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Frequency dependency of temporal contrast adaptation in normal subjects

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ABSTRACT

The aim of this study was to determine the influence of temporal frequency of temporal contrast adaptation on contrast sensitivity in healthy subjects. Temporal contrast sensitivities (TCS) were measured monocularly in seven healthy subjects with a modified ERG full-field bowl stimulator at eight different test temporal frequencies (9, 15, 20, 25, 31, 37, 44, 51 Hz) using a two-alternative-forced-choice strategy. Before each presentation of the test stimulus, a 100% contrast adapting flicker stimulus was presented (frequencies: 9, 15, 20, 25, 31, 37, 44, 51, 100 Hz). At each adapting frequency, a complete set of TCSs was measured. All temporal contrast sensitivities decreased with increasing temporal frequencies. Adaptation led to a general temporal contrast sensitivity decrease. Largest adaptation effects were seen at an adaptation frequency of 25 Hz. Reduction of contrast sensitivity was significantly larger at 25 Hz adaptation than at 9 Hz adaptation (*t*-test of paired samples, Bonferroni corrected). The results of this study showed a general TCS decrease with the largest effect at an adaptation frequency of 25 Hz. This finding indicates that the contrast adaptation probably occurred in the magnocellular-pathway. In future clinical studies adaptation effects could be investigated in patients with reduced temporal contrast sensitivity.

1. Introduction

Neurons in sensory systems often are desensitized by a continuously presented stimulus. This process, called "adaptation", is possibly a protection against overstimulation as well as a method to adjust the sensitivity for optimal stimulus detection. In the visual system, many forms of adaptation are active and they occur at different levels. In contrast adaptation, the response to a temporal or spatial modulation is adjusted. Contrast adaptation can be present as early as the retina (Baccus & Meister, 2002; Chander & Chichilnisky, 2001). Especially the bipolar cells are involved in a fast contrast adaptation process (Kim & Rieke, 2001; Rieke, 2001). Even in subcortical centres like the dorsal lateral geniculate nucleus and the pretectum (Ibbotson, 2005; Pasley, Mayes, & Schultz, 2004) and in cortical structures contrast adaptation has been reported to be present (Maffei, Fiorentini, & Bisti, 1973; Movshon & Lennie, 1979; Ohzawa, Sclar, & Freeman, 1985). Contrast adaptation occurs for the spatially and for temporally modulated stimuli.

To achieve temporal contrast adaptation, visual neurons are exposed to a temporally modulating adapting light. The sensitivity to another temporally modulating stimulus is subsequently adjusted by the adapting modulation. Psychophysically, contrast adaptation can be quantified by comparing the contrast sensitivities to a temporally modulating stimulus in the presence and the absence of an adapting modulation. Temporal contrast adaptation, as in all adaptation processes, involves feedback mechanisms.

Unlike spatial contrast adaptation, temporal contrast adaptation does not only occur at stimulus frequencies that are close to the adapting frequency (Smith, 1971). Instead two (Cass & Alais, 2006) and possibly three (Mandler & Makous, 1984) temporal frequency channels are proposed. A low temporal frequency channel (up to about 4 Hz) probably has a cortical origin because cortical neurons respond only at these temporal frequencies. A high temporal frequency channel probably has a sub-cortical origin. In psychophysical experiments in which the effects of masking gratings on the detection of target gratings were measured, the two channels were found to have distinct properties: low temporal frequency masking gratings affected the detection of targets only when the two gratings had the same orientation. In contrast, high temporal frequency masks were effective in changing target detection for iso-oriented and cross-oriented gratings (Cass & Alais, 2006). These data are in agreement with the notion of a low temporal frequency channel with cortical origin and a high temporal frequency channel that has a sub-cortical origin. It was found that LGN cells belonging to the magnocellular but not those of the parvocellular channel show contrast adaptation to luminance stimuli (Solomon, Peirce, Dhruv, & Lennie, 2004).

