The time course of contrast adaptation measured with a new method: Detection of ramped contrast

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Abstract. The present study introduces a new method to measure contrast detection thresholds before and after adaptation to contrast. A sinusoidal testing grating increased contrast at a constant rate from an initial subthreshold level. Subjects indicated when the grating was just visible, which terminated its presentation. The stimulus contrast at the time of response was taken as a measure of relative threshold. We used the method to measure the time courses of changes in threshold following adaptation, for several adapting contrasts (9, 19, 29, or 39 dB, ref. 1%) and adapting durations (10, 100, or 1000 s). The buildup and decay of adaptation to contrast was described well by a power function of time. These results agree with previous findings, but are more efficient in terms of subject time. This method promises to be a useful tool for studying the dynamics of adaptation to spatial contrast.

Keywords: contrast adaptation, ramp detection

1 Introduction

Adaptation is a fundamental process that allows the visual system to adjust to the environment; one intensively studied form is contrast adaptation. Viewing a high-contrast pattern causes desensitization to a similarly oriented test stimulus (eg Blakemore & Campbell, 1969; Blakemore, Muncey, & Ridley, 1973), whereas depriving observers of visual input at a specified orientation improves their sensitivity to the deprived orientation (Bao & Engel, 2012; Zhang, Bao, Kwon, He, & Engel, 2009). One account of such findings is that adaptation enables neurons with limited dynamic range to represent a much larger range of contrasts present in the visual world (Gardner et al., 2005; Greenlee & Heitger, 1988; Ohzawa, Sclar, & Freeman, 1985).

The natural environment changes continuously on many time scales. Thus, to be effective, the visual system should be capable of adapting to the changes of the world dynamically with a similar diversity of time scales. To test this possibility in the laboratory, a number of researchers have investigated the time course of contrast adaptation by tracking the buildup and decay of sensitivity changes (ie the threshold elevation aftereffect; Greenlee, Georgeson, Magnussen, & Harris, 1991; Lorenceau, 1987; Magnussen & Greenlee, 1985; Pavan, Marotti, & Campana, 2012).

Staircases are a traditional method for measuring contrast thresholds. Some studies measured the effects of adaptation with multiple interleaved staircases (eg Fang, Murray, Kersten, & He, 2005; Snowden, 1994; Zhang et al., 2009), but because the interleaving limits the temporal sampling of trials, this method may be not able to track the fast dynamics of adaptation's effect. Other studies used a single one-down–one-up staircase to measure the time course of aftereffect (Bao & Engel, 2012; Bao, Fast, Mesik, & Engel, 2013; Greenlee et al., 1991; Vul, Krizay, & MacLeod, 2008). This procedure has a higher sampling rate. However, it does not directly measure the actual strength of the aftereffect, but defines only upper and lower bounds (whether a step was 'down' or 'up', respectively). One solution is to pool trials from a number of repetitions (eg 5–10 repetitions per condition in Greenlee

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et al., 1991) within a range of time bins and then estimate contrast threshold within each time bin by fitting psychometric functions. However, such pooling inevitably causes a loss of temporal precision of the measurement and an increase of subject time.

Another disadvantage of staircases is difficulty in determining a starting test contrast for the first trials following continuous adaptation, because immediate effects of adaptation are dependent on both adaptation conditions (eg adapter contrast and duration, Greenlee et al., 1991) and individual subject sensitivity. Conventional solutions to this issue included using preliminary estimates as a 'best guess' (Greenlee et al., 1991), pilot psychophysical measurements (Lorenceau, 1987), and adopting larger staircase step sizes at the start of testing (Bao & Engel, 2012). Preliminary estimates are likely to be inaccurate unless they are based on pilot measurements, which require additional subject time. Using larger initial step sizes is unable to give a timely and precise estimate of immediate effects of adaptation.

To overcome these disadvantages, in the present study we introduce a new method that we term 'ramp detection'. This method promises to measure contrast threshold time courses in a more convenient and efficient way, since it saves subject time and is free of preliminary guess or additional pilot tests in estimating immediate effects of adaptation. Each trial contains a sinusoidal testing grating whose contrast increases over time. Subjects make a response when the grating is just visible to them, which terminates the trial. The stimulus contrast at the time of response is taken as a measure of threshold. Adaptation to high-contrast stimuli is expected to reduce sensitivity to the test, and thus prolong the response latency and increase the threshold of the postadaptation tests, especially for testing stimuli that are similar to the adapters in orientation and spatial frequency.

To examine the efficiency and validity of this method, we measured effects of adaptation duration (10, 100, and 1000 s) and adapter contrast (9, 19, 29, and 39 dB) on the time course of the recovery of aftereffects. Conditions were similar to the experiment of Greenlee et al. (1991), who used more traditional methods. With fewer sessions per subject (4 sessions per condition as compared with 5–10 sessions per condition in Greenlee et al.'s study), our results mostly replicated Greenlee et al.'s findings, and suggested that the method was particularly useful for measuring aftereffects from longer adapting durations and higher adapting contrasts.

