Central luminance flicker can activate peripheral retinotopic representation

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We aimed to study cortical responses to uniform luminance stimulus in different conditions. We stimulated the central visual field with luminance flicker and reversal of checkerboard pattern contrast and mapped the visual field representation up to 50 degrees of eccentricity. Our results show spreading of cortical BOLD responses when visual stimulus contains mean luminance change in dark surround and no spreading when stimulus surround has bright illumination. No cortical region was more sensitive to luminance flicker than to pattern reversal during both stimulation setups. We suggest that the spread of luminance responses in retinotopic cortical areas results from intraocular scattering of light. Light scattered inside the eye spreads visual stimulation on the retina, and the contrast of the scattered light is strongest when the surround of the stimulus is dark. The stray light is potential and often neglected source of an artefact in visual experiments, and the responses due to stray light can erroneously be interpreted as indicators for local cortical sensitivity to luminance.
Introduction

Previously, human primary visual cortex has been shown to respond to uniform illuminated surface (Haynes, et al. 2004) and increased sensitivity to luminance flicker has been suggested in extrastriate cortical areas (Dechent and Frahm 2003). Many visual paradigms comprise variations in the mean luminance of the stimuli either intentionally or unintentionally, and these luminance changes form a potential source of an error in visual neuroscience. Examples of unintended luminance stimuli could be uncontrolled blinks or saccades with lights on. In addition, in natural stimulation paradigms, where photographs or videos are presented, luminance is typically poorly controlled.

The aim of this work was to study sensitivity to luminance flicker in the human visual cortex. Originally we started this work by searching for functional cortical areas that were more sensitive to luminance flicker than pattern reversal stimulus. However, when we discovered that most of the light-sensitive response was coming from the peripheral part of the primary visual cortex, we were obliged to search for alternative explanations to our original hypothesis of a distinct light-sensitive functional area. We approached the question of luminance sensitivity by comparing the stimuli containing and not containing mean luminance change with dark and illuminated stimulus surround. The idea to illuminate the stimulus surround was derived from studies of patients with cortical blindness. In these studies intraocular scattering of light from the blind hemifield is a potential source of an error, but the effect of stray light can be attenuated by increasing the illumination of the healthy hemifield (Barbur, et al. 1994; Weiskrantz, et al. 1995).

Methods

Subjects and stimuli

We studied eleven healthy right-handed volunteers (23–40 years, mean age 27 years, 7 males and 4 females). The study was approved by the Ethics Committee of Hospital District of
Helsinki and Uusimaa, and all subjects gave their written informed consent before participation in the study. All eleven subjects were measured in the first experiment, and a subgroup of four subjects (2 males and 2 females) attended the second control experiment.

In two experiments we presented three different visual stimuli in a block-paradigm: (i) A luminance stimulus (black = 0.4 cd/m², white = 25 cd/m²) flickering at 4 Hz, (ii) a checkerboard pattern-reversing contrast at 8 Hz (no change in the mean luminance), and (iii) a fixation point with a grey background (11 cd/m²) for the fixation condition. We examined the responses to luminance vs. responses to fixation and pattern vs. fixation in both experiments.

Fig. 1 visualizes the stimulus presentation system used in both experiments. In the first experiment we minimized illumination to the peripheral visual field around the stimuli. To avoid reflections from the coil and the bore structures, we covered the interior of the head coil with black matte cloth. In addition, all subjects wore a black mask. The mask was constructed of plastic goggles and black wool cloth. Two apertures in front of both eyes formed two artificial pupils at 30 mm distance from the eyes. The diameters of the apertures were 22 mm, and their depths were 10 mm. All surfaces of the goggles, including the interior of the two apertures in front of eyes, were covered with cloth. The mask covered the peripheral part of the visual field. The stimulus was roughly a circle with 10 cm radius. With 35 cm viewing distance this resulted in approximately visual stimulus with 30 degrees of diameter.

Even though the mask was made of thick coarse black wool, leakage of light through the mask is a potential source of peripheral stimulation. To examine the leakage of light we compared the luminance changes under the mask during different stimulus conditions. We placed a tip of an optic cable between the eyes to detect the luminance changes. The optic cable was connected to optical amplifier that converted the luminance to voltage, and we measured the voltage changes with an oscilloscope (Hewlet Packard Inc.). This setup enabled comparison of illumination under the mask during different stimuli in the real experimental conditions inside the magnet. We did not find difference between the stimuli indicating that illumination under the mask was similar during all stimulus conditions. In addition to leakage, reflections from the interior of the apertures in front of the eyes form another source of peripheral
responses. To examine the reflections from the structures covered with the cloth, we illuminated the cloth with a light source and measured the reflected luminance from the cloth. The measurement showed that approximately 0.04 cd/m² was reflected when the cloth was illuminated with 25 cd/m² luminance stimulus.