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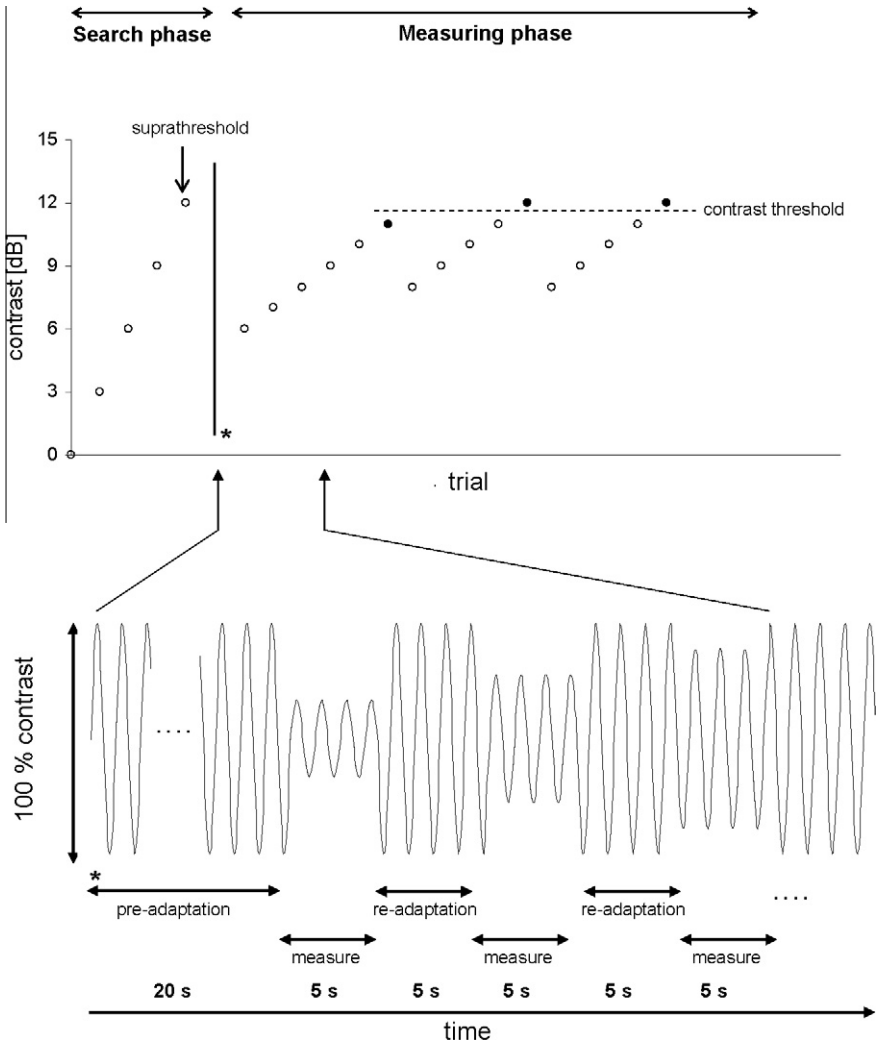

Fig. 1. Upper plot: A schematic drawing of the strategy for determining threshold contrast. A search phase was used prior to the actual measurements to approximate the threshold contrast. The measuring phase started about 6 dB below the estimated threshold. In the measuring phase the contrast was increased in 1 dB steps when the stimulus was not detected. After detection of the stimulus, the contrast was decreased by 3 dB. The threshold was the mean of the contracts of the three presentations that were detected. Lower sketch: Sketch of the presentation procedure in the measuring phase. After a pre-adaptation (20 s) with a 100% contrast adapting stimulus the measuring and re-adaptation periods were presented alternately for 5 s.

Temporal contrast adaptation that occurs in the retina probably involve feedback mechanisms with an inner retinal origin (Freeman, Grana, & Passaglia, 2010). But temporal contrast adaptation may also be present in cortical areas. It is not known, however, if a psychophysically measured temporal contrast adaptation has a cortical or a subcortical (and probably retinal) origin. Because cortical mechanisms are more specialized for processing specific aspects of the visual scene it can be expected that cortical contrast adaptation has more specific effects (Dragoi, Rivadulla, & Sur, 2001; Dragoi, Sharma, & Sur, 2000; Movshon & Lennie, 1979), whereas retinal adaptation processes would have a more general effect. As a result, if psychophysical contrast adaptation would have a cortical origin then adaptation to a temporal frequency can be expected to have an effect on the sensitivity to this particular temporal frequency leaving the sensitivities to other temporal frequencies unchanged. On the other hand, psychophysical contrast adaptations with a retinal origin would result in a more general sensitivity change at all temporal frequencies.

The aim of the present study was to measure the influence of adaptation frequency on the magnitude of adaptation on the temporal contrast sensitivity (TCS) of a modulating test stimulus. The temporal frequencies of both adaptation and test stimuli were at least 9 Hz, so that adaptation likely had a sub-cortical origin. Luminance stimuli were used, to which only magnocellular cells adapt (Solomon et al., 2004).

Because, as mentioned above, adaptation probably involves inner retinal mechanisms, a more complete description of the effects of the influence of adaptation on TCS may help in choosing the optimal conditions for diagnosing disorders of the inner retina. The adaptation frequency that most effectively changes the TCS could be the condition of choice for finding disease related changes in adaptation effects.

With a modified version of the ‘‘Erlangen flicker test’’ temporal contrast adaptation can be studied psychophysically. The ‘‘Erlangen flicker test’’ is a full-field temporal contrast sensitivity test, which uses a Xenon-arc lamp for lighting and a sinusoidally flickering white light as stimulus (Horn, Jonas, Korth, Junemann, & Grundler, 1997; Horn, Korth, & Martus, 1994; Horn, Link, Dehne, Lammer, & Junemann, 2006; Nguyen et al., 2002). In the present study, this test set-up has been modified. The illumination of the full-field bowl was achieved by white light emitting diodes. Because the ‘‘Erlangen flicker test’’ involves luminance modulation the subcortical mechanism, underlying the psychophysical test, probably resides in the magnocellular (M-) pathway (Horn et al., 2006; Korth et al., 2000).