2 Method

2.1 Subjects
Eight subjects (one male and seven females, ages ranging from 23 to 33 years old) participated in the present study. Five were naive to the experimental hypotheses. All participants had normal or corrected-to-normal vision. Experimental procedures were approved by the Institutional Review Board of the Institute of Psychology, Chinese Academy of Sciences, and informed consent was obtained from all subjects.

2.2 Apparatus
Stimuli were presented binocularly on a gamma-corrected CRT monitor (1024×768 resolution at 85 Hz). The display was driven by a Bits# 14-bit video card (Cambridge Research Systems) and calibrated with a Photo Research PR-655 spectrophotometer. To calibrate the display, we measured the luminance gamma curves and inverted them with a look-up table. All stimuli were viewed from a distance of 57 cm in a dark room, and a chin-rest was used to minimize head motion. The monitor mean luminance was 44.49 cd m^{-2}.

2.3 Stimuli
Stimuli were sinusoidal gratings whose edges had been smoothed with a Gaussian filter. The spatial frequency of the gratings was 1.5 cycles deg^{-1}. The patches subtended 5 deg for the testing stimuli and 7 deg for the adapters, and were presented foveally on a mean luminance gray background with a central fixation.

The adapter gratings drifted at 5 Hz, and were oriented either vertically or horizontally. The orientation of the adapter was orthogonal to the drifting directions, and was kept constant throughout the experiment for each subject but was counterbalanced across subjects. To minimize motion aftereffect, drifting direction was randomly determined for the first 5 s of every 10 s period, while in the other 5 s the grating drifted to the other direction. Randomization made it difficult to predict the drifting direction, allowing relatively constant attentional level over time, especially during longer adapting duration conditions.

The test stimulus was a vertical or horizontal grating. The test contrast increased logarithmically from 0.05% to 12% over a period of 3.5 s (13.6 dB s^{-1}).

2.4 Procedure

Each session started with a pretest where no adapter was presented. Subjects were asked to fixate on a black circle (0.48 deg). A brief tone cued the start of each trial. After a randomly selected delay (100∼700 ms), a stationary test grating appeared whose contrast progressively increased. Its spatial phase was randomized across trials. The orientation of the grating was either horizontal or vertical, selected randomly on each trial, to avoid anticipation of any particular orientation.

Subjects pressed a key as soon as they were just able to perceive the grating. The button press terminated the presentation of the test grating, and presentation of the next trial followed after a 200 ms delay. If no response was made after 3.5 s, then the test grating was removed and the next trial began.

To establish a relatively stable response criterion, subjects practiced the baseline measurements intensively (0.65 ± 0.24 h, around 20 two-minute practices) before running the formal experiment. The variation of the baseline thresholds in the formal experiment reflected the response variation of the ramp detection method, which in turn could be used to examine the reliability of the measured adaptation effect. The immediate effects of adaptation (the values at 1 s on the fitted regression lines) were then compared with the baseline thresholds.

Subjects performed two blocks of trials in each session, a 120 s pretest which was run following 60 s of viewing the mean field, and a 180 s posttest which followed a variable number of seconds of viewing an adapting grating. The first posttest trial started 200 ms after the offset
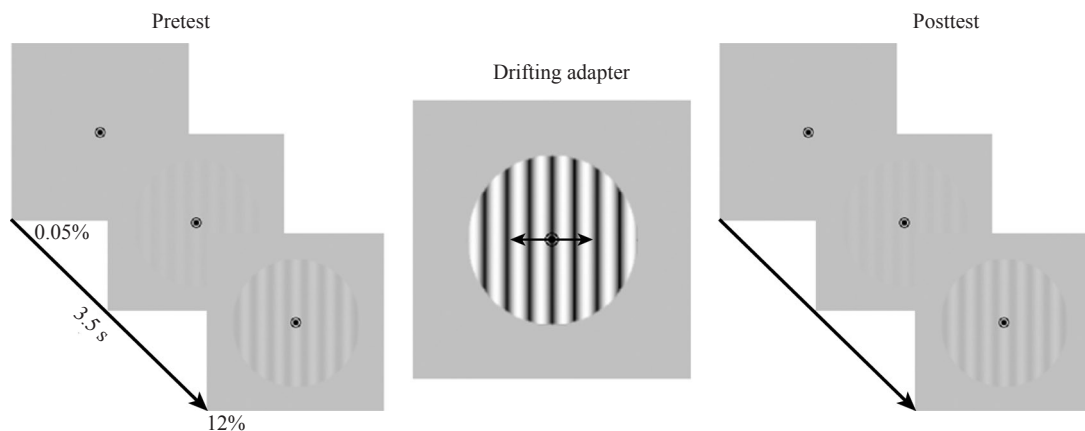

