Evidence for two types of lateral interactions in visual perception of temporal signals

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The aim of this work was to investigate the mechanisms of lateral interactions involved in flicker perception. Furthermore, the spatial properties of the monoptic and dichoptic components of these mechanisms were studied. We quantified the perceived flicker strength (PFS) in the center of a test stimulus, which was simultaneously modulated with a surround stimulus of variable size. The modulation depth of a separate stimulus, identical to the center test stimulus but without the surround, was determined using a two-alternative forced choice procedure. Using LCD goggles synchronized to the frame rate of a CRT screen, the center and surround of the test stimulus were presented either monoptically or dichoptically. In the monoptic condition, center-surround interactions have subcortical and cortical origins. In the dichoptic condition, center-surround interactions must have a cortical origin. The difference between the dichoptic and the monoptic data is an estimate of the contribution of the subcortical mechanisms. At each condition (surround stimulus size; monoptic or dichoptic presentation), the PFS was measured for phase differences between center and surround stimuli. The PFS changed systematically with phase difference. It also was observed that the PFS in the center stimulus changed merely by the presence of a surround stimulus independently of the center-surround phase difference. We propose that this is a phase-independent mechanism related to contrast adaptation owing to the presence of surround modulation. Our data suggest that both phase-dependent and -independent mechanisms have cortical and subcortical origins. There were no systematic differences between the spatial properties of subcortical and cortical components involved in PFS modulation.

**Introduction**

The perception of properties of a central stimulus can be altered by its surround. Several psychophysical studies have described this effect on the perception of brightness (De Valois, Webster, De Valois, & Lingelbach, 1986; Rossi & Paradiso, 1996; Spehar, Debonet, & Zaidi, 1996; Zaidi, Yoshimi, Flanigan, & Canova, 1992; Zaidi & Zipser, 1993), color (Atetrusseau & Shevell, 2006; Christiansen, D’Antona, & Shevell, 2009; Krauskopf, Zaidi, & Mandler, 1986; Shevell & Cao, 2006), motion (Tadin, Lappin, Gilroy, & Blake, 2003; Tadin, Paffen, Blake, & Lappin, 2008; Tadin, Lappin, & Blake, 2006), perceived synchrony (Shapiro et al., 2004; Shapiro, 2008), and spatiotemporal signals (Chubb, Sperling, & Solomon, 1989; Petrov & McKee, 2009; Singer & D’Zmura, 1994, 1995; Xing & Heeger, 2000, 2001). In addition, many physiological studies have searched for the neural basis of the center-surround interactions involved in the mentioned perceptual effects (Bair, Cavanaugh, & Movshon, 2003; Born & Tootell, 1992; Conway, Hubel, & Livingstone, 2002; Rossi & Paradiso, 1999; Webb, Dhruv, Solomon, Tailby, & Lennie, 2005).

Lateral interactions are also involved in the perception of temporal flicker: The perceived flicker strength in a modulating central stimulus depends strongly on the phase difference with a simultaneously modulating surround (D’Antona et al., 2011; Teixeira et al., 2011). The lateral interaction was reminiscent of receptive field center-surround interactions in the responses of LGN cells suggesting that mechanisms of subcortical origins were involved (Kilavik, Silveira, & Kremers, 2003). The LGN cells’ response is modulated by the phase difference between center and surround stimuli in a similar way as the perceived flicker strength (PFS) in the central stimulus (Kremers, Kozyrev, Silveira, & Kilavik, 2004). A model linking the responses of an array of LGN cells with different receptive fields’ locations to perception was proposed (Kozyrev, Silveira, & Kremers, 2007). Additional evidence strengthened this hypothesis: PFS modulation by a surround stimulus depended on the surround size in a way similar as can be expected from receptive field sizes of sub-cortical cells (Kremers & Rimmle, 2007). However, as in these experiments the stimuli were presented to the same eye, it was not possible to distinguish experimentally between lateral interactions with subcortical and with cortical origins.

Recently, two different psychophysical studies compared the lateral interaction in dichoptic (presentation of the center and surround stimuli to separate eyes) and monoptic (presentation to the same eye) conditions, thereby enabling a separation between cortical and subcortical contributions (D’Antona et al., 2011; Teixeira et al., 2011). In the dichoptic conditions, the interactions can only have a cortical origin, whereas in the monoptic conditions the interactions have cortical as well as sub-cortical origins. The difference between the results with the monoptic and with the dichoptic conditions therefore has subcortical (and possibly early cortical) origins. The mentioned studies showed that lateral interactions in the perception of flicker strength have not exclusively subcortical but also cortical origins. The two sites have distinct temporal properties influencing the visual perception of temporal signals in distinct ways.