Figure 1 approximately here

In the second experiment the background illumination was increased in order to minimize the luminance contrast in the peripheral part of the retina around the stimuli. Four subjects wore a white mask with a similar coverage of the periphery compared to the first experiment, and the interior of the mask was illuminated with bright light (> 100 cd/m²). Light was directed to the mask via two bundles of thick optic fibres, one for each eye. This setting resulted in two brightly lit rings in front of subjects’ eyes and thus also around the stimuli.

The visual stimuli were controlled with Presentation™ software (Neurobehavioral Systems Inc.), and they were presented with a data projector comprising three micromirror units (VistaPro, Electrohome Ltd). The stimuli of the block experiments were projected on a semi-transparent screen, attached behind the subjects’ head to an open head coil. The subjects viewed the stimuli via a mirror inside the head coil and were asked to fixate to a point in the centre of the visual field.

We mapped the occipital retinotopic areas of three subjects who attended the second control experiment, and analysed their data also on the cortical surface. We delineated the borders of the retinotopic areas for Subjects 1 and 2 with standard phase-encoded retinotopic mapping using polar phase information (Sereno, et al. 1995). We used 15 degree radius stimuli and the same stimulus presentation system as in the block paradigm. In addition, we mapped medial occipital retinotopic areas of Subjects 1, 2, and 3 with multifocal fMRI (Vanni, et al. 2005), which is based on the simultaneous stimulation of multiple visual field locations with an orthogonal temporal sequence. We used the stimuli covering visual field up to a radius of 50 degrees for the horizontal meridian and 40 degrees for the vertical meridian, and we presented
the stimuli with a near-view stimulus presentation system that enables mapping of the peripheral parts of the visual field (Stenbacka and Vanni, unpublished observation). Both phase-encoded and multifocal mapping comprised of checkerboard pattern-reversal stimuli with the contrast of the checks reversing at 8 Hz and with no mean luminance change.

**MR data acquisition**

We measured signals with a 3-tesla MRI scanner (Signa™, General Electric Corp.) using a single-channel head coil. We performed functional imaging with a T2*-weighted gradient-echo echo-planar imaging (EPI) sequence. The measurement parameters for block designs were TR = 2 s, TE = 40 ms, flip angle = 90 deg, acquisition matrix = 64 x 64, FOV = 190 x 190 mm². With slices of 3-mm thickness, this resulted in isotropic 3 x 3 x 3 mm³ voxels. We acquired 27 slices approximately orthogonal to PO sulcus to cover most of the cortical visual areas. The duration of each block was 20 s, comprising 10 functional volumes. One run contained five blocks of each stimulus in a pseudorandom and counterbalanced order, thus resulting in altogether 150 functional volumes. One session comprised four runs in both experiments.

Major data acquisition parameters in the phase-encoded retinotopy measurement were TR = 1.3 s, TE = 40 ms, flip angle = 90 deg, acquisition matrix = 64 x 64, FOV = 200 x 200 mm², 16 slices, slice thickness 4 mm, resulting in 3.1 x 3.1 x 4.0 mm³ voxels. Duration of each run was 7 min 22 s comprising 354 functional volumes. The measurement parameters of the multifocal experiments were TR = 2 s, TE = 30 ms, flip angle = 60 deg, acquisition matrix = 64 x 64, FOV = 190 x 190 mm², 27 slices, slice thickness 3 mm, and 3 x 3 x 3 mm³ voxels. Both upper and lower visual fields were measured with two runs, each comprising 240 functional volumes (eight min).

We acquired low-resolution anatomical images with a T1-weighted spoiled gradient-echo sequence after each functional experiment. The 124 slices were 1.5 mm thick, FOV was 230 x 230 mm², and matrix size 128 x 128. We segmented the borders between the grey and the white matter from high-resolution T1-weighted anatomical images, acquired with slice thickness of
0.9 mm, FOV 230 x 230 mm², and acquisition and reconstruction matrices of 256 x 256, resulting in isotropic 0.9 x 0.9 x 0.9 mm³ voxels.