Figure 1. Experimental procedure and stimuli. In each pretest and posttest trial a test grating appeared with contrast ramped up logarithmically from 0.05% to 12%. Subjects indicated when the grating was just visible, which terminated its presentation. The orientation of the grating was either horizontal or vertical, selected randomly in each trial. After a 120 s pretest, subjects were exposed to a drifting adapter for 10, 100, or 1000 s with a contrast of 9, 19, 29, or 39 dB. The orientation of the adapter was horizontal or vertical but remained the same for each subject. Following adaptation, a 180 s posttest started which was similar to the pretest.

of the adapter. Stimuli and timing for the posttest were the same as those for the pretest. During adaptation, the drifting grating was presented for 10, 100 or 1000 s, with a contrast of either 9, 19, 29, or 39 dB [dB = 20 $*\log_{10}(C/0.01)$, where C is absolute stimulus contrast].

Each of the 12 conditions was repeated 4 times, yielding a total of 48 sessions. To minimize the carryover of adaptation effect across successive sessions, subjects had to rest in the normal viewing condition for 10 min, 35 min, and 2 h after the session with adapting duration of 10, 100, and 1000 s.

2.5 *Analysis*

Stimulus contrast at the time of response was taken as a measure of relative threshold. Thresholds in the pretest trials were averaged to estimate a baseline value for each repetition. Thresholds in the posttest were concatenated to form a time series that was used to track the time course of the aftereffect as it recovered. Raw data from the 4 repetitions of the same condition were first pooled to create a single vector of time and threshold pairs.

Functions were then fitted to the pooled data. Because subjects were more sensitive later in the time course, they responded more quickly, and there were many more data points at longer times. Since the error term of traditional functional fitting is weighted by the number of points, we divided the later stage of the posttest into time bins, whose widths were constant on a log scale, and then averaged values within each time bin. These averages along with the raw data from the initial part of the time course, were used for function fitting. A histogram analysis indicated that in most (~75%) cases 3 data points for the adapting orientation were measured within the first 10 s following adaptation, and on average the third trial ended 8.52 s after adaptation. We began binning the data following 8.52 s, and the bin width was 0.205 log s, which insured a roughly equal number of data points in each bin. Note that the linear width of time bin depended on where the time window was located on the log axis. For example, the four points [0.205 0.410 0.615] determine 3 time bins with equal width (0.205 log s) on the log axis. Transformed back to the linear axis, these four points would be [1 1.60 2.57 4.12]. The linear widths of the 3 time bins become 0.60 s, 0.97 s, and 1.55 s. A t-test comparison suggested that in the 10 s and 100 s conditions the effects of adaptation did not differ significantly from the baseline in the last two data points (10 s: $t_{63} = 0.93$, $p > 0.35$, 100 s: $t_{63} = -0.08$, $p > 0.93$), so the last two data points of all conditions were removed when fitting with power and exponential functions. Keeping the last two data points for the 1000 s condition did not produce different results.

Both power and exponential functions were then fitted to each subject's binned time series using MATLAB's fminsearch routine. The values at 1 s on the fitted regression lines of the power function were regarded as the immediate, maximal effect of adaptation, and were then entered into a 3 (adapting duration) × 4 (adapting contrast) ANOVA.

To fit pooled data across subjects, each subject's binned time series was nearest-neighbor interpolated with a step size of 0.205 log s, and then the grand average time series of each condition was fitted with a power function. For contrast conditions of 29 and 39 dB, which had robust adaptation effects, a one-way ANOVA was used to compare the slopes of fits among different adapting durations. If there was no significant main effect of adapting duration, we further refitted the individual and grand average time series but constrained the slope to be the same across adapting durations (Greenlee et al., 1991).

A successful refitting with a common slope for different adapting durations indicates that adaptation simply shifts the recovery function to the right on log–log axes (Greenlee et al., 1991). If this is the case, and the shift is by an amount proportional to the adapting duration, then plotting all grand average time series as a function of 't', where $t = \log_{10}$(recovery time/adapting duration), should cause the data to fall onto a single regression line.

In addition to a power law fit, we also fitted the individual and grand average time series with an exponential, in order to determine which function described the data better. The goodness of fit on the individual data for the two models was compared using a paired *t*-test.

