

**Shading & Texture:
separate information channels with a common adaptation mechanism ?**

Mark A. Georgeson §#

Andrew J. Schofield§

§ School of Psychology, University of Birmingham, Birmingham B15 2TT, UK

#*Present address*: School of Life & Health Sciences, Aston University, Birmingham B4 7ET, UK, e-mail: m.a.georgeson@aston.ac.uk

Abstract

We outline a scheme for the way in which early vision may handle information about shading (luminance modulation, LM) and texture (contrast modulation, CM). Previous work on the detection of gratings has found no sub-threshold summation, and no cross-adaptation, between LM and CM patterns. This strongly implied separate channels for the detection of LM and CM structure. However, we now report experiments in which adapting to LM (or CM) gratings creates tilt aftereffects of similar magnitude on both LM and CM test gratings, and reduces the perceived strength (modulation depth) of LM and CM gratings to a similar extent. This transfer of aftereffects between LM and CM might suggest a second stage of processing at which LM and CM information is integrated. The nature of this integration, however, is unclear and several simple predictions are not fulfilled. Firstly, one might expect the integration stage to lose identity information about whether the pattern was LM or CM. We show instead that the identity of barely detectable LM and CM patterns is not lost. Secondly, when LM and CM gratings are combined in-phase or out-of-phase we find no evidence for cancellation, nor for ‘phase-blindness’. These results suggest that information about LM and CM is not pooled or merged - shading is not confused with texture variation. We suggest that LM and CM signals are carried by separate channels, but they share a common adaptation mechanism that accounts for the almost complete transfer of perceptual aftereffects.

Keywords:

Vision, Shading, Texture, Detection, Adaptation, Tilt aftereffect, Luminance, Contrast, Modulation

Introduction

Spatial variations of shading and texture are clearly both important cues in the process of forming a perceptual representation of object boundaries, surface shape and 3-D form. Our broad aim in this paper is to study some aspects of the linkage between early spatial filtering mechanisms and these later perceptual processes. To do this we have used two kinds of grating pattern (cf. Fig. 2), and have adopted the working assumption that luminance-modulated gratings (LM) and contrast-modulated gratings (CM) are useful probes of the mechanisms underlying the analysis of shading and texture respectively.

Previous psychophysical and physiological work has supported the idea that LM and CM gratings are detected by separate processing channels that might imply a parallel analysis of shading and texture cues. Firstly, there was no facilitation or sub-threshold summation between barely detectable LM and CM gratings, but there was summation between gratings of the same type (Schofield & Georgeson, 1999). Secondly, when detection thresholds for luminance gratings and CM gratings were measured after adaptation to such gratings, there was a highly selective loss of sensitivity. Spatial frequency tuned threshold elevation was substantial only after adaptation to gratings of the same type (Nishida, Ledgeway & Edwards, 1997). Together these findings suggest that detection is mediated by separate, adaptable LM and CM channels.

Other lines of evidence, however, have suggested that LM and CM information may be later integrated in the visual system. Physiological studies of cat visual cortex have revealed that some cells, especially in area 18, respond well to both types of stimulus, but closer analysis of the response selectivities suggested that these cells might be combining the inputs from separate LM and CM analyzers (Zhou & Baker, 1993; Zhou & Baker, 1996). Studies of motion perception have also suggested separate LM and CM analyzers (Ledgeway & Smith, 1994; Lu & Sperling, 1995) in a 2-stage integrative scheme (Wilson, Ferrera & Yo, 1992; Nishida & Sato, 1995) rather like that shown in Fig. 1b. In this paper we ask similar questions about LM/CM integration in spatial vision. The logical possibilities include: no separate channels at all (Fig 1a), entirely separate channels (Fig. 1c), and a hybrid in which separate channels are combined at a later stage (Fig. 1b).

