., 2004a). Briefly, the subjects were allowed to view the reference stimulus foveally. No temporal Gaussian envelope was used, to give the subjects the possibility to view the stimulus as long as they wished. To avoid on-set phenomena, the subjects were instructed to view the stimulus at least several seconds. The subjects were encouraged to make small eye movements across the center stimulus to avoid Troxler's fading. By pressing a button the reference stimulus was replaced by the test stimulus. After the test stimulus appeared, the subjects were forced to indicate, by pressing a button, whether the perceived flicker in the test stimulus was stronger or weaker than the perceived flicker in the center of the reference stimulus. After making this decision, the reference stimulus appeared again and the procedure was repeated. To enable direct comparisons, the reference and test stimuli were immediately replaced without interstimulus intervals. During one run, the reference stimulus was not changed (i.e. a constant phase difference between center and surround stimuli was used), whereas the contrast in the test stimulus was altered. The contrast in the test stimulus was decreased when the subject indicated that the perceived flicker in the test stimulus was stronger than the perceived flicker in the center of the reference stimulus. Conversely, the contrast in the test stimulus was increased when the flicker of the test stimulus appeared to be weaker than in the center of the reference stimulus. To exclude the possibility of guessing, two randomly interleaved staircases of the test stimulus, one starting at 0% and the other at 100% contrast, were used. Therefore, two independent estimates of the PFS were obtained in each run. At the beginning, the contrasts in the test stimulus were changed in steps of 60% (i.e. from 0% to 60% and from 100% to 40%). After a reversal in direction of the contrast change, the contrast steps were halved. When the contrast change in the test stimulus was less than $0.14\times$ the actual contrast (in % contrast), it was assumed that the PFS in the test stimulus and the center of the reference stimulus matched. Each run was repeated three times in most measurements. In a few cases, the variability in the data was small enough after two runs so that a third run was not necessary (mainly for subject DK; no systematic effects of stimulus condition on variability were observed). Thus, each data point is the mean of four or six settings. This procedure was chosen instead of the measurement of a flicker detection threshold in the center stimulus because the surround modulation could induce a flicker percept at low contrasts, preventing reliable measurements of a threshold. After a run was completed, the measurements were repeated at another phase difference between center and surround in the reference stimulus. The different runs were presented in quasi-random order. One trial, defined as the measurements of the perceived flicker strength at all phase differences between center and surround stimulus but with a constant annulus diameter and temporal frequency, was completed before a new trial (i.e. another annulus size and/or another temporal frequency) was started. The different trials were presented in quasi-random order. The data were acquired in several sessions.

3. Results

The subjects had to set the contrast in the test stimulus so that the perceived flicker strength (PFS) in the test stimulus and the center of the reference stimulus matched. Fig. 1 shows the averaged PFS (\pm SD) as a function of the phase difference between center and surround in the reference stimulus for three different annulus sizes (1.224° , upper panels; 1.632° , middle panels; 7.14° , lower panels), for the two temporal frequencies and for each subject. Clearly, the PFS is modulated by the center-surround phase difference at all frequencies and for larger surround stimuli. The PFS is not only weakly modulated when