3 Results

Before and after adaptation to contrast, we used our new 'ramp detection' method to measure subjects' detection thresholds. The method allowed us to characterize the time courses of threshold changes under different adapting conditions. Figure 2 shows the raw time series of one subject's 100 s–39 dB and 1000 s–39 dB adapter conditions, with data pooled from all 4 repetitions.
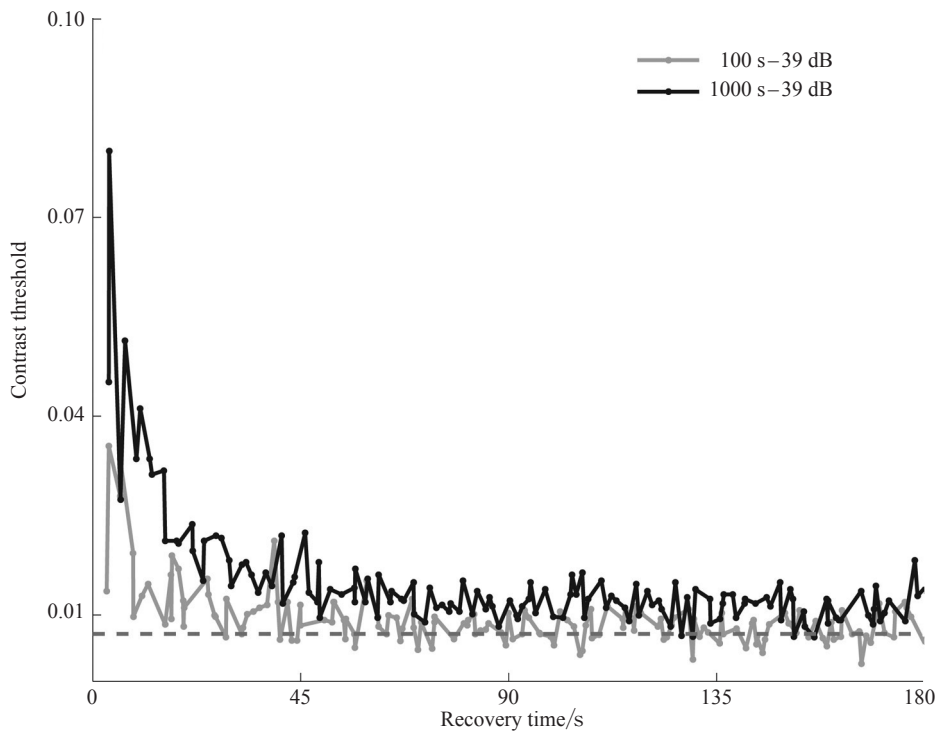

Figure 2. The time course of the effect of adaptation from one subject after adaptation to the 39 dB contrast for 100 s and 1000 s, respectively. The contrast threshold is defined as 1 for full contrast and 0 for the mean field. The dashed line represents the baseline.

Effects of adaptation on detection thresholds were estimated by fitting functions to the time series (see methods). To identify which conditions generated reliable adaptation effects, we compared thresholds immediately after the end of adaptation to the baseline. As shown in table 1, the immediate adaptation effects were significantly above baseline in most conditions

Table 1. Comparison between *t*-statistics for immediate adaptation effects versus baselines (df = 7).

Adapt/dB	Adapt/s		
	10	100	1000
9	2.06	4.96**	7.69***
19	2.69*	5.82**	5.02**
29	4.90**	9.46***	12.01***
39	10.63***	21.20***	13.72***

*p < 0.05; ** p < 0.01; *** p < 0.001.

except the 9 dB–10 s condition, plausibly because adaptation effects for that condition were not robust enough to survive the variation of response. Robust adaptation was present in all the 100 s and 1000 s conditions. Note that insufficient sensitivity of measurements often produces negative results, and so should not necessarily lead to the conclusion that exposure to 9 dB contrast for 10 s is unable to produce adaptation.