Data analysis

Data were analysed with SPM2 software (Wellcome Department of Imaging Neuroscience, for an extensive review, see Friston 2003). Raw data were corrected for head movements and high pass filtered with a cut-off period of 160 s. The design matrix was convolved with a standard hemodynamic response function, and the temporal autocorrelation of the system noise was taken into account in the statistical analysis.

For the group analysis of eleven subjects, we normalized all data to a standard anatomical space by using a T1-weighted MNI template provided by SPM2. The data were recalculated to 3 x 3 x 3 mm³ voxels and the normalized EPI images were smoothed with a Gaussian kernel of 10 x 10 x 10 mm³. We performed random-effects analysis with one sample t-test to investigate the results at the group level (Friston, et al. 1999) and used a false discovery rate (FDR; Benjamini and Hochberg 1995; Genovese, et al. 2002) of 5% (pFDR < 0.05) to correct for multiple comparisons. We defined both luminance against fixation and pattern against fixation contrasts and compared them in three-dimensional space. The results were projected into a normalised anatomical MR template image provided by SPM2.

Data of four subjects who attended also the control experiment were examined at individual level. We used unsmoothed data for the individual level analysis, and the locations of the responses were examined by projecting the active functional voxels to the 3D T1-image of each subject. In both experiments, we defined an individual peripheral luminance response, as a response to luminance stimulus with a voxel threshold of pFDR < 0.05, excluding regions with responses (p < 0.05, uncorrected) to pattern stimuli, and a cluster size above 10 voxels.

In addition, the results of three control subjects were inspected and located in relation to the retinotopic areas on a reconstructed cortical surface with Matlab® toolbox; Brain à la Carte (BLC) provided by INSERM unit 594/Université Joseph Fourier, Grenoble, France (Warnking, et al. 2002). We created individual 3D anatomical models along the border of the
white and the grey matter of the medial part of the occipital lobe, and the 3D models were unfolded onto a 2D surface. We assigned the t-maps to the surface, and smoothed the t-values (SD 1.5 mm) along the cortical sheet.

In addition, we calculated the BOLD signal changes in V1 for these three control subjects to compare the BOLD signal in different eccentricities during luminance flicker and pattern reversal stimuli. We divided the cortical sheet of area V1 for 16 approximately transverse sets of samples, placed in about 5 mm intervals on the surface model. These samples were converted to 3D space, indicating the voxels where parameter estimates were sampled. The signal change equals the division of the signal-of-interest by the mean signal of the session and multiplied by 100.

*Figures 2 and 3 approximately here*

**Results and discussion**

*Group analysis and the stimuli with dark surrounds*

Fig. 2 shows group results for pattern vs. fixation and luminance vs. fixation contrasts of the first experiment with the dark stimulus surround. This setup corresponds to visual experiments, where stimuli are presented against dark background and peripheral reflections are carefully controlled. Both pattern and luminance stimuli activate visual areas in the occipital lobe. For both stimuli the activation extends from the medial part of the occipital lobe, most likely corresponding to the activation in functional areas V1/V2/V3, to the lateral part of the occipital lobe, approximately to the region of the area V5 (Zeki, et al. 1991; Watson, et al. 1993) and to the dorsal cuneus possibly corresponding to activation in V3A (Tootell, et al. 1997). However, the response to the luminance stimulus extends further anteriorly in the medial part of the occipital lobe. This discrepancy is clear bilaterally around the calcarine sulcus, and extends upwards and towards the midline approximately at the depth of the parieto-occipital (PO) sulcus.
Only the pattern reversal stimulus activated cortex around the intraparietal sulci and in the ventral occipital cortex (data not shown). In addition, the pattern reversal stimulation resulted in responses in the posterior part of the thalamic region likely reflecting activation in the lateral geniculate nucleus. The responses in these regions during pattern reversal but not during luminance flicker are presumably due to more contrast energy in the pattern stimulus. Several contrast borders activate large amount of cortical neurons and the following BOLD response exceeds the statistical threshold whereas the uniform luminance stimulus fails to activate sufficient amount of neurons. Similarly pattern reversal resulted in higher t-values than luminance flicker in the cortical regions with significant BOLD responses during both stimuli. In addition, we found a response to pattern reversal in the junction of the left temporal and occipital lobe, bilaterally in six out of eleven subjects, approximately at the region of the angular gyrus.

