



The temporal course of recovery from brief (sub-second) adaptations to spatial contrast

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ABSTRACT

Visual adaptation is a critical and ubiquitous mechanism that occurs for any stimulus feature and involves a continuous adjustment of the neuronal contrast gain. These adjustments prevent our visual system from dropping in sensitivity for the prevailing ranges of stimulus features that are processed at a given time. In addition to the classical adaptation, which arises over several seconds to minutes, a number of psychophysical, electrophysiological and interference studies have documented a much faster form of adaptation occurring with motion stimuli. This faster adaptation operates on a sub-second scale. In the present study, we investigated whether a fast form of adaptation also exists for spatial contrast and whether its characteristics (e.g., dependence on the duration of adaptation, time course of recovery) are similar to the classical, slower contrast adaptation. We found that a fast form of adaptation does exist and is maximal at intervals of 16–50 ms after the offset of the adapting stimulus. Similar to what previous studies have found regarding the classical contrast adaptation, the initial threshold elevation of this study did not depend on the duration of the adapting stimulus, but only on its contrast. Our results showed that the function which best describes the decay of brief adaptations to high-contrast stimuli was a double exponential decay function, whereas the best function for describing adaptation to low-contrast stimuli was a single exponential decay function with a very fast recovery rate. Thus, adapting contrast influences both the threshold elevation, which rises with increasing adapting contrast, and the time course of recovery from adaptation. Overall, our data suggest the presence of a mechanism that is similar to the classical contrast adaptation involved in longer adaptations, but it operates over much shorter timescales.

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1. Introduction

Visual adaptation is one of the most important functions of the visual system, because it produces relevant perceptual outcomes (Kohn, 2007; Krekelberg, Boynton, & van Wezel, 2006). For example, studies of cats and monkeys' striate cortices (Ohzawa, Sclar, & Freeman, 1985; Sclar, Lennie, & DePriest, 1989) showed that cortical cells can adjust their gain to the prevailing contrast level. Adaptation shifts the contrast response function to another operating range, thereby increasing the slope of the function and thus the sensitivity of the system in the other contrast range (Heeger, 1992). Traditionally, studies have investigated the effects of adaptation by using long stimulus durations (ranging from seconds to minutes; for a review, see Mather et al., 2008). However, other studies have observed neurophysiological and psychophysical evidence that adaptation occurs not only over long time periods, but also at a variety of timescales, indicating that even a few

milliseconds of stimulus presentation can produce adaptation (Campana et al., 2011; Chance, Nelson, & Abbott, 1998; Glasser, Tsui, Pack, & Tadin, 2011; Kanai & Verstraten, 2005; Pavan et al., 2009, 2010; Priebe, Churchland, & Lisberger, 2002; Priebe & Lisberger, 2002; Varela et al., 1997, 1999).

In the present study, we investigated the time course of recovery from brief adaptations to spatial contrast in order to assess whether brief adaptations exhibit the same dynamics as do longer adaptations but over different timescales. A striking number of studies (for a review, see Foley & Boynton, 1993) have investigated the timescales of contrast adaptation. Again, most of these studies assessed the recovery functions after long adaptation durations. Greenlee et al. (1991), by using a contrast detection task (i.e., yes/no task), adapted subjects to flickering gratings presented for either 1, 10, 100 or 1000 s. Overall, their results showed that: (i) the recovery function from contrast adaptation was approximated by a power function that is a linear function on log–log coordinates (i.e., log contrast threshold vs. log recovery time; for similar results see Blakemore & Campbell, 1969; Blakemore & Nachmias, 1971; Georgeson & Harris, 1984; Stecher, Sigel, & Lange, 1973; Swift &

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Smith, 1982; Tolhurst, 1972); and (ii) across all the adapting contrast levels, the recovery function was invariant/independent of all adapting durations employed, as the slope of the (log–log) linear recovery function was represented by a single decay constant for all the adaptation durations. The recovery functions were parallel, but those relative to the higher adapting durations were shifted upwards with respect to the functions relative to the lower adapting durations. Thus, the time required to complete recovery depended on the adapting time but not on the initial threshold elevation, whereas the slope of the recovery function depended on the adapting contrast, but not on the adapting time. Other studies have similarly pointed out that desensitization (i.e., threshold elevation) and recovery from contrast adaptation varied linearly in log–log coordinates (Magnussen & Greenlee, 1985; Rose & Evans, 1983). From this perspective both desensitization and recovery from contrast adaptation can be described as a power function of time.