The influence of surround stimulus size, as described by Kremers and Rimmle (2007), was based solely on monoptic presentations of the center-surround stimulus and thus could not separate between the influences of cortical and subcortical components. A more detailed description of the spatial effect on subcortical and cortical lateral interactions is therefore still lacking. In the present manuscript, we describe the results of monoptic and dichoptic measurements of the PFS in the central stimulus while varying the size of the surround stimulus. Thus, the influence of the surround size could be separately studied for subcortical and cortical components.

The results of this work support the idea that lateral interactions involved in the PFS of the center stimulus have subcortical and cortical contributions. However, until now the data were only interpreted in terms of lateral interactions influencing the change of flicker perception. The mean level of flicker perception was not considered. We here extend the previous interpretations by proposing two mechanisms of lateral interactions: one mechanism that results in a phase-dependent modulation of the PFS (and that was considered in previous work) and a second mechanism that does not depend on the phase difference between center and surround stimuli and results in a general decrease of PFS (possibly through processes similar to contrast adaptation). Although present in previous data, this distinction was not recognized before. Both types were influenced by the size of the surround stimulus and have cortical as well as subcortical components. The cortical “contrast adaptation” component does not vary strongly with surround stimulus size whereas the subcortical component increases with increasing surround size. Because the phase-independent “lateral contrast adaptation” mechanism limits the results for the phase-dependent mechanism, the cortical and sub-cortical components resulting in PFS modulation depend in a complex manner on surround size.
Methods

Participants

The experiments were performed in Erlangen and Belém. In Erlangen, three healthy subjects participated as observers in the present study, two authors (CT and JK, age 36 and 50 years, respectively) and one subject who is an experienced observer but was naïve concerning the goals of the experiments (GP, aged 32 years). In Belém, two subjects (SW and LA, age 20 and 21 years, respectively) who are experienced observers but were naïve concerning the goals of this work participated in the experiments. All subjects had normal color vision, and an extensive ophthalmological examination did not reveal any ocular disorder. All psychophysical measurements were performed under dim light conditions in a darkened room, using natural pupils and full optical correction. The experimental procedures adhered to the Helsinki Declaration.

Apparatus

In the experiments performed in Erlangen, the stimuli were presented on an EIZO L360 monitor (EIZO NANAO Corporation, Ishikawa, Japan; frame rate 120 Hz) controlled by a Matrox Millennium G550 graphic card (Matrox, Plattsburgh, USA) using commercially available software (VisionWorks™ 4.0 for Windows, Vision Research Graphics Inc., Durham, USA).

Two different stimuli (a test stimulus and a matching stimulus) were displayed simultaneously. The test stimulus consisted of a spatially homogenous circular center and a spatially homogenous annular surround. The diameter of the center stimulus was 1°, the inner diameter of the surrounding annulus was 1.1°, and various outer diameters were used: 1.2°, 1.6°, 3° and 5°. There was a small annular gap (inner-outer diameters of 1°–1.1°) between the center and the surround stimuli. This annular gap enabled a perceptual separation of the center circle from its surround at all stimulus conditions.

The center and surround test stimuli had equal mean luminance (45 cd/m²) and chromaticity (10, 30, and 5 cd/m²), mean luminance of the red, green, and blue phosphors, respectively), resulting in a white with coordinates x = 0.3330, y = 0.3263 in the CIE1964 chromaticity diagram for the 10° standard observer. The background had the same chromaticity but with a slightly higher mean luminance (50 cd/m²; 11.11, 33.33, and 5.55 cd/m² mean luminance of the red, green, and blue phosphors, respectively) to reduce the effects of stray light. Stray light would result in an increased flicker perception when center and surround were modulated in-phase and a decreased flicker perception when they were modulated in counter phase. However, the results were reversed, strongly suggesting that stray light had a minor effect.

The stimuli were viewed through goggles with LCD shutters (NuVision 60GX, MacNaughton, Inc., Beaver, OR, USA). The LCD shutters were synchronized to the monitor’s refresh rate by infrared connection. When the shutters were opened, they transmitted 20% of the light. Transmission was similar for all wavelengths. As a result, the center and surround stimuli had mean luminances of 9 cd/m² (2, 6, and 1 cd/m² mean luminance of the red, green, and blue phosphors, respectively).