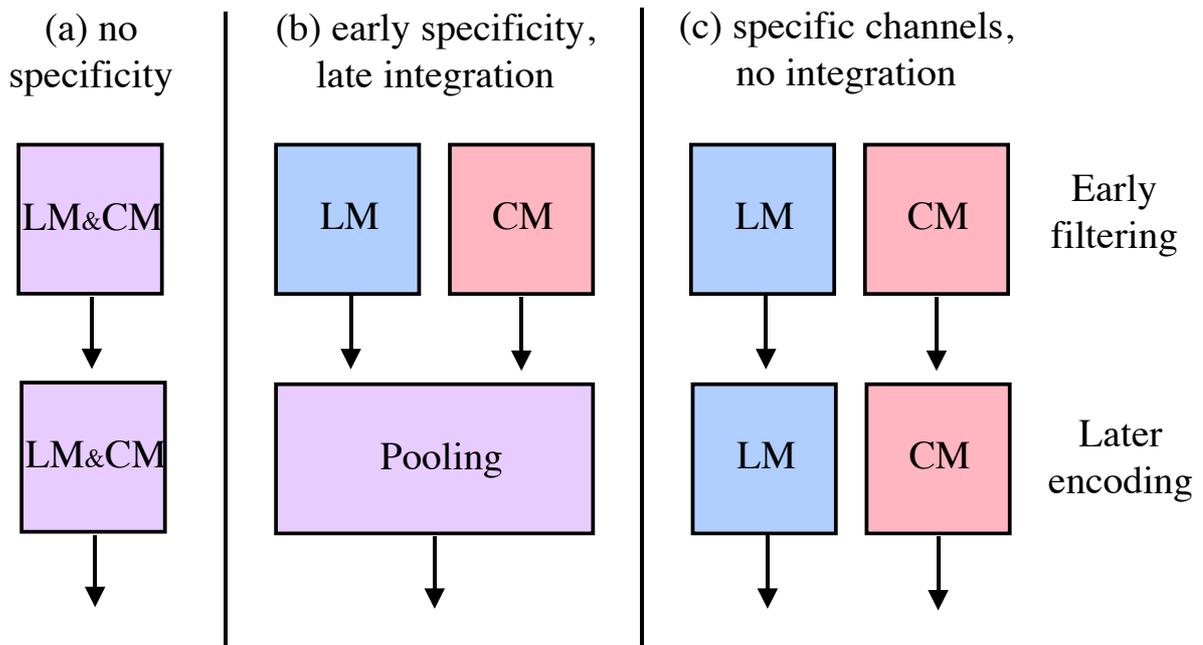


Fig 1. Three views of LM/CM information processing. (a) Common channel, no specificity at any stage; (b) initially separate channels, followed by signal combination with a single output; this is the 'single-channel integration' discussed in the text; (c) separate channels at early and late stages.

We have addressed these questions through two types of experiment. In part 1 (experiments 1 and 2), we look at two perceptual aftereffects from adapting to LM and CM gratings to determine whether adaptation to LM (or CM) transfers to a CM (or LM) test, or not. A high degree of transfer would imply some integrative process. In part 2 (experiments 3 and 4), we compare detection and recognition of LM and CM gratings, without adaptation, but again with the aim of learning about the independence or integration of LM and CM information. Watson and Robson (1981) were the first to suggest that, with certain assumptions, if the ability to recognize (identify) two very weak stimuli (A, B) was as good as performance in detecting them, then this would point to the existence of separate channels for A and for B. This amounts to a 'labelled-line' model, in which the response of one channel (with no response from the other) signals both the presence and identity of the stimulus. The expectation of equal detection and recognition performance holds only when stimuli A and B are sufficiently far apart along some dimension (such as spatial frequency, orientation, etc) to stimulate non-overlapping channels (Graham, 1989). We therefore applied this idea to test for separate LM and CM channels.

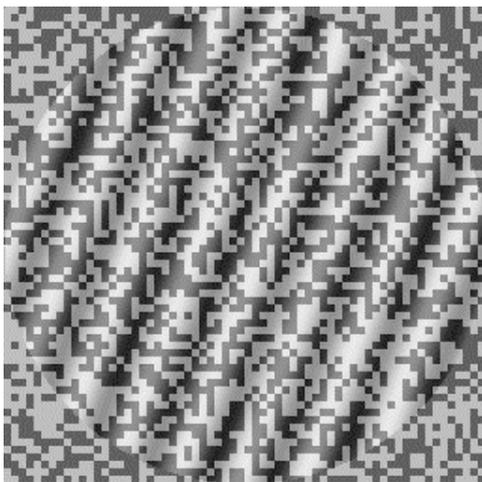
Part 1: Perceptual aftereffects

Experiment 1. The Tilt aftereffect

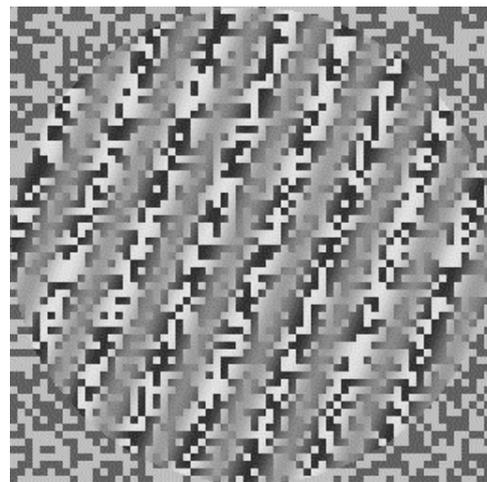
The purpose of this experiment was to measure the tilt aftereffect (if any) for LM and CM gratings, and to determine the extent to which the aftereffect transferred from LM to CM, and vice-versa.

Method

Images were generated and displayed using NIH Image 1.61 software on a Macintosh 7300 computer with a greyscale CRT monitor (Eizo 6600M). The screen luminance (27 cd/m^2) was measured with a Minolta digital photometer LS110, and the internal look-up tables were calibrated both to linearize the system (gamma correction) and to set image contrast to the desired level. Individual images contained 256×256 pixels, and subtended 4 deg at the viewing distance of 136 cm. The rest of the screen (16.4 deg wide, 11.8 deg high) was set to a uniform grey (mean luminance) background. Viewing was binocular, in a dimly lit room illuminated only by the monitor, with head position constrained by a chin and forehead rest.



Adapt LM (0.4)



Adapt CM (0.8)

Fig. 2. Examples of LM and CM adapting gratings tilted 20° clockwise (CW) from vertical.