Analysis of the immediate adaptation effect of all conditions disclosed a main effect of adapting contrast ($F_{3,21} = 47.35$, $p < 0.001$) and adapting duration ($F_{2,14} = 78.25$, $p < 0.001$). There was also a significant interaction ($F_{6,42} = 6.01$, $p < 0.001$; see figure 3a). However, as shown in table 1, robust effects of adaptation were not reliably observed in some conditions of shorter adapting duration and lower adapting contrast. To avoid the bias from these weak adapting conditions, we performed the ANOVA on the conditions with 9–39 dB adapting contrast and 100–1000 s adapting duration, and found no significant interactions. The main effects of adapting contrast ($F_{3,21} = 54.13$, $p < 0.001$) and adapting duration ($F_{1,7} = 19.00$, $p < 0.01$) remained significant (see figure 3b), suggesting that contrast threshold elevated with the increase of adapting contrast and adapting duration.
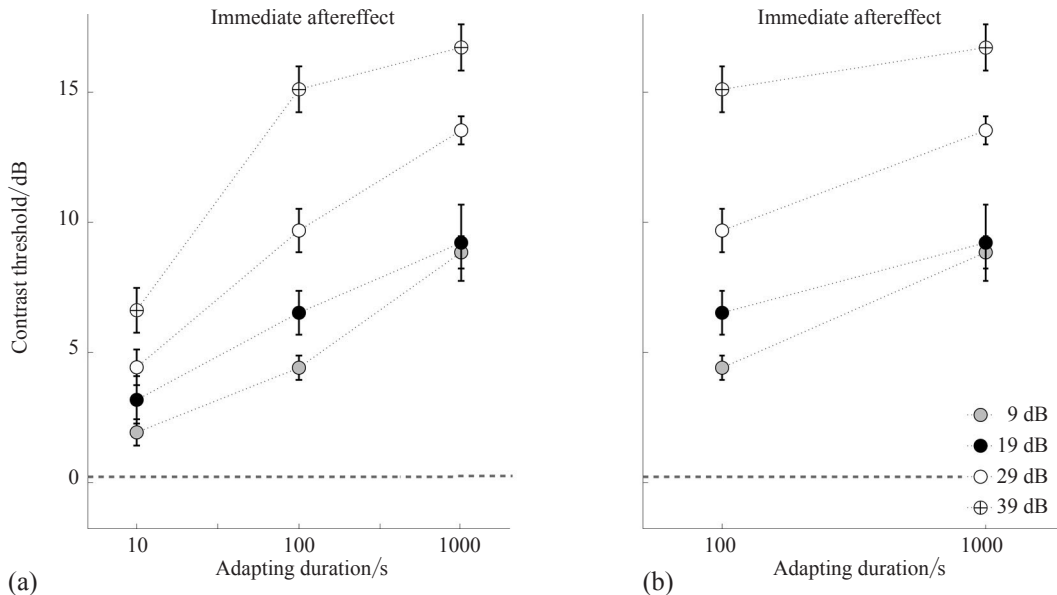

Figure 3. (a) The immediate adaptation effect as a function of adapting contrast and duration. (b) The same plots as in (a), but the data points of all the 10 s conditions (9–39 dB) were excluded. Error bars represent standard error of the mean.

3.1 *Power law recovery of adaptation*

To characterize the time course of the recovery of adaptation, we fitted power functions to the across-subjects grand average time series of threshold values that followed the end of adaptation. The slopes of the fits did not differ significantly across the various adapting conditions, and so we refitted the data but constrained the fits to use a common slope for different adapting duration conditions (see figure 4). This power function fit, which is linear when both axes are logarithmic, accounted for more than 92% of the variance in the data (9 dB: 92.96%, 19 dB: 94.10%, 29 dB: 95.71%, 39 dB: 93.24%). By contrast, an exponential function explained only 42% of the variance. The good fit of the power functions to the recovery curves is consistent with previous work (Greenlee et al., 1991; Magnussen & Greenlee, 1985). To test this statistically, we fitted data from individual subjects with both types of curves, and found that power functions reliably explained more of the variance than did exponentials (table 2).
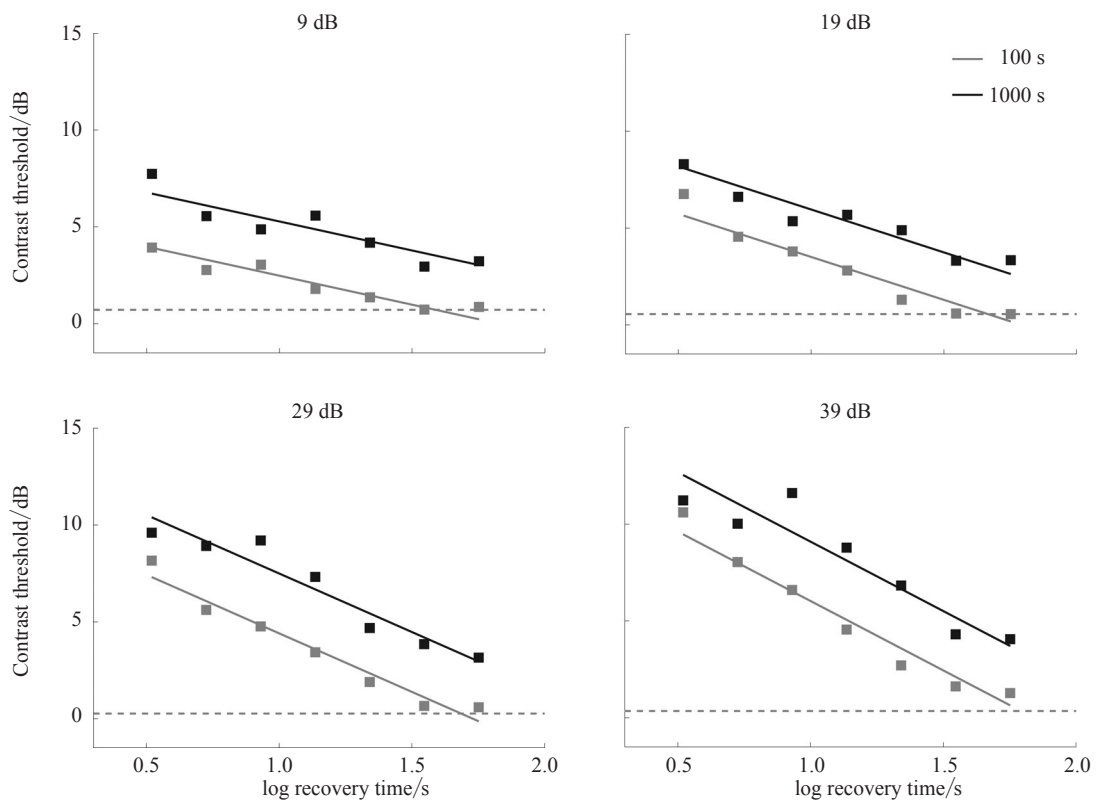
Figure 4. Binned grand average time courses of effects of adaptation. The time courses of threshold (contrast thresholds in dB, re. 1%) changes were fitted with a power function which was constrained by using a common slope for different adapting contrast conditions. Fits explained more than 92% of the variance in each curve (9 dB: 92.96%, 19 dB: 94.10%, 29 dB: 95.71%, 39 dB: 93.24%), which suggests that effects of contrast adaptation decay as a power function of the recovery time.