The luminance of the center and surround stimuli was sinusoidally modulated in time with 0.5 Michelson contrast with equal temporal frequency. This relatively high contrast ensured that we obtained reliable psychophysical data at all stimulus conditions. As the contrast of the test stimulus was constant for all conditions, contrast-dependent saturation does not influence the results. The measurements were performed at a 3 Hz temporal frequency, at which previous data (D’Antona et al., 2011; Teixeira et al., 2011) showed that both cortical and sub-cortical perceived flicker strength (PFS) components could be reliably analyzed. In subject CT, the measurements were repeated at 6 and 12 Hz.

The matching stimulus consisted of a single stimulus with the same shape, size, temporal frequency, time-averaged luminance, and time-averaged chromaticity as the center of the test stimulus. The distance between the edges of the surround test stimulus and the matching stimulus was 5°. The contrast of the matching stimulus was variable and set by the observer to match the PFS in the center of the test stimulus.

The matching stimulus and the center of the test stimulus were presented to the left eye. The measurements were performed in two conditions: one in which the surround of the test stimulus was also presented to the left eye (monoptic condition) and one in which it was presented to the right eye (dichoptic condition). An unmodulated light of equal time-averaged luminance was presented to the other eye.

In the experiments performed in Belém, visual stimuli were physically identical to those described above. They were programmed with MATLAB® (MathWorks, Inc., Natick, MA, USA) and presented on a Mitsubishi Diamond Pro 2070SB monitor (frame rate: 160 Hz) using a VISAGE system (Cambridge Research System, Rochester, UK). The only exceptions were that the inner and outer diameters of the surrounding annulus were fixed at 1.1° and 3°, respectively. In addition, the stimuli were viewed through FE-1 Shutter goggles (Cambridge Research
System, Rochester, UK). The LCD shutters were synchronized with the monitor’s refresh rate through a cable connection. When the shutters were opened, they transmitted 20% of the light. Therefore, similar to the above-described experiments performed in Erlangen, transmission was similar for all wavelengths and the center and surround stimuli had a mean luminance of 9 cd/m² (2, 6, and 1 cd/m² mean luminance of the red, green, and blue phosphors respectively).

Procedure

In the experiments performed in Erlangen, the PFS measurements were carried out at 13 randomly presented relative phases between center and surround test stimulus: −180°, −150°, −120°, −90°, −60°, −30°, 0°, 30°, 60°, 90°, 120°, 150° and 180° (the −180° and 180° phase conditions were measured separately although they were physically identical). A two-alternative forced-choice method was used to match the PFS in the matching stimulus to the PFS in the center of the test stimulus. Subjects were requested 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 matching stimulus. The subjects viewed the matching stimulus and the center test stimulus as long as necessary and were free to make eye and small head movements.

In each PFS measurement, the contrast in the matching stimulus was varied without changing the test stimulus. If the subject indicated that the perceived flicker in the matching stimulus was stronger than in the center test stimulus, the contrast in the matching stimulus was decreased. It was increased when the subject indicated that the perceived flicker of the matching stimulus was weaker than in the center test stimulus. A staircase procedure was used to match the center of the test and the matching stimulus. Two staircases, one starting at 0.0 and the other at 1.0 Michelson contrast, were used. The contrasts in the matching stimulus were initially changed in 0.1 steps. After a first change in response (from a weaker to a stronger PFS in the test stimulus or vice versa), the direction of contrast change was reversed and the step size was decreased to 0.05. Subsequent changes in response led to a change in step direction and further decreasing step sizes (0.03, 0.02, and 0.01 respectively). Once a 0.01 contrast step was reached, two additional changes in response resulted only in a direction reversal without a change in step size. After six changes in response, it was assumed that the PFSs in the matching stimulus and in the center test stimulus matched. In each PFS measurement run, two independent estimates of the PFS in the center test stimulus were obtained (one from each staircase). Each run was repeated three times. The means and standard deviations of the six matching PFS estimates were calculated. The standard deviation of the results shows that the PFS could be estimated with a reliability of about one tenth of the mean PFS. However, the reliability was much better in most cases.