Examples of the LM and CM adapting images are shown in Fig. 2, at the standard 20 deg adapting orientation. Luminance-modulated (LM) images contained a sinusoidal luminance grating in a circular aperture (4 deg diameter for adapters, 3 deg diameter for test images), added to a binary noise image that filled the whole 4 deg square area of the image. In contrast-modulated (CM) images, the sinusoid was used to modulate the local contrast of the noise, rather than being added to it. The equations that define LM and CM images are given by Schofield & Georgeson (1999). Noise elements were 4×4 pixels (3.75 min arc) square, and the noise contrast was 0.4, except where noted (Table 1). Spatial frequency of the adapting and test images was 2

c/deg. Schofield & Georgeson (1999) found that modulation thresholds were about a factor of two higher for CM than LM under conditions fairly similar to these, and so in an effort to equate the visibility or effectiveness of the two types of grating, the standard adapting and test modulation depths were 0.4 for LM and 0.8 for CM. Where noted, these values were halved to create ‘low’ contrast or ‘low’ modulation depth. Note that halving the overall contrast of an image halves the noise and LM grating contrasts, but does not alter the CM modulation depth. In other cases we selectively halved the LM contrast or CM modulation while keeping the noise contrast fixed at 0.4. The purpose was to ensure that any conclusions about TAE transfer did not depend on the particular contrast and modulation levels used. Table 1 gives a complete specification of the 6 adapting conditions. The condition names aim to summarize the way that the various conditions deviate from the ‘standard’ (condition 2). For example, “LowAdaptCon” means that the adapt contrast was ‘low’ and (by default) the test images were ‘standard’, while “LowTestMod” means that the adapt images were standard and the test modulations (LM or CM) were ‘low’.

Observers fixated the centre of the display binocularly. During adaptation the phase of the adapting modulation reversed abruptly, and the noise switched back and forth between two different random samples, every 0.25 sec to minimize negative afterimages. In each session, the initial adapting period was 2 min, with a ‘top-up’ period of 2 sec after each trial. On each trial, the test grating (LM or CM) was shown for 0.5 s and the observer pressed a key to indicate whether the test grating looked tilted to the left or right of vertical. The boundaries of the test image and the edges of the monitor screen were clearly visible and provided visual reference information for the judgement of orientation. This should exclude non-visual adaptation (such as a change in the sense of gravitational vertical) from contributing to the TAE. A simple staircase procedure (1 up, 1 down) adjusted the test orientation in 1 deg steps from trial to trial by selecting from a set of pre-computed images. The staircase began at a randomly chosen test orientation, and across trials it homed in on the point of subjective equality, at which the test grating looked vertical, taken as the average orientation at the last 10 reversals of the staircase. This procedure estimates the TAE by finding how much physical tilt is needed to null it. Four staircases (2 for LM test, 2 for CM test) were run concurrently within each session. Each adapting condition was run 4 times (twice with clockwise adapting tilt, twice with anti-clockwise), yielding 8 TAE estimates per condition per observer. This design makes it unnecessary to collect unadapted control data (since the latter cancel out when CW and ACW measures of the TAE are combined).

Sessions lasted 8-9 mins, and we allowed at least 20 mins between sessions to minimize carry-over of adaptation from one session to the next. As a further safeguard, the adapting orientation alternated between clockwise and anti-clockwise orientations across sessions so that any residual TAE from one session should be swamped by the opposite TAE in the next. After a few practice sessions, two observers (MVJS, SJG) naïve to the purpose of the study were tested in all 6 different adapting conditions (Table 1) – a total of 48 experimental sessions each. A third observer (ZLC) was tested in conditions 1, 2, 3 and 5 but was unavailable to complete conditions 4 and 6.

Results

All three observers showed clear and consistent TAEs averaging around 3 degrees of tilt for both LM and CM adapting gratings, and the aftereffect transferred very substantially from LM to CM and vice-versa. Table 2 gives results for individual observers and their means for all 6 adapting conditions, and our main finding is summarized in Fig. 3 as the average across conditions 1-3 whose results were quite similar. Fig. 3 shows that when the adapting and test gratings were of the same type (both LM or both CM) the TAE averaged 3.6° and when they were different the TAE averaged 2.8° . We can define the percentage TAE transfer as:

$$\text{Transfer}(\%) = 100 * (\text{Mean_TAE_different}) / (\text{Mean_TAE_same})$$

and from this we get a mean transfer of 77% in conditions 1-3. Table 2 gives more detail and shows that observers consistently showed 60-85% transfer in all cases 1-3.

The similarity of TAE magnitude and its transfer between LM and CM in both the standard and low contrast conditions (1-3) is quite important, since it makes it unlikely that the effects for CM are based on an early visual nonlinear distortion that introduces an effective LM component into the CM grating. Such a distortion product should decrease as the square of contrast (Scott-Samuel & Georgeson, 1999) and so would be 4 times smaller in the low contrast CM conditions. Indeed Scott-Samuel & Georgeson (1999, Fig. 4) measured the amount of distortion psychophysically and their data imply that any distortion products in the present experiments would be tiny - an order of magnitude below the LM detection threshold of about 4% in these conditions (Schofield & Georgeson, 1999).

Modulation depth, however, does appear to influence the TAE, in that low adapting modulation combined with standard test modulation (LM or CM; condition 5) gave about half the TAE when compared with the reverse (condition 4), for both observers tested (Table 2). Weaker adapters give smaller effects, but weaker test gratings show larger TAEs. This is consistent with the

TAE's dependence on relative contrast (adapt:test contrast ratio) observed for noise-free gratings (Parker, 1972; Georgeson, 2000).