Other studies, however, have shown that different functions could describe the time course of desensitization and recovery. For example, Bodinger (1978) found that the recovery function was described by a sum of two exponential decay functions. One of these exponential functions has a time constant of a few seconds and describes the earliest part of the recovery, whereas the other exponential function has a much longer time constant and describes the later stage of the recovery. Hammett, Snowden, and Smith (1994) showed similar exponential decays from initial contrast threshold elevation, but they demonstrated it only for temporal frequencies of the adapting and test patterns above 4 Hz. Foley and Boynton (1993) using a two-position spatial forced-choice task (2PSFC) and adapting for 200 ms, 2 s and 2 min, found that threshold elevation was very rapid: indeed, the contrast thresholds did not increase much as the adaptation duration increased (~ 1 dB from 200 ms to 2 min adaptation). Moreover, different adapter durations did not produce different desensitization in the first few milliseconds (from 10 to 50 ms) after the offset of the adapting stimulus. It is possible that Foley and Boynton achieved this result because they measured the contrast thresholds immediately or very shortly after the offset of the adapting stimulus (Foley & Boynton, 1993; Georgeson & Georgeson, 1987), whereas other studies (e.g., Greenlee et al., 1991; Magnussen & Greenlee, 1985; Rose & Evans, 1983) measured the contrast thresholds several milliseconds after the adapting offset (e.g., 300 ms after the adapting offset in the case of Greenlee et al., 1991), thus showing a different effect of adapting duration on initial threshold elevation as well as showing different recovery functions. As suggested by Foley and Boynton (1993), power functions can hardly describe the recovery function for very short inter-stimulus intervals (ISIs), since these functions should imply that thresholds would tend towards infinity immediately after the adaptation period. Moreover, they found that the relation between contrast threshold elevation and recovery function could be described accurately by a weighted sum of two decay exponential functions, with the shorter decay constant (50–100 ms) that was independent of adaptation duration and the longer decay constant (above 1 s) that increased with the adapting duration. Contrarily to what Hammett, Snowden, and Smith (1994) had observed, Foley and Boynton also pointed out a relatively small effect of the temporal frequency of the adapting pattern on the initial threshold elevation over a range of 0–15 Hz.

In the present study, by using a yes/no contrast detection task similar to that used by Greenlee et al. (1991), we assessed: (i) the timescales of desensitization and recovery from brief adaptations to spatial contrast, focusing on sub-second adapting durations; (ii) whether the recovery functions can be described by a power function or an exponential decay function (or a sum of two decay functions; Bodinger, 1978; Foley & Boynton, 1993) for two levels of adapting contrast (i.e., 19 and 39 dB); and (iii) whether the initial threshold elevation depends on the adapting

durations in the case of brief adaptations. Since Foley and Boynton (1993) showed that the adapter duration beyond 200 ms had no effect on the initial contrast threshold elevation in the first few milliseconds (10–50 ms) after the offset of the adapting pattern, we used initial ISIs of either 16.7 or 50 ms, depending on the contrast of the adapting patterns.

2. Method

2.1. Subjects

Two authors and five naïve subjects participated in the experiment. Subjects sat in a dark room at a distance of 57 cm from the screen. Viewing was binocular. They were instructed to fixate on the center of the screen. All subjects had normal or corrected-to-normal visual acuity. All subjects participated voluntarily, and all received compensation (except for the two authors and one naïve subject). In addition, all participants gave their informed consent prior to their inclusion in the experiment.

2.2. Apparatus

Stimuli were displayed on a 19-in. CTX CRT Trinitron monitor with a refresh rate of 60 Hz. We generated the stimuli with Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997). The screen resolution was 1280×1024 pixels. Each pixel subtended ~ 1.9 arc min. The minimum and maximum luminances of the screen were 0.2 and 101.05 cd/m², respectively, and the mean luminance was 46.7 cd/m². Luminance was measured with a Minolta LS-100 photometer. A gamma-corrected lookup table (LUT) was used so that luminance was a linear function of the digital representation of the image.

2.3. Stimuli

The adapting stimuli consisted of vertically oriented sinusoidal gratings (size: 11×11 deg) that were presented for a duration of 200, 400 or 800 ms. The sinusoidal gratings had a spatial frequency of 3 cycles/deg (Greenlee et al., 1991). The initial spatial phase was randomized across trials and reversed as a sinusoidal function of time at a rate of 5 Hz; that is, the spatial phase of the adapting gratings was changed by 180 deg during the stimulus presentation. The contrast of the gratings was expressed in decibels (dB) relative to 1% (i.e., dB re. 1 = $20 \log_{10} C$, where C is contrast; Greenlee et al., 1991). The contrast of the adapting stimuli could be either 19 dB (8.913%) or 39 dB (89.13%). Moreover, we used a baseline condition in which the contrast of the adapting grating was set at 0% (see Section 2.4). The test grating was presented for 100 ms and had the same size and spatial frequency of the adapting grating. The initial spatial phase of the test grating was randomized across trials. We varied the contrast of the test gratings on a trial basis with two modified up–down staircases (Levitt, 1971).

2.4. Procedure

The adapting gratings were displayed at the center of the screen and were counterphase flickered at 5 Hz. High-contrast adapting gratings (39 dB), low-contrast adapting gratings (19 dB) and the baseline conditions were presented in separate blocks. Adaptation durations (i.e., 200, 400 or 800 ms) were also varied in separate blocks. Subjects fixed their eyes upon a black point (0.2 cd/m², dia. 0.32 deg) displayed at the center of the screen. The fixation point overlapped with the center of the gratings. After the termination of the adapting stimulus, the presentation of the test stimulus (100 ms) was cued by a brief (16 ms) tone. We used different recovery times (i.e., an ISI) of 50, 150, 450, 1350 and 4050 ms for

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