In the experiments performed in Belém, in addition to the measurements in the presence of a modulating surround at the same temporal frequencies with 13 varying phases, as described above, additional measurement conditions with the central test stimulus modulating at 3, 6 and 12 Hz were used: with the test stimulus consisting of only the center stimulus in the absence of a surround stimulus; with the test stimulus having a steady (non-modulating) surround, and with the test stimulus having a surround modulating at 25 Hz (and thus with a varying phase difference between center and surround modulation). A staircase procedure also was used to match the center of the test stimulus and the matching stimulus. Two staircases, one starting at 0.0 and the other at 1.0 contrast, were used. The contrasts in the matching stimulus were changed in steps of 0.05 contrast. After a first change in response (from a weaker to a stronger PFS in the test stimulus or vice versa), the direction of contrast change was reversed. After thirty changes in response, it was assumed that the PFSs in the matching stimulus and in the center test stimulus matched. Then, the mean and standard deviation contrast values at the last ten changes in response of both staircases were used to calculate the PFS. The standard deviation of the results shows that the PFS could be estimated with a reliability of about one tenth of the mean PFS. However, the reliability was much better in most cases. Simulations with this staircase procedure performed by García-Pérez (1998) showed a reliability of about 80% in contrast threshold measurements.

Results

Perceived flicker strength

Figures 1 through 5 (left panels) display the PFS (mean and SD of six estimates) as a function of the phase difference between center and surround test stimuli presented in the monoptic and dichoptic conditions and for four different surround sizes (1.2°, 1.6°, 3°, and 5°). Figures 1 through 3 display the measured PFS for three subjects (CT, JK, and GP) at 3 Hz stimulus frequency. Figures 4 and 5 display the measured PFS for subject CT at two additional temporal frequencies (6 and 12 Hz). The right panels describe the subtraction of the dichoptic PFS data from the monoptic data to estimate how the subcortical
component is influenced by phase difference between center and surround test stimuli. Here, a contrast of 0.5 (the physical contrast) has been added to the estimated sub-cortical component data to compensate for the subtraction of the mean contrast levels and to avoid the fact that contrasts can have negative values.

The monoptic and dichoptic PFSs are modulated by the center-surround phase difference at all surround sizes, indicating the presence of a phase-dependent lateral interaction. The PFS modulation in the monoptic condition increased with increasing surround size (except with the $5^\circ$ surrounds in certain conditions).

There were stimulus conditions where almost no flicker was perceived when the phase difference between center and surround stimuli was between $-30^\circ$ and $30^\circ$. In addition, most PFSs are smaller than the physical contrast of the center stimulus (0.5), indicating the presence of an additional and phase-independent lateral interaction.

As mentioned above, while the PFS modulation in the monoptic condition can have cortical and subcortical origins, the PFS modulation in the dichoptic condition probably has exclusively a cortical origin. Assuming that subcortical and cortical components do
not interact and are completely independent, an estimate of the subcortical component contribution to the phase-dependent PFS can be obtained by subtracting the dichoptic PFS from the monoptic PFS data (Figures 1 through 5, right panels). Therefore, we will henceforth refer to the difference between the monoptic and dichoptic interactions as the “sub-cortical PFS component.”

Linear vector addition model

In previous work, it was found that a linear vector addition of the responses to the center and to the surround stimuli can describe the responses of LGN neurons to a combined stimulus (Kozyrev et al., 2007; Kremers et al., 2004). A similar equation was used to describe psychophysical data (D’Antona et al., 2011; Kremers & Rimele, 2007; Teixeira et al., 2011):

\[
PFS = \sqrt{R_C^2 + R_S^2 - 2R_C \times R_S \times \cos(S - P)}
\]  

(1)

where \(R_C\) and \(R_S\) are the selective psychophysical responses to the center and surround stimuli, respectively (\(R_S\) quantifies the phase-dependent modulation of the PFS and thus the strength of phase-dependent lateral interactions; \(R_C\) quantifies the mean phase-independent PFS level). The description with the linear model is an approximation because the model does not consider nonlinear center-surround interaction. These nonlinear interactions may have subcortical and cortical origins. Kozyrev et al. (2007) described a model that links psychophysical data with responses of an array of LGN cells in which several nonlinearities are considered.
As the PFS modulation cannot be larger than the mean level, $R_C$ was always larger than $R_S$. Thus, a PFS modulation can only be present when the averaged PFS, quantified by $R_C$, is large enough. $S$ is the phase of the surround stimulus relative to the phase of the center stimulus, and $P$ is the relative phase of the response to center and surround stimuli at a minimal PFS. Equation 1 was fitted to the data using the Solver routine of the Microsoft Excel 2007 program. In the fitting routine, there were three free parameters: $R_C$, $R_S$ (both expressed in Michelson contrast), and $P$ (expressed in degrees). The curves in Figures 1 through 5 are fits of Equation 1 to the mean value of the six PFS measurements. The fits of Equation 1 to each of the six PFS measurements were used to obtain estimates of the free parameters $R_C$, $R_S$, and $P$, for which mean values ($\pm SD$) are shown in Figures 6 through 8.