Finally, since perceptual aftereffects are subjective phenomena, we should consider the possible role of response bias or expectation. The use of naïve subjects and the nulling method should both minimize expectation, since the observers are not led to expect an aftereffect, and the staircase nulling method always drives the test stimuli to roam around the perceived vertical, with or without an aftereffect. However, it is possible that an observer's responses might be biased by the adapting stimulus. If s/he had a tendency to guess that the test stimulus was tilted in the opposite direction to the adapter, this could produce an 'aftereffect' in the data. We evaluated this possibility by adapting the observers to orientations ± 70 deg from vertical where we should expect similar guessing, but either no genuine TAE, or perhaps a reversed 'indirect effect' (Gibson & Radner, 1937). The mean TAE was very close to zero (Table 2, condition 6), and so response bias is likely to have contributed very little to our data.

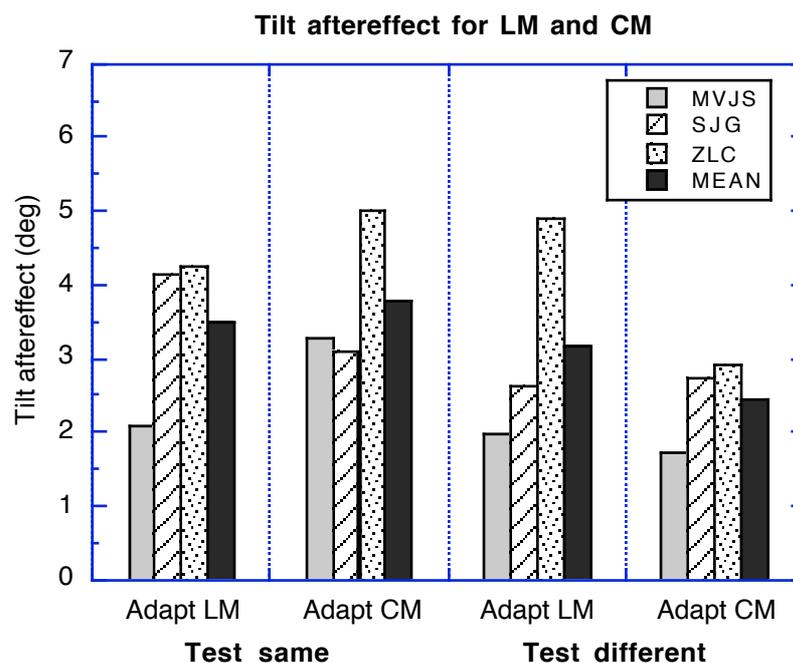


Fig.3. Experiment 1. Tilt aftereffect for the 3 individual Ss, and their mean, averaged over contrast conditions 1-3.

Experiment 2. Contrast reduction aftereffect

Experiment 1 showed strong transfer of the tilt aftereffect between LM and CM gratings. To test the generality of this finding we studied a second aftereffect – the reduction of perceived contrast (or modulation depth) of LM and CM gratings after adaptation to LM or CM.

Method

The display apparatus and staircase procedure were broadly similar to experiment 1, but the task of matching contrast or modulation depth required a pair of test and reference images to be presented side by side, as shown in Fig. 4b. All gratings were vertical.