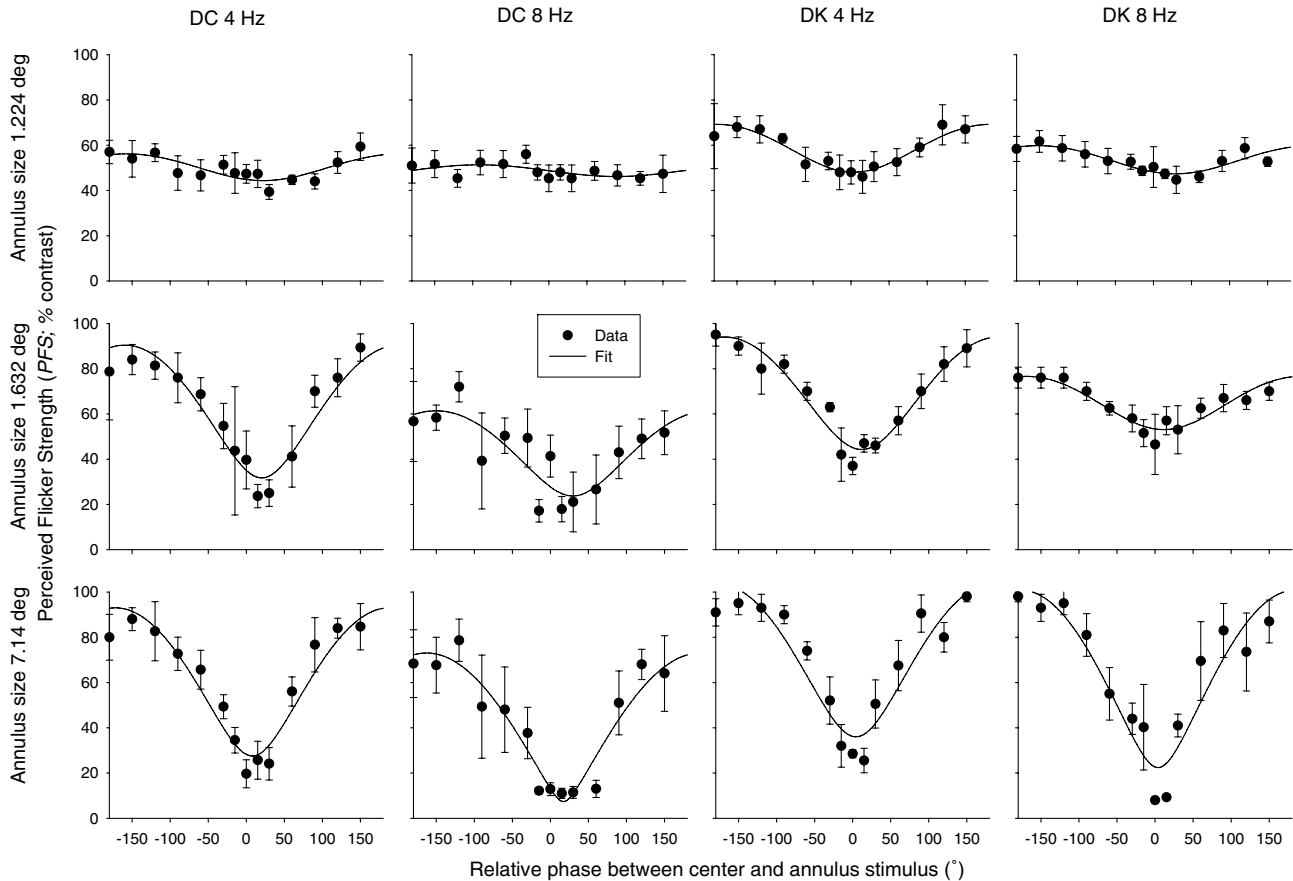


Fig. 1. Contrasts in the test stimulus to match the perceived flicker strength (PFS) in the center of the reference stimulus given as a function of center-surround phase differences in the reference stimulus. Data are shown for three different outer diameters of the annulus in the reference stimulus (1.224°, 1.632°, and 7.14°), two different temporal frequencies (4 and 8 Hz) and for the two subjects (DC and DK). Clearly, the PFS in the center stimulus is modulated by the phase difference. The curves are fits of Eq. (1) to the data. The modulation of the PFS becomes more pronounced with increasing size of the surround stimulus and the surround stimulus leads the center stimulus when the PFS is minimal (the minimum of the fitted curves is at positive relative phases), indicating that the response to the surround stimulus lags the response to the center stimulus.

the outer diameter of the annulus is 1.224° and strongly modulated with an annulus with 1.632° outer diameter, indicating that a slight increase in annulus size has a large effect upon the modulation of the PFS. A further increase in annulus size to 7.14° has a relatively minor effect. At all conditions in which the PFS is strongly modulated, the PFS is minimal at positive phase differences where, by definition, the surround stimulus leads the center stimulus. It should be noted that the physical contrast in the center and surround stimuli was constant in all conditions (50%).