This model described the psychophysical data satisfactorily. However, the phases were not well constrained when the phase-dependent modulation of the PFS (quantified by $R_S$) was small. Therefore, we disregarded the phase estimates from those fits in which the difference between the maximal and minimal values of the PFS was less than three times the average of the standard deviations at all data points. All phase estimates could be used, except for the sub-cortical PFS component at 3 Hz (surround sizes of 3° and 5°) and at 6 Hz (surround size of 1.2°) for subject CT.

Figure 6 displays the estimates of $R_C$ as a function of the spatial frequency of the surround stimulus outer diameter for three subjects (CT, JK, and GP) at 3 Hz stimulus frequency (left panel) and for subject CT at two additional temporal frequencies (6 and 12 Hz; right panel). The dichoptic (cortical) $R_C$ value was always
smaller than 0.5 contrast (the physical contrast of the center stimulus) but larger than the monoptic $R_C$. As mentioned above, this is indicative for a phase independent (possibly contrast adaptation-related) lateral interaction that has both cortical and subcortical origins. Moreover, the monoptic $R_C$ decreased more strongly with increasing surround size, suggesting that the phase independent cortical mechanism is not strongly influenced by surround size. In addition, this result also suggests that either the phase independent subcortical mechanism depends strongly on surround size or the phase independent monoptic mechanism results from subcortical and cortical phase independent mechanisms that are similarly influenced by surround size. It was not possible to verify which of these two possibilities better explain the present psychophysical data because the estimate of the strength of the subcortical $R_C$ mechanism was influenced by the addition of a contrast of 0.5 (the physical contrast) to the estimated subcortical component data to compensate for the subtraction of the dichoptic PFS data from the monoptic PFS data, as mentioned above.

Figure 7 displays the cortical $R_S$ mechanism (dichoptic interactions) and the estimated subcortical $R_S$ mechanism (monoptic-dichoptic interactions) for the three subjects (CT, JK, and GP) at 3 Hz stimulus frequency (left panel) and for subject CT at two additional temporal frequencies (6 and 12 Hz; right panel). Although there is a large interindividual variability in the data, there is a tendency for $R_S$ to increase with increasing surround sizes, except with the largest surrounds where $R_S$ magnitude can even decrease. We attribute this decrease in $R_S$ magnitude to the phase-independent (contrast adaptation-related) mechanism, which can be so strong at the largest...
surround resulting in a small value of $R_C$, thereby limiting also $R_S$ and the PFS modulation.

Figure 8 displays the estimates of phase $P$ as a function of surround stimulus outer diameter for three subjects (CT, JK, and GP) at 3 Hz stimulus frequency (left panel) and for subject CT at two additional temporal frequencies (6 and 12 Hz; right panel). Generally, the phase at minimal PFS was positive, suggesting a phase lag of the phase dependent mechanisms that respond to the surround stimulus.

These data indicate the presence of two types of lateral interactions: a phase dependent mechanism, which results in a modulation of the PFS by the different relative phase between center and surround stimuli, and a phase-independent mechanism leading to an overall decrease of the PFS.

To study the origin of the phase independent mechanism, additional experiments were performed in Belém with three subjects. Figures 9 through 11 display the results of PFS measurements (mean ± SD) obtained for three different temporal frequencies. The monoptic (left panels, empty circles) and dichoptic (right panels, empty squares) PFS data were measured in the presence of a modulating center and surround test stimuli at the same temporal frequencies with varying phases, similar to the experiments described above. The subtraction of the dichoptic data from the monoptic data (not shown) is in agreement with the data shown above. The curves are fits of Equation 1 to the mean value of two PFS measurements. The estimated values of $R_C$ (i.e., the estimate of the influence of the phase independent mechanism) are shown to the right of these data (filled triangles). The fits of Equation 1 to each of two PFS measurements were used to estimate the values of $R_C$ (mean ± SD) displayed in Figures 9 through 11. In addition, the
results of the other PFS measurements [in the presence of a surround stimulus modulating at 25 Hz (filled diamonds); in the presence of a steady surround (filled circles); and in the absence of a surround stimulus (crosses)] also are shown.