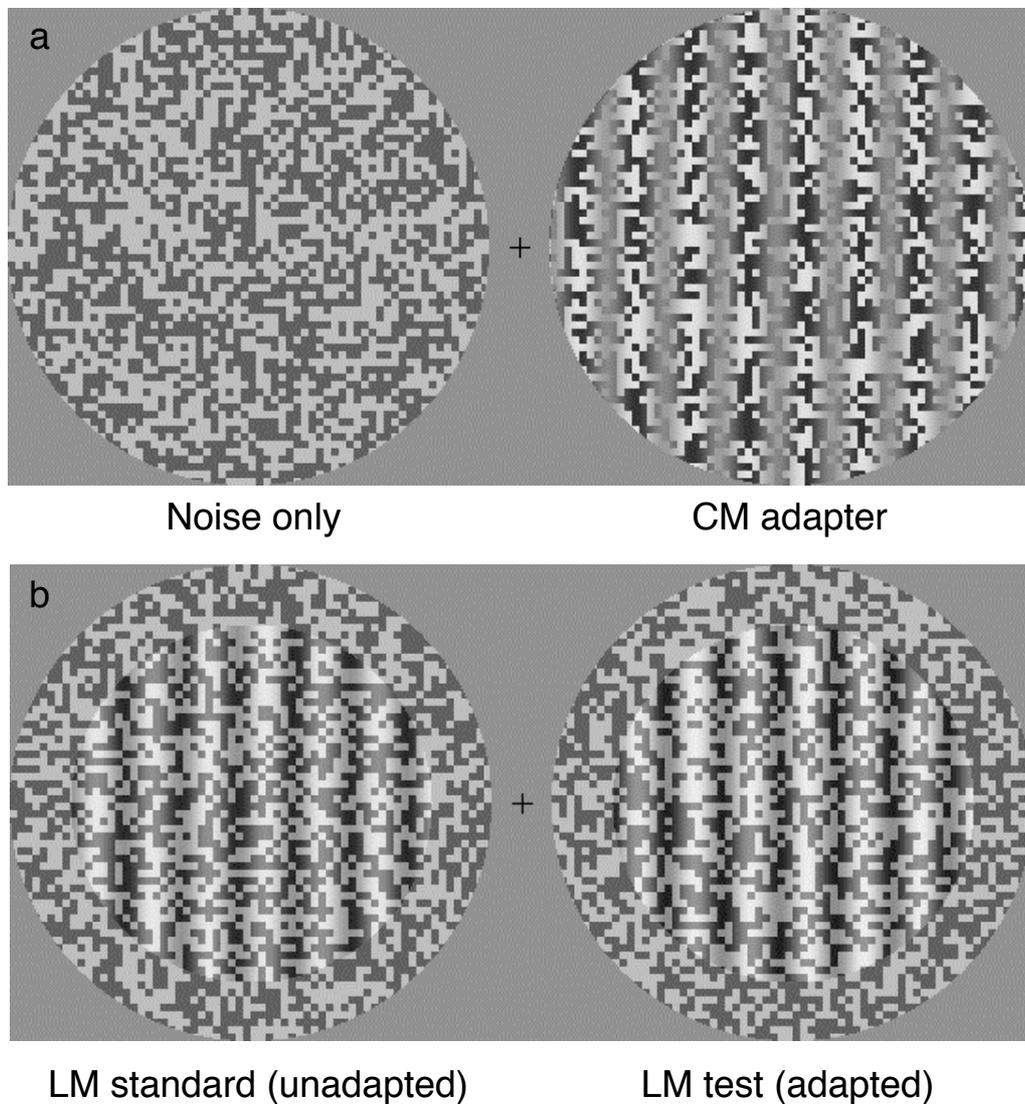


Fig. 4. Experiment 2. (a) example of CM adapting display. (b) example of LM test display

The observer fixated the central cross. The adapter was on the left or right in different sessions while the opposite field contained unmodulated noise. Both the left and right fields subtended 4 deg diameter. As before, the pattern of adapting modulation was 4 deg in diameter, while the test was 3 deg (see Fig. 4). Noise contrast was always 0.4 and spatial frequency 2 c/deg. The adapter was either LM (contrast 0.4), CM (modulation 0.8), or noise-only (control). As in experiment 1, the adapter reversed phase at 2 Hz for 3 mins initially, with a topup period of 2s after each trial. The test pair of images was presented for 0.5s. It consisted of a reference grating on the unadapted (noise-only) side of the display and a test grating on the adapted side. The LM

reference had a contrast of 0.2 ('low') or 0.4 ('high') and the CM reference had modulation of 0.4 ('low') or 0.8 ('high'). Note that the 'high' values equalled the corresponding LM or CM adapting values. All four reference images were tested via interleaved staircases within a session. The observer had to indicate whether the left or right grating had the higher contrast or modulation. The staircase procedure adjusted the test grating contrast (LM) or modulation depth (CM) in 1 dB steps to find the point of subjective equality with the reference. If adaptation reduces perceived modulation then the test modulation will be increased to match the reference. Thus the aftereffect magnitude (in dB) is defined as the average match made after adaptation minus the average control match. Five naïve observers were tested with different random ordering of sessions. Practice was given before the main sessions.

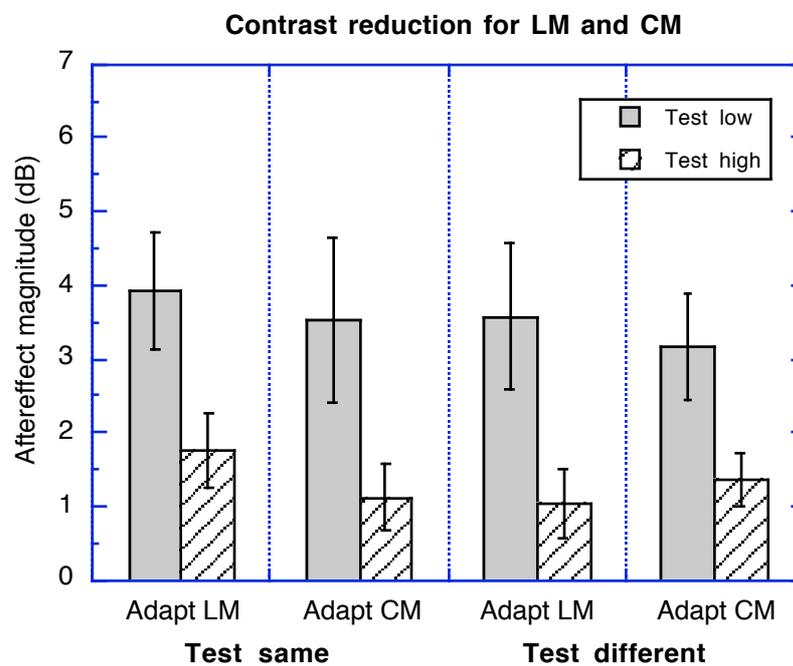


Fig. 5. Experiment 2. Mean (± 1 s.e.) reductions in perceived contrast or modulation for LM and CM gratings

Results

Fig. 5 shows the mean aftereffects for the group of observers. When the reference level was 'low' the aftereffect was 3-4 dB in all cases, but when the reference was 'high' the aftereffect reduced to about 1 to 1.5 dB.