Table 2. Comparing *t*-statistics of goodness of fit for power versus exponential functions for each subject (df = 7).

Adapt/dB	Adapt/s		
	10	100	1000
9	2.50*	2.67*	3.86**
19	2.54*	4.81**	3.71**
29	3.26*	10.86***	5.76***
39	6.96***	9.67***	8.22***

*$p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.
Note: Power functions described each subject's recovery function better than exponentials, especially in the conditions of longer adapting duration and higher adapting contrast.

3.2 *Effects of adaptation duration and contrast*

The parallel curves shown in figure 4 suggest that the effect of increasing adapting duration is to shift the time courses measuring recovery from adaptation to the right along the log time axis. This would correspond to a multiplicative scaling of time by a constant, such that every *x* s of recovery following shorter adaptation would correspond to *cx* s of recovery following longer adaptations. If increasing adapting duration simply shifts the recovery function to the right along the horizontal axis by an amount proportional to the adapting duration,

then plotting the data as a function of t, where $t = \log_{10}$(recovery time/adapting duration), should align the data from all adapting durations along a common curve (Greenlee et al., 1991). Figure 5 plots the data as a function of t, and a single linear fit (which represents a power function since both axes are logarithmic) does account for the data well, explaining more than 78% of the variance on average (9 dB: 92.86%; 19 dB: 86.35%; 29 dB: 85.85%; 39 dB: 78.87%). Since the time course of the threshold changes was better described by a power law than an exponential, the fits on the log–log axes were essentially linear. Therefore, a vertical multiplicative shift could also account for the results of parallel curves for different adapting durations.
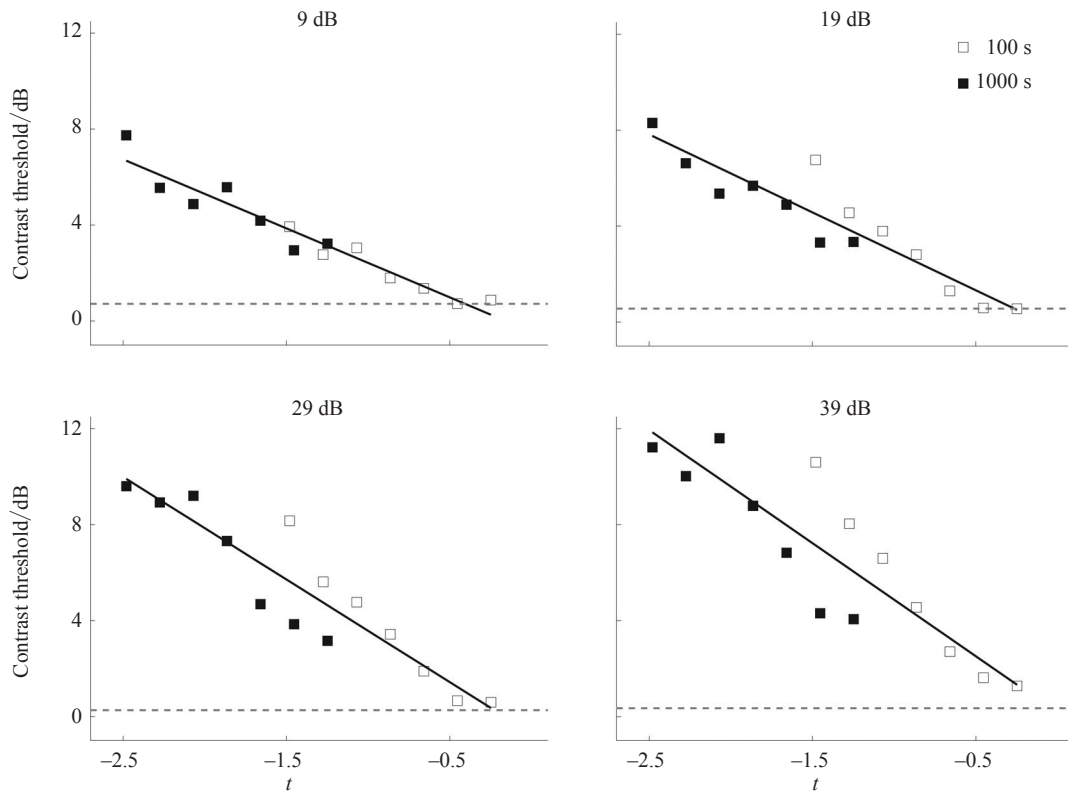