Despite intersubject variability, for each subject the PFS in the absence of a surround was close to the physical contrast, independent of stimulus temporal frequency. This outcome indicates that the subjects were able to reliably compare the test and the matching stimuli. However, subject LA always underestimated the physical contrast. The presence of a steady surround had little influence on the PFS.

On average, the PFS in the presence of a 25 Hz modulating surround was smaller than either the PFS in the absence of a surround or the PFS in the presence of a steady surround (except for subject EC, dichoptic condition, 6 and 12 Hz), indicating that the presence of a modulating surround is sufficient to decrease the PFS in the center stimulus. Because in the presence of a 25 Hz modulating surround there is no constant phase difference between center and surround stimuli, a phase-independent mechanism, possibly related to temporal contrast adaptation, must be responsible for this PFS decrease. At least in subjects SW and EC this effect seems to be larger in the monoptic presentations.

In agreement with the data given above, the estimated (phase-independent) $R_C$ values were smaller in the monoptic presentations. In subjects SW and EC, the $R_C$ values were smaller than any of the other PFS values, indicating that a surround with equal temporal frequency as the center is more efficient for the phase-independent mechanism. For subject LA, the 25 Hz surround was more effective, possibly indicating the results of another effect.

**Discussion**

The results support the hypothesis that two distinct mechanisms contribute to the lateral interactions influencing the PFS in the center stimulus: a phase-dependent mechanism and a phase-independent mechanism. The phase-dependent lateral interactions, resulting in a modulation of the PFS, was described previously and is quantified by the strength of the response to the surround stimulus and is quantified by
the parameter $R_S$ in the fits (D’Antona et al., 2011; Kozyrev et al., 2007; Kremers et al., 2004; Kremers & Rimmele, 2007; Teixeira et al., 2011). Our data confirm previous data that this mechanism ($R_S$) has both cortical and subcortical origins (D’Antona et al., 2011; Teixeira et al., 2011). With increasing surround stimulus size, the strength of both sub-cortical and cortical $R_S$ components generally increases although its value is constrained by $R_C$. In most cases, the subcortical $R_S$ component was smaller than the cortical component (Figure 7).

The physiological basis of the subcortical component of this phase-dependent mechanism may lie in the linear center-surround interaction of retinal ganglion and LGN cells (Kozyrev et al., 2007; Kremers et al., 2004). Similar simple center-surround interactions might also be present in the responses of cortical cells, which may be the basis of the cortical component of phase-dependent interactions (Jones, Grieve, Wang, & Sillito, 2001; Sillito & Jones, 1996; Williams, Singh, & Smith, 2003; Xu, Shen, & Li, 2005).

On the other hand, we found evidence that the PFS in the center stimulus is also influenced by a, hitherto not described, phase-independent mechanism that is quantified by the strength of the selective response to the center stimulus ($R_C$). The results show that this phase-independent mechanism also has both cortical and subcortical origins and results in a general decrease of the PFS in the center stimulus when a surround stimulus is present. The strength of this mechanism increases with increasing surround stimulus size. Additional experiments showed that the decrease in monoptic (subcortical + cortical) $R_C$ is influenced by the temporal modulation in the surround. This effect was smaller but still present for the dichoptic (cortical) conditions, suggesting that the phase-independent monoptic mechanism might result either from a joint effect of subcortical and cortical phase-independent mechanisms. We propose that the phase-independent mechanism, represented by $R_C$ in the fits, is mainly related to temporal contrast adaptation at subcortical and cortical sites (Brown & Masland, 2001; Gardner et al., 2005; Heinrich & Bach, 2001; Hohberger, Rössler, Jünemann, Horn, & Kremers, 2011; Smirnakis, Berry, Warland, Bialek, & Meister, 1997).