The size of these aftereffects – up to 4 dB – may appear small when compared with the previous literature on contrast reduction for sine gratings (Blakemore, Muncney & Ridley, 1973; Georgeson, 1985). However, we note that the reference values here were either equal to the adapter, or only a factor of 2 below it. The contrast reductions we observed are quite similar to

previous ones when these levels are borne in mind. Contrast reduction becomes large when the reference level is well below the adapter (Georgeson, 1985), but here the high thresholds for LM and CM gratings made it impossible to test lower reference levels. With that in mind, it is interesting that contrast modulation – a second-order cue – does suffer a very similar loss of perceived signal strength to that observed for LM after first-order (LM) or second-order (CM) adaptation. Importantly, in both cases, the transfer of adaptation from one image type to the other was almost complete. Using a definition equivalent to that given above, the mean transfer was 90% in the ‘low’ test condition and 84% in the ‘high’ condition.

The substantial transfer of the contrast & tilt aftereffects implies some common mechanism in the processing of LM and CM signals. Since previous work on detection thresholds (see Introduction) has supported the idea of separate, specific LM and CM channels, a possible resolution of these findings is the second scheme of Fig. 1: early specificity, with later integration. This type of scheme has been widely suggested for the architecture of motion processing (Wilson et al., 1992; Wilson, 1994; Nishida et al., 1997). But there is another possibility that we now address, by asking whether LM and CM really share a later stage of information processing, or whether they might instead share an adaptation process whilst maintaining separate channels for LM and CM information. In short, what is processed in common - Information or Adaptation ?

For clarity, we shall call the scheme of Fig 1b ‘single-channel integration’ because the pooling or integration stage has 2 input sources (LM and CM) but a single output path. LM and CM images are physically different, but it has been widely supposed (especially in the motion literature) that a rectification or squaring stage in the CM path could serve to recover the contrast envelope (the modulation signal) and thus effectively convert LM and CM signals into a common format (Chubb & Sperling, 1988; Solomon & Sperling, 1994; Sperling, Chubb, Solomon & Lu, 1994). If LM and CM signals were converted into a common format they could be readily combined, either (a) by linear summation that would preserve the sign (or phase) of the input signals, or (b) by some nonlinear combination that might throw away relative phase information [e.g. $\text{abs}(\text{LM}) + \text{abs}(\text{CM})$, or $(\text{LM}^2 + \text{CM}^2)$].

We next test several predictions from this single-channel integration scheme. Firstly, with a single output path, information about the input source is lost and it should be difficult to identify whether a grating is LM or CM. This has not previously been tested. Secondly, in experiment 4, we test whether the combination is sign-preserving, or not, by studying compound gratings that

contain both LM and CM. With signed summation we should expect detection of out-of-phase compounds (denoted LM-CM) to be harder than in-phase compounds (LM+CM) because of partial or complete cancellation at the summation stage.

Part 2: Detection and Recognition

Experiment 3 - Detection and Recognition of LM and CM gratings

In this study we ask whether it is harder to recognize LM and CM gratings than it is to detect them. Operationally we define detection as the percentage correct in a 2AFC task in which the observer has to distinguish between patterned noise (LM or CM) and noise only (N). Different blocks of trials tested (LM vs N) and (CM vs N). Recognition performance is defined as the percent correct on a 2AFC (LM vs CM) task in which the LM and CM gratings have been matched for detectability. This matching is important in order to prevent a difference in visibility serving as an artefactual cue to recognition (e.g. “if it’s more visible it must be LM”).

Method

Apparatus and procedure were similar to that described by Schofield & Georgeson (1999), except that performance was measured at several fixed stimulus levels (method of constant stimuli) and not via the staircase method. In brief, LM and CM images (512x512 pixels) were generated on a PC with a VSG graphics card and shown on a greyscale monitor (Eizo 6500M). The display was carefully calibrated and linearized via look-up tables. Fine control of modulation depth was achieved with frame-interleaving, described by Schofield & Georgeson (1999). The binary noise contrast was always 0.4. All gratings were vertical with a spatial frequency of 1 c/deg in a soft-edge window of 5.7 deg outer diameter. Viewing was binocular from a distance of 200 cm. On each trial the two test intervals lasted for 555 msec, including 111 msec smooth onset (and offset), separated by a blank (mean luminance) interval of 555 msec. Within a session the observer’s 2AFC task was either detection (LM vs N, or CM vs N: “which interval contained a grating?”) or recognition (LM vs CM: “which interval contained the LM grating?”). Practice sessions were used to select the 4 stimulus levels (in 3dB steps) to be used for each observer in the main sessions, such that performance ranged from about 60-95% correct across the 4 levels. Data were collected over several sessions in order to obtain at least 200 trials for each stimulus and each signal level per observer.

Experiment 4 - Detection and Recognition of compound LM and CM gratings

This study was in all respects similar to experiment 3, except that the stimuli were compound gratings, containing both LM and CM modulations. The two modulations could be in-phase (LM+CM) or in anti-phase (LM-CM). Absolute phase was randomized. Observers either had to detect the compound grating (LM+CM vs N, or LM-CM vs N in separate blocks of trials) or recognize the phase relation (LM+CM vs LM-CM). Note that the LM and CM signal levels were adjusted for each observer to make them equally detectable and, because compound gratings are more detectable than their components (Schofield & Georgeson, 1999), the component levels here would be around 2-3 dB lower than in experiment 3.