Individual analysis and stimuli with dark surrounds

Below, we define individual peripheral luminance activation as the luminance responses ($p_{FDR} < 0.05$) after the regions responding also to the pattern-reversal stimuli ($p < 0.05$, uncorrected) were excluded. The clusters of the peripheral luminance activation extended bilaterally from the lingual gyrus and the anterior part of the calcarine sulcus medially and upwards along the PO sulci in all four individually analyzed subjects, and all three subjects with the cortical surface analysis had these luminance responses in the peripheral parts of V1 and V2.

Fig. 3 shows that the most peripheral part of the retinotopic mapping response obtained with the multifocal stimuli directly overlaps with the peripheral luminance response. The peripheral luminance response extends approximately from 20 to over 30 degrees of eccentricity, even though the stimuli reached only 15 degrees radius. The missing signal at 15-20 degrees of eccentricity may be related to the spread of the cortical BOLD responses. A cortical response and also a BOLD signal can spread several millimetres along the cortex most likely through local lateral connections (Parkes, et al. 2005; Tolias, et al. 2005). The spread of the pattern related activation results in lack of the luminance responses in the region bordering
the 15 degree representation, because we defined the peripheral luminance activation as the response to luminance flicker after exclusion of the responses to pattern reversal.

*Figures 4 and 5 approximately here*

**Comparison of the responses to stimuli with dark and illuminated stimulus surrounds**

When peripheral illumination was increased in the second control experiment, the activation for luminance in the representation of peripheral visual field disappeared in all four subjects. Fig. 4 visualizes the analysis for two subjects. The upper row shows similar strong central visual field activation during pattern reversal both when the periphery was dark and light. In contrast, the activation for the luminance stimuli behaves differently in these two situations. When the periphery is dark, the response to the luminance stimulus extends to a clearly larger area of cortex than the response to the pattern stimulus. However, when the periphery is illuminated luminance-related activation shows no extension beyond the pattern response. Accordingly, one of the authors (SV) spontaneously reported flickering sensation in the peripheral visual field during luminance flicker with dark stimulus surround and this flickering disappeared when the peripheral illumination was increased. The dark periphery condition and the phase-encoded retinotopic mapping extending only to 15 deg eccentricity (Fig. 4, Subject 1) gives an impression of a cortical area anterior to V1 with special sensitivity to luminance stimulation. However, when retinotopic mapping is extended to cover the peripheral visual field up to 50 deg of eccentricity (Fig. 4, Subject 2), majority of the peripheral luminance response remains within retinotopic areas V1, V2, and V3.

Fig. 5 visualizes cortical signals during different conditions for three subjects. The pattern reversal stimulus resulted in stronger signal changes than luminance flicker with both dark and illuminated periphery in all three subjects. Luminance flicker with illuminated surround and both pattern reversal conditions evoked responses in the cortical regions corresponding to the more central visual field representations. However, luminance flicker with the dark stimulus surround resulted in responses also in the visual field periphery. These peripheral responses
continued without interruption along V1 and were weaker than the responses in the region representing the actual stimuli.

*Intraocular scattering of light may cause responses in peripheral visual field representations*

Our results showed that the luminance flicker stimulus with dark surround evoked cortical responses outside the retinotopic representation of the stimulus. However, when the visual stimuli did not contain mean luminance change or when the surround area of the stimulus was illuminated, the cortical responses were restricted roughly to the stimulus representation. Our results are in line with the earlier finding, showing sensitivity to luminance in visual areas V1, V2, and V3. It is known that increment and decrement of surface luminance evokes positive BOLD responses in V1 and V2/V3 (Haynes, et al. 2004). In addition, Goodyear and Menon (1998) have found that the spatial extent of V1 responses related to a flickering LED stimulus in the central visual field increased with the increasing contrast of the stimulus, and Cornelissen, et al. (2006) reported the spread of responses to stimulus edge in V1. In our data the luminance responses extending beyond the pattern responses were located in the deep calcarine sulcus and the ventral part of posterior PO sulcus. The retinotopic mapping with the stimuli subtending 50 degrees of the horizontal meridian and 40 degrees of the vertical meridian confirmed that the luminance responses in the calcarine and PO sulci mainly corresponded to the peripheral visual field representation in V1 and not to a separate functional area.