Figure 5. Grand average data plotted as a function of t, where $t = \log_{10}$(recovery time/adapting duration). After the recovery time was normalized by adapting duration, the fits converged to a single curve. A linear fit accounted for more than 78% of the variance and indicated that increasing adapting duration shifted the recovery function to the right along the horizontal axis.

To examine the influence of adapting contrast on recovery from adaptation, time series for each adapting contrast were fitted as separate functions of t for 100 s and 1000 s of adapting durations, respectively (figure 6). The fits were again linear on log–log axes, representing a power function. The fits were good overall (ranging from 84.02% to 96.59% of the variance explained) and tended to converge at a common x-intercept. Constraining the fits to have a common intercept reduced the percent variance explained only slightly. Constrained fits explained 82.09% to 96.11% of the variance, on average only 1.20% less than the unconstrained fits (maximum reduction: 5.19%). Consistent with Greenlee et al. (1991), these results indicate that, after adapting to a grating for the same amount of time, the time required for thresholds to reach the unadapted level was not much affected by the adapting contrast. In order to achieve this, however, the slope of the decay functions varied substantially wit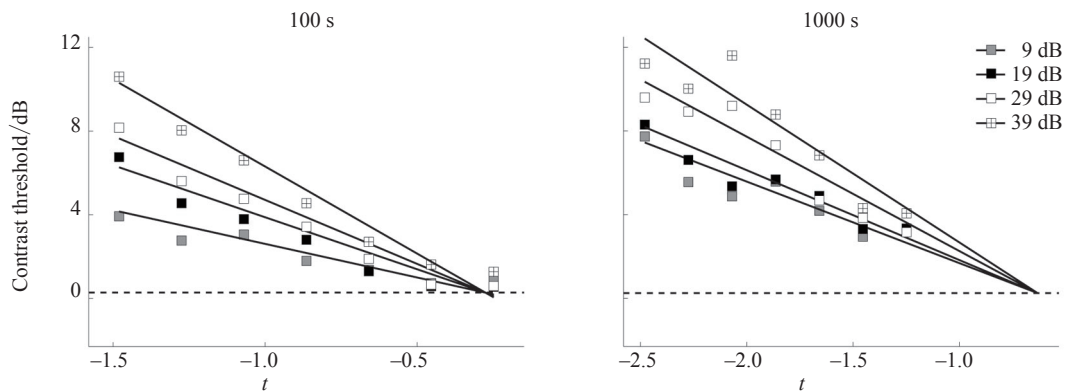h the adapting contrast (100 s: $F_{3, 28} = 10.72$, $p < 0.001$; however, it was nonsignificant for 1000 s: $F_{3,28} = 0.62$, $p > 0.6$).

Figure 6. Time series for each adapting contrast as a function of *t* were fitted with power functions constrained to have a common *x*-intercept. Results are shown for two adapting durations. The fit accounted for more than 82% of the variance overall, suggesting that adapting contrast did not affect the recovery time *t*, but significantly modulated the slopes of the fits.

4 Discussion

In the present study we have developed a new method to measure contrast thresholds by using response time. The contrast of a test grating ramped up at a constant rate, and subjects responded when the test was visible. We used the contrast presented during the response as our measure of relative threshold. We used this method to track the time course of threshold changes following adaptation to varied spatial contrasts for different adaptation durations (a set of parameters used in a previous study, Greenlee et al. 1991).

Our results revealed robust aftereffects of adaptation that increased in strength with increasing adapter duration and contrast. The recovery function of the adaptation effect observed in the present study was described well by a power function. The main effect of adapter duration was to shift the functions along the log–time axis, and the main effect of adapter contrast was to increase the rate of recovery.

These results closely resemble the findings in Greenlee et al.'s (1991) study with similar parameters and design but a different method of threshold measurement, suggesting that our method is a valid measure of contrast threshold. It should be noted that which function (eg power or exponential) best describes recovery from adaptation is still under debate (Bodinger, 1978; Foley & Boynton, 1993; Greenlee et al., 1991; Ho & Berkley, 1988; Lorenceau, 1987; Magnussen & Greenlee, 1985; Pavan et al., 2012; Rose & Evans, 1983). The goal of the present study is not to resolve the debate, but to validate the ramp detection method by comparing Greenlee et al.'s (1991) findings with ours.