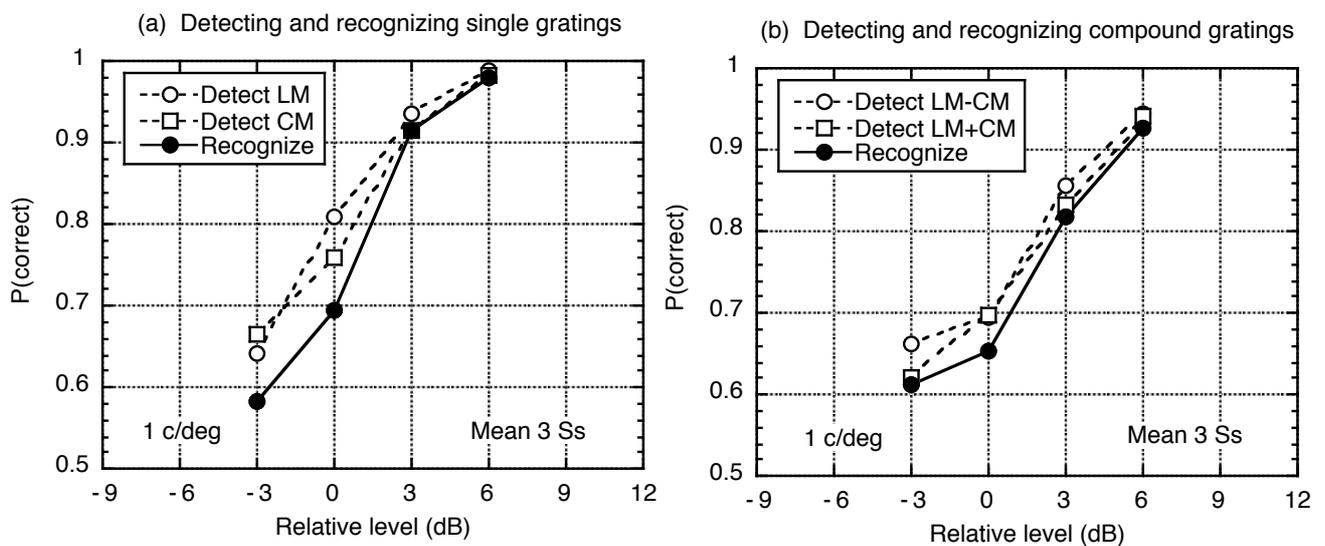


Fig.6 (a) Experiment 3; mean performance of 3Ss detecting and recognizing single LM and CM gratings. (b) Experiment 4; mean performance of 3Ss detecting and recognizing compound (LM+CM, LM-CM) gratings. Note that absolute levels of LM and CM modulation were not the same in (a) and (b).

Results

Fig 6 shows the results of experiments 3 and 4, expressed as percent correct for the detection and recognition tasks, averaged over the 3 observers. In Fig 6a, we see that (by design) performance levels for detection were similar for the LM and CM gratings. This confirms that a difference in detectability would not have been a cue to recognition. Recognition performance was, on average, just a little below the performance in detecting the same gratings, mainly at the lower signal levels. Viewed as a horizontal shift in the psychometric function, this difference corresponds to a small (1-2 dB) reduction in effective signal strength for the recognition task. On closer inspection, this difference was evident in the data for 2 of the 3 observers, even after further practice, while for the third observer recognition performance was the same or marginally better than detection. These results show that, although recognition was on average a bit worse than detection, there was no

major loss of perceptual identity for barely detectable LM and CM gratings. This argues against a strong version of the single-channel integration model outlined above.

Fig 6b shows that detectability of compound gratings was almost identical for in-phase (LM+CM) and anti-phase (LM-CM) images, and again recognition performance (LM+CM vs LM-CM) was slightly lower than detection, by an amount equivalent to about 1 dB reduction in signal level. These results provide further evidence against the single-channel integration model. Firstly, if there were a signed summation of the LM and CM signals, we should expect detection of LM-CM to suffer from cancellation between the two inputs, but in fact its detectability was the same as for LM+CM. This could be consistent with unsigned summation. But with unsigned summation of the signals we should expect phase-blindness – a substantial loss of performance in phase recognition, relative to detection, since the two compounds differ only in the relative sign (phase) of the LM and CM inputs. No major loss was found. Instead, recognition of the phase relation was nearly as good as compound detection. Since these results argue against signed summation, and against unsigned summation, we must conclude that there is no simple summation of LM and CM signals at all in near-threshold detection and recognition tasks. In summary, these results provide strong evidence against the single-channel integration model, either with or without preservation of the sign of the signals.

Discussion

In part 1, we found substantial transfer of two perceptual aftereffects between adapting and test gratings of different types (LM and CM). These findings echo previous reports that the tilt aftereffect generalizes between gratings defined by very different cues, such as luminance, colour, motion and stereo depth (Berkley, Debruyn & Orban, 1994), and between real and ‘illusory’ contours (Smith & Over, 1975; Paradiso, Shimojo & Nakayama, 1989). One attractive view of these findings is that a first stage of contour processing in vision is cue-specific, while a second stage is cue-invariant and serves to encode orientation (and perhaps contour ‘strength’) irrespective of the image cue that defines the contour (Bruce, Green & Georgeson, 1996, chapter 5; Regan, 2000, chapter 7). The generalization or pooling of signals at stage 2 would mediate the transfer of aftereffects from one cue to another.