Because the contrasts in the reference stimulus were not changed, the responses of LGN neurons to such a stimulus can be described by a linear vector addition of the responses to the center and to the surround stimuli. This vector addition model could also adequately describe the PFS although saturation may be involved at high PFS and threshold mechanisms at low PFS (Kremers et al., 2004a). The averaged PFS data were fitted by Eq. (1):

$$\text{PFS} = \sqrt{R_c^2 + R_s^2 - 2R_c \times R_s \times \cos(S - P)} \quad (1)$$

in which R_c and R_s are estimates of the PFS due to selective stimulation by the center and surround stimuli, respectively: S is the relative phase of the surround stimulus and P the relative phase for a minimal PFS. The equation was fitted to the data using the solver routine of the Excel98 program. The curves in Fig. 1 are the best fits of Eq. (1) to the data. The modulation of the PFS (MPFS), defined as the difference between the maximum and the minimum in the fitted curves (and thus is twice R_s), increases with increasing size of the surround stimulus.

The MPFS is shown in Fig. 2 as a function of the annulus size plotted separately for the two subjects and the two temporal frequencies. The MPFS equals twice R_s . Initially, the MPFS in the center stimulus increases steeply with increasing annulus sizes and reaches a plateau for outer diameters of the annulus above about 2° (the inner diameter is always 1.02°). The curves are fits of Eq. (2) to the data:

$$\text{MPFS} = A \left(1 - \exp \left(\frac{-(x - 1.02)^2}{2\sigma^2} \right) \right) \quad (2)$$

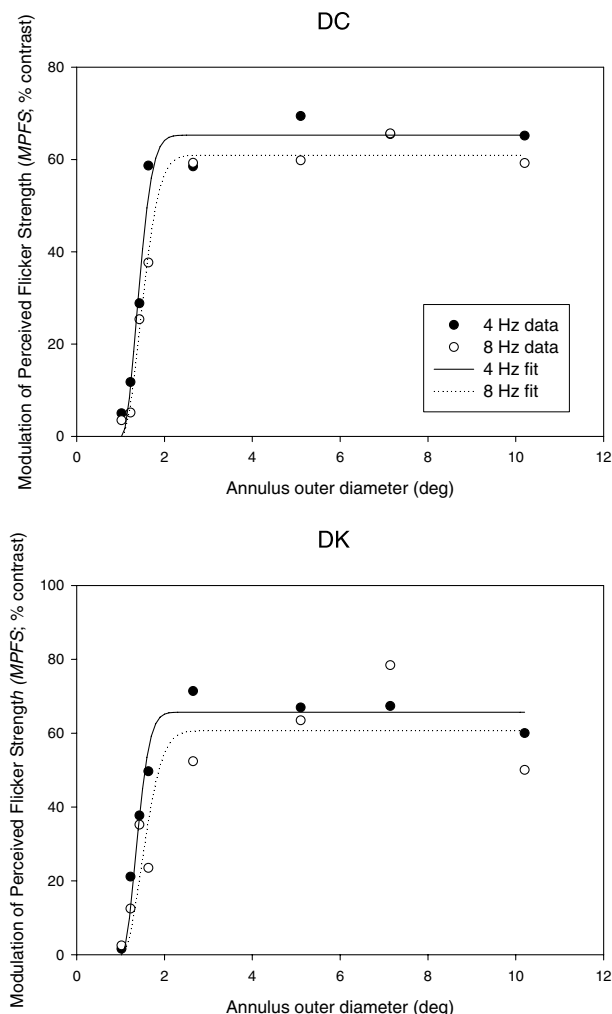


Fig. 2. The modulation of the perceived flicker strength (MPFS) as a function of the outer diameter of the annulus in the reference stimulus for 4 and 8 Hz stimuli and for the two subjects. The MPFS initially increases steeply with increasing annulus size and reaches a plateau for annulus sizes above 2° . At 8 Hz, the MPFS is slightly smaller for nearly all sizes of the surround stimulus.