It is interesting that varying the adapting contrast altered the slope but not the duration of the decay functions. This was observed first in Greenlee et al.'s 1991 paper and replicated in ours, indicating that adapting duration was the main determinant of how long the aftereffect will persist. Systematically investigating the underlying reason is beyond the scope of the present study, but we tend to interpret it using the idea that multiple mechanisms control visual adaptation (Bao & Engel, 2012; Bao et al., 2013; Mesik, Bao, & Engel, 2013). According to our model (Bao & Engel, 2012), the longer the visual system adapts, the stronger those mechanisms with longer time scale activate. Aftereffects caused by those longer term mechanisms are also expected to persist for longer. However, adapting contrast is thought to inform the visual system about which responsiveness level the neurons should adjust to. Accordingly, adapting contrast is mainly responsible for the strength of aftereffect. Future work is needed to systematically address this issue.

A close examination of the curves in figure 5 revealed worse fits for the higher contrast adapters than for the lower contrast adapters. In the high-contrast plots, the 1000 s condition appeared to be systematically to the left of 100 s condition. Interestingly, this same phenomenon was present, though uncommented upon, in Greenlee's et al.'s original study (see their figure 3). This leftward shift of the 1000 s condition means that adaptation was weaker than expected (note equivalently that the 1000 s data points were below the 100 s points on the part of the curve that overlaps). Why might adaptation for 1000 s be weaker than expected? It is possible that adaptation could show a law of diminishing returns, where longer durations produce less adaptation than expected, but this would be expected to be equally visible at all contrast levels. One speculative reason for adaptation to be lower than expected at only high-contrast levels is that some component of it may have asymptoted, leaving total adaptation below what it would have been otherwise. For example, our prior work suggests that adaptation is likely controlled by multiple mechanisms tuned to different time scales, whose summed activity sets overall adaptation (Bao & Engel, 2012; Bao et al., 2013; Mesik et al., 2013). It is possible that the shorter term mechanisms asymptote at high-contrast values, leading them to make smaller than expected contributions to the total for longer durations.

Unlike the results of Greenlee et al. (1991), there was no significant threshold elevation after adaptation to 9 dB contrast for only 10 s. Our pilot experiment on three subjects failed to find reliable immediate effect for adapting duration of 1 s, either. One recent study demonstrated that subsecond exposure to spatial contrast could induce adaptation, but these effects decayed as fast as 50 ms (Pavan et al., 2012). Foley and Boynton (1993) also found very rapid (~200 ms) desensitization of short-term adaptation (eg 2 s). Such short-lived effects are often labeled 'masking' in the literature. Considering the random intertrial interval (0.1–0.7 s) in the present study and that it usually takes about 1 s for the stimulus contrast to increase to be just visible in the unadapted condition, very brief adaptation would not be captured by the ramp detection method. Moreover, response variability is present among even well-practiced subjects, which could swamp weak adaptation effects. Accordingly, our method might be particularly suitable for measuring the effect of relatively longer term (eg > 100 s) adaptation and higher adapting contrasts (eg > 29 dB).

Since our method is based on response latency, the measured threshold is likely inflated by the amount of time subjects take to respond following detection. However, our subjects practiced the task intensively before starting our main measurements. This likely helped establish a relatively stable criterion for judgment, making the measured thresholds likely to be offset by a constant amount from true ones. For this reason we refer to our data as 'relative thresholds'.

It should also be noted that the decision criterion problem exists in all subjective measures, including many still in use in the field—for example, matching methods. There are nevertheless times in research when one wishes to use such methods if there is no reason to believe that criteria vary with condition. In our research, 2AFC methods are too time-consuming to adequately delineate the time course of threshold changes following adaptation (eg Zhang et al., 2009). In this and other situations, ramp detection should be a useful complement to current psychophysical methods. In some of these cases it may be worthwhile to test for criterion effects using 2AFC methods for a subset of conditions; for the current work we rely on the many previous 2AFC studies that have documented effects of contrast adaptation (eg Graham, 1989).

One prior study (Lorenceau, 1987) also used response latency to measure the time course of threshold changes following contrast adaptation. The method was mainly used to measure baseline thresholds and the relatively flat parts of decay curves: for the first 5 postadaptation trials a fixed test grating was presented abruptly at one of five predetermined contrast levels.

In addition, the start of ramp contrast in this study varied across trials, being defined as a 10 dB drop in contrast from the threshold at the preceding trial. The current paper validates the response latency method by using it to measure full response curves and comparing the pattern of results with prior work.

In summary, the ramp detection method proposed in the present study is a useful option for measuring the time course of the contrast adaptation effect efficiently and accurately, especially for longer adapting durations and higher adapting contrasts.

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