Why the peripheral part of V1 was activated with luminance flicker and not with pattern reversal and why the activation disappeared when the illumination of the stimulus surround was increased? First, a peripheral BOLD response could be modulated by central stimulus. Changing luminance outside the receptive field affects responses in striate cortex of cat (Rossi, et al. 1996; Rossi and Paradiso 1999). However, in our study the modulation of the peripheral responses should be seen also with the illuminated stimulus surround. On the other hand, previous studies have found sensitivity to visual motion in PO sulcus (Dupont, et al. 1994;
Kleinschmidt, et al. 2002), and a flickering stimulus activates some of the functional areas responding also to a motion stimulus (Sunaert, et al. 1999). Theoretically, if the representations of the visual field periphery were more sensitive to flicker or to visual motion, the luminance flicker stimulus would activate them more than the pattern reversal stimulus. However, most likely such peripheral sensitivity to luminance flicker would result in responses also with the illuminated stimulus surround.

Secondly luminance flicker may cause behaviour which results in responses in the PO region. Previous studies have found responses in PO sulcus during eye movements (Anderson, et al. 1994; Dejardin, et al. 1998; Law, et al. 1998), and voluntary saccades in darkness activate V1 (Sylvester and Rees 2006). However, our subjects were asked to fixate to a point in the center of the screen to prevent voluntary eye movements, and the dark stimulus surround is unlikely to distract spontaneous eye movements.

It is unlikely that the peripheral response to luminance flicker is due to eye movements or increased sensitivity of the peripheral representation to flicker or visual motion as these would affect responses also with illuminated stimulus surround. However, response to light reflected from the stimulus presentation structures or scattered intraocularly would behave differently with dark and illuminated stimulus surround because the change of background illumination affects the contrast of reflected and scattered light.

Intraocular scattering of light is defined as the retinal illumination that does not optically correspond to the direction of light (Ijspeert, et al. 1990). This scattering causes a phenomenon called disability glare; bright light in a field of view results in a veil of light and lower contrast elsewhere. The main sources of the intraocular stray light are the cornea, the lens, and the fundus of the eye, and the amount of scattered light increases with the age of the subject (Vos 2003).

When the mean luminance change of the stimulus is minor or close to the detection threshold, scattered light has little contrast. However, when the mean luminance difference between the stimulus and the surround of the stimulus is large and scattered light has high contrast, it can stimulate the retina outside the intended region. The intensity of stray light
decreases with inverse square relationship with increasing angular distance from the light source. With non-linear contrast response function in V1 (Boynton, et al. 1996), where low contrast gives relatively high signal, scattered luminance contrast could result in rather linear spread of the response, as in our study.

*Figure 6 approximately here*

Vos (2003) presented a modified Stiles-Holladay disability glare formula that describes the relationship between the equivalent veiling background and the illuminance at the eye by the glare source as function of the angular distance between the line of sight and the glare source. Figure 6 shows the veiling glare luminance as a function of angular distance in our stimulation setup assuming a point glare source. The results give an approximation of intensity of scattered light at different eccentricities.

We suggest that in our study the responses to luminance flicker outside the stimulus representation are mainly due to intraocular scattering of light. The measurement of illumination under the mask during stimulation convinced that no light leaked through the mask. Even though the stimulus system was carefully constructed to prevent light reflections, we detected 0.04 cd/m² of light reflection from black cloth during luminance stimulation which may contribute to responses to luminance flicker. This affects more the inner aperture of the mask, approximately from 15 to 20 degrees of eccentricity. Cortical activation compounding more than 30 degrees of eccentricity is more likely explained by intraocular scatter which contain 0.14 cd/m² veiling luminance against dark background (Fig 6).

*No cortical region is specifically sensitive to luminance flicker, implications to human V6 studies*

Previously Dechent and Frahm (2003) showed with fMRI that two different clusters of activation emerged for luminance flicker but not for pattern reversal, one deep in the calcarine sulcus and the other more superficially in the parieto-occipital sulcus above the junction with the calcarine sulcus. They proposed that the luminance response in the PO sulcus originates
from a human homologue of monkey V6/V6A complex. The monkey V6 is located in the bottom of the PO sulcus. It is retinotopically organized with large receptive fields and, compared to the other retinotopic areas, has relative weighing of sensitivity on the peripheral visual field (Galletti, et al. 1999). Our data suggest that at least the deeper part of the luminance response defined by Dechent and Frahm reflects peripheral V1 activity with contribution from V2.