This equation can be expected when the RF of the physiological mechanism underlying the psychophysical task has a Gaussian responsivity profile (Kremers, Kozyrev, Silveira, & Kilavik, 2004b). A represents the plateau level of the MPFS. σ is the space constant of the MPFS. The values of σ were 0.34 (DC, 4 Hz), 0.42 (DC, 8 Hz), 0.32 (DK, 4 Hz), and 0.46° (DK, 8 Hz).

Fig. 3 shows the values of R_c and of P as a function of annulus outer diameter. The values of R_c are relatively constant and seems to be slightly smaller at 8 Hz (Fig. 3, left panels). For small annulus sizes, values of P (Fig. 3, right panels) could not be estimated reliably because the MPFS was too small. Therefore, values of P were disregarded if the MPFS was smaller than 20% contrast. For those annulus sizes at which the MPFS was large, P had positive values, indicating that the surround stimulus had to lead the center stimulus to obtain a minimal PFS. This is in agreement with previous data and indicates that the physiologi-

cal response to the surround stimulus lags the response to the center stimulus (Kremers et al., 2004a). The data further seem to indicate that P increases when the annulus is smaller than about 2° .

4. Discussion

The presented data confirm our previous observation (Kremers et al., 2004a) that the PFS in a center stimulus is modulated by the relative phase of a surrounding stimulus. Psychophysically this was already shown by Kelly (1969). We further confirm our previous observations that the surround stimulus has to be phase advanced relative to the center stimulus to obtain a minimal PFS and that, if stimulus contrast is kept constant, the modulation of the PFS can be adequately described by a vector addition of the physiological responses to the center and the surround. We previously found, however, that when the stimulus contrast changes in the center and/or surround, nonlinearities play a role, which change mainly the phase lag in the response to the surround stimulus (Kremers et al., 2004a).

Our data show that the MPFS depends on the size of the surrounding stimulus. When no surround is present (as is the case when the annulus has a 1.02° outer diameter which is identical to the diameter of the center stimulus) then the PFS is not modulated, equal to R_c and about 50% (Fig. 3, left panels) which is the physical contrast of the center stimulus. This shows that the procedure of measuring the PFS by matching the contrast in the test stimulus can give reliable results.

The MPFS increases with increasing annulus size (Fig. 2) with space constants that are similar to those of the RF surrounds of parafoveal subcortical cells [typically about 0.5° ; see e.g. Croner and Kaplan (1995) for the macaque and Kremers and Weiss (1997), Solomon, White, and Martin (2002) Kilavik, Silveira, and Kremers (2003) for the marmoset taking into account a correction for the smaller eye size of the marmoset (Kremers & Weiss, 1997)] and much smaller than the spatial extent of cortical horizontal connections and feedback mechanisms which are larger than 2° (Sceniak et al., 1999; Angelucci et al., 2002). The classical receptive fields of cells in area V1 may have similar sizes as the surround in the psychophysical stimulus, but it is possible that the interactions within the classical receptive field also have a subcortical origin. Furthermore, the MPFS is slightly smaller at 8 Hz, confirming previous psychophysical and physiological data (Kremers et al., 2004a). The data therefore are in agreement with our proposition that the physiological basis of perceived flicker in a center stimulus can be found at a subcortical level. On the basis of the present data a cortical origin of the lateral interactions cannot completely be excluded, but it seems likely that a subcortical mechanism is involved. Nevertheless cortical decision mechanisms need to be involved. We have shown that the psychophysical data can be adequately explained when a cortical peak to