Previous work has shown that the temporal contrast sensitivity to a test stimulus can be affected by the presence of a steady surrounding stimulus (Cornsweet & Teller, 1965; Harvey, 1970; Keesey, 1970; Kelly,
There is also evidence that the dynamics of lateral contrast adaptation in a center field is dependent of the contrast level in a flickering surround (Snowden & Hammett, 1998). Snowden and Hammett (1998) showed that at high mean luminance levels (150 cd/m²) the perceived contrast in a central field decreases when the contrast in the surround increases. A similar process is possibly also involved in the phase-independent PFS decrease described in the present work. In contrast, Kremers et al., (2004) found that the monoptic PFS could increase (e.g., $R_C$ increased) in comparison to the central field stimulus contrast (0.5) when the contrast in the surround is smaller (0.25) but decrease (e.g., $R_C$ decreased) if the surround had equal contrast as the center. These data suggest that the relative contrast in center and surround may influence lateral contrast adaptation. However, in the work of Snowden and Hammett (1998), the surround had a different spatial and temporal frequency than the center, and they argue that their results are probably more related to masking processes.

On the basis of the present data, it seems that the phase-independent PFS decrease is mainly associated with the presence of flicker (e.g., temporal contrast) in the surround. It is difficult to speculate on the subcortical and cortical physiological origins for this psychophysical phase-independent lateral contrast adaptation mechanism. At the subcortical level, bipolar cells show some modest change in gain after pooling from photoreceptors and horizontal cell inputs. Ganglion cells pool from bipolar and amacrine cell inputs and have a further possibility to adapt to surrounding stimuli (Baccus & Meister,

Figure 8. Estimates of $P$ as a function of surround stimulus outer diameter. Data for three subjects at 3 Hz (left) and for subject CT at 6 and 12 Hz (right) are shown. Symbols as in Figure 1.
The evidence that both RF’s center and surround of retinal ganglion cells can adapt independently to subtle changes in contrast level (Brown & Masland, 2001) suggests that ganglion cells’ contrast adaptation may not spread laterally over the retina. The presence of extraclassical receptive fields in LGN cells, i.e., stimuli outside the classical receptive field of LGN cells suppressing the responses to stimuli presented within the classical receptive fields (Solomon, White, & Martin, 2002), suggests that LGN cells can be another physiological source of the psychophysical phase-independent mechanism described here. In agreement with this notion, Kremers et al. (2004) showed that values of $R_C$ (expressed in spikes/s) estimated from responses amplitudes of LGN cells elicited by similar center-surround stimuli as used in the present study always decrease in comparison to the responses amplitudes elicited by the center stimulus alone. That is, a modulating stimulus in the surround led to a decrease of the response to a central stimulus. These data suggest a similarity between the dynamics of the phase-independent mechanisms ($R_C$) estimated from LGN physiology and from psychophysical data. However, at the LGN level, contrast adaptation is present mainly in M cells responses (Solomon, Peirce, Dhruv, & Lennie, 2004): If the contrast adaptation and the lateral interactions are related, then these results would suggest that a subcortical phase-independent suppression would be weak or not present with red-green chromatic stimuli to which mainly P cells respond. However, Kremers et al. (2004) found similar effects in M and P cells. It therefore is not clear if the effects can be attributed to particular subcortical pathways or if it is a general feature of all subcortical pathways.

Extraclassical receptive field suppression may also be a physiological basis for the cortical phase-independent mechanism. There is evidence supporting the idea that geniculo-cortical inputs, V1 horizontal connections and top-down extra-striate feedback connections might be involved in lateral contrast adaptation interactions similar to those described in the present work.
Angelucci et al., 2002; Angelucci & Bullier, 2003; Ichida, Schwabe, Bressloff, & Angelucci, 2007; Schwabe, Ichida, Shushruth, Mangapathy, & Angelucci, 2010).

The psychophysical separation of subcortical and cortical center-surround interactions and the quantitative understanding of the mechanisms involved in these interactions can potentially be used as a clinical tool for the evaluation of neurological and/or ophthalmological defects because it may reveal early disease-related changes in receptive field organizations of subcortical and/or cortical neurons. Consistent with this proposal, we found differences between lateral interaction in glaucoma patients and in normal subjects (Teixeira, Silveira, & Kremers, 2010).

Figure 10. PFS data for different stimulus conditions (subject LA). Three different temporal frequencies were used: 3 (upper plots), 6 (middle plots) and 12 Hz (lower plots). Symbols as in Figure 1.

Conclusion

The lateral interactions involved in flicker perception of a central field are the result of phase-dependent and phase-independent mechanisms, each having subcortical and cortical components and diverse spatial properties.

Keywords: subcortical lateral interactions, cortical lateral interactions, contrast adaptation, flicker perception

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