However, (Pitzalis, et al. 2006) have found a human homologue of monkey V6 in the dorsal part of the PO sulcus. Given that the peripheral dorsal V1, V2 and V3 are abutting V6, without detailed mapping of all these areas with more than three subjects, we cannot determine the source of the more dorsal part of the luminance response. They can either emerge from V6, relatively sensitive to peripheral stimulation, or from the peripheral part of the dorsal V1, V2 and V3. By and large, our data suggest that the parieto-occipital luminance responses result from indirect stimulation of peripheral visual field rather than from luminance sensitivity itself. We found no evidence of cortical region responding specifically to luminance flicker.
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References


Figure legends

Fig.1. A) Schematic visualization of the stimulus presentation system. Different parts of the system are not in scale. B) The black mask used in the first experiment. In the second control experiment the mask was similar except it was white.

Fig.2. Group average fMRI results for stimulation with luminance flicker and pattern contrast reversal with dark periphery. The results of random effect group level analysis ($p_{FDR} < 0.05$) are presented on anatomical MNI template images of SPM2. White lines on the sagittal MR slice indicate the level of the axial slices below. The white numbers in the left upper corner of the axial slices indicate elevation ($z$-values) in MNI space.

Fig.3. The peripheral luminance response with dark stimulus surround on top of the eccentricity mapping of Subject 2. The white-grey matter border of the left occipital lobe is reconstructed and unfolded, and data from functional experiments is assigned on the surface model. Response from 1-14 degrees of eccentricity is coded as blue, 14-32 degrees yellow and 32-50 degrees red. The eccentricity data have been obtained with multifocal mapping. The threshold for visualization is $t = 5$ and the colour of the region reflects only the strongest response for each location. The black contours show the peripheral luminance response ($t$-isocontours above $p_{FDR} < 0.05$) after removal of the regions responding also during pattern reversal ($p < 0.05$, uncorrected, see Fig. 4).

Fig.4. SPM-t maps assigned onto the segmented and unfolded cortex of Subject 1 (right occipital lobe) and 2 (left occipital lobe) thresholded at $t = 3$. The upper row shows the responses to pattern reversal ($p_{FDR} < 0.05$) and the lower row the responses to luminance flicker ($p_{FDR} < 0.05$) after voxels responding to pattern reversal ($p < 0.05$, uncorrected) have been excluded. The black lines indicate the borders of retinotopic areas, defined up to 15 degree radius for Subject 1, and 40 degree radius vertically and 50 degree horizontally for Subject 2.
Fig. 5. Percent signal changes (contrast between parameter estimates) for three subjects as a function of distance from central representation (excluding fovea). The 16 sampling points are placed at approximately 5 mm intervals on the modelled cortical surface. The grey area highlights the peripheral region, where the luminance vs. fixation contrast with dark stimulus surround exceeds other conditions.

Fig. 6. The luminance of veiling background in logarithmic scale as a function of angular distance according age-adjusted Stiles-Holladay formula (Vos 2003). The formula
\[
L = 10 \times E \left(1 + \left(\frac{\text{age}}{70}\right)^4/\theta^2\right)
\]
gives the luminance of the equivalent veiling background in cd/m². \(E\) is the illuminance at the eye by the glare source in lux, and \(\theta\) is the angular distance between the line of sight and the glare source. The mean age of our subjects was 27. The illumination created by the glare source was integrated over the surface of the source.
Figure 1: Stenbacka

A: Head-coil, Mirror, Back-projection screen

B: Projector, Mask

Figure 1: Stenbacka

A: Head-coil, Mirror, Back-projection screen

B: Projector, Mask
Dark periphery Dark periphery Illuminated periphery Illuminated periphery

Subject 2
Right hemisphere
Dark periphery Illuminated periphery

Subject 1
Left hemisphere
Dark periphery Illuminated periphery

Retinotopy mapped up to 15 deg of eccentricity Retinotopy mapped up to 50 deg of eccentricity

Figure4Stenbacka
Figure 5. Stenbacka

The figure illustrates the signal change (in %) over different subjects (Subject 1, Subject 2, Subject 3) and hemispheres (Left hemisphere, Right hemisphere) under various conditions: Luminance vs. fixation and Pattern vs. fixation. The x-axis represents the relative position (mm) ranging from 5 to 75, and the y-axis represents the signal change (%). The data are shaded to indicate specific areas of interest or significance.
Figure 6: Angular distance (degrees) vs. Equivalent veiling luminance (log cd/m²)