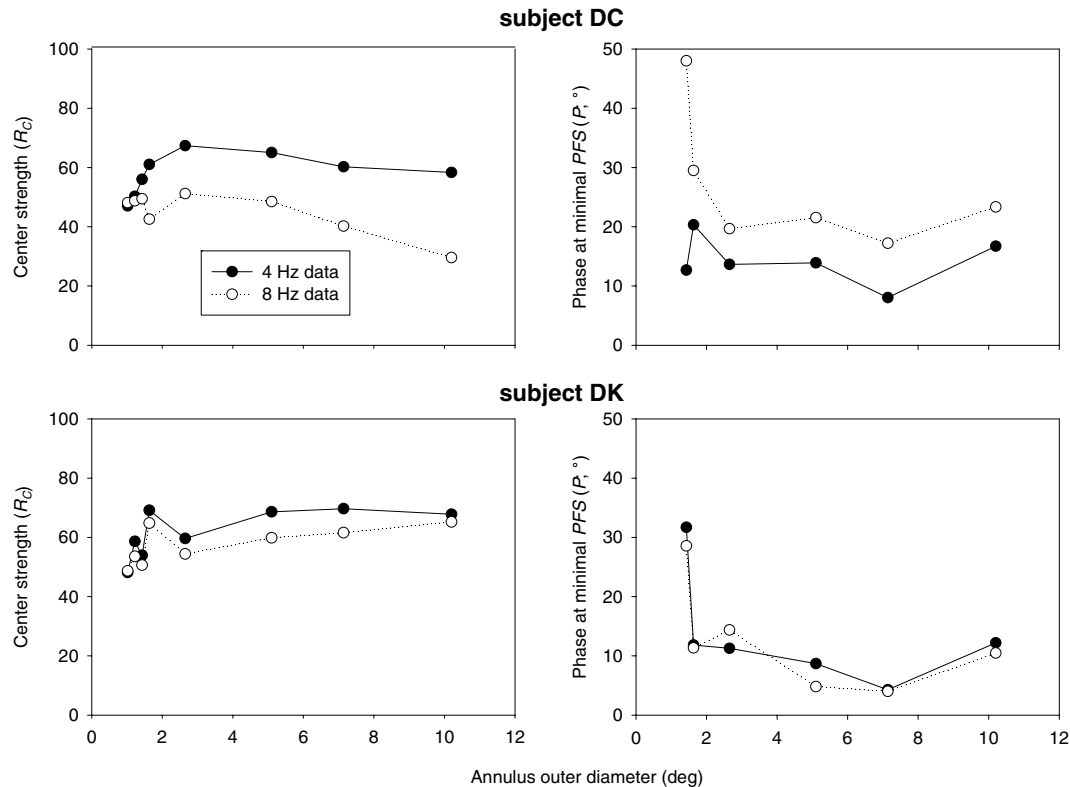


Fig. 3. The amplitudes of the center response (R_c ; left panels) and the phase at minimal PFS (right panels) displayed as a function of surround stimulus size for 4 and 8 Hz frequency and for the two subjects. At 8 Hz, R_c is lower for all sizes of the surround stimulus. The positive phase in all conditions indicates a phase lead of the surround stimulus at a minimal PFS and a phase lag of the physiological response to the surround stimulus.

trough detector with a subsequent saturation and threshold mechanism processes the input from the LGN (Kozyrev, Silveira and Kremers, submitted for publication). The proposed cortical detector provides an important link between the physiological and psychophysical data. The output of the putative cortical peak to trough detector is proportional to the difference between the maximal and the minimal responses in an array of responding LGN cells. When the size of the surround stimulus is reduced, the response difference decreases, because of a decrease in the influence of the surround stimulus on the responses of the LGN cells.

It is difficult to compare the psychophysically determined receptive field sizes with those obtained from other tasks. As we discussed previously (Kremers et al., 2004a), the perceived flicker strength is most probably not identical to the phenomenon of brightness induction. The present data confirm this notion, because changes in perceived brightness may be induced by targets that are as remote as several degrees (Rossi, Rittenhouse, & Paradiso, 1996); although in other tasks, brightness induction can have much smaller space constants (Hong & Shevell, 2004).

The data seem to indicate that the phase at a minimal PFS increases when the surround stimuli are very small (Fig. 3, right panels) suggesting an increasing phase lag of the response to the surround stimulus. In these conditions, the surround stimuli are so small that only

parts of the RFs surrounds of the subcortical cells are stimulated. Although, the phase data are not very reliable at these conditions, they suggest that different subfields of RF surround may have distinct response properties.

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