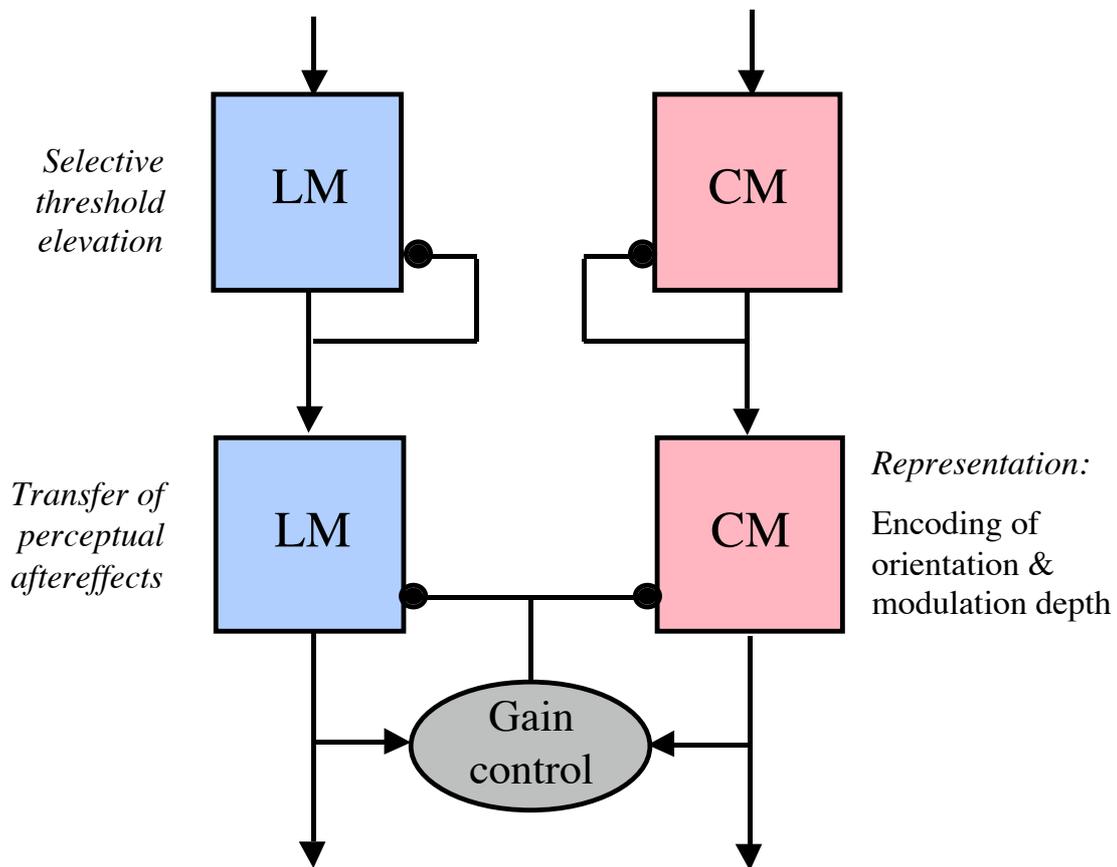


Fig. 7. A parallel processing scheme for LM and CM signals consistent with our results and others. Adaptation (filled circles) at the first stage would be orientation-tuned, spatial frequency-tuned, and selective for LM or CM. It would be responsible for selective threshold elevations. For the TAE, adaptation at the second stage has to be orientation-tuned, but not selective for LM or CM because each channel affects the other through a common gain control that mediates the observed transfer of suprathreshold aftereffects.

In part 2, however, we saw that a single-channel integration scheme of this kind (Fig 1b) has great difficulty with the results on detection and recognition. There was no substantial loss of identity for single gratings near threshold, and no cancellation or phase-blindness for compound gratings. Fig. 7 outlines a different 2-stage scheme that is more consistent with our results and others. Its key features are:

1. separate channels for LM and CM at both stages
2. selective adaptation of LM and CM channels at stage 1
3. common or pooled adaptation at stage 2.

The separateness of channels was suggested by our earlier finding of no sub-threshold summation between LM and CM gratings (Schofield & Georgeson, 1999) and, using the logic of Watson & Robson (1981), is further supported by the similarity of detection and recognition performance for single LM and CM gratings. The presence of selective adaptation at stage 1 is implied by the

selectivity of threshold elevation reported by Nishida *et al* (1997), but it has to be reconciled with the lack of LM/CM selectivity in suprathreshold (perceptual) aftereffects seen in Experiments 1 and 2. This can be understood if adaptation at stage 1 is (approximately) subtractive (cf. Georgeson, 1985). Subtracting a small constant value from all signals has, in proportional terms, a large effect on small signals (at threshold) but a small effect on large signals (suprathreshold). Thus stage 1 adaptation effects would be selective, but confined to near-threshold stimuli. On the other hand, if adaptation at stage 2 were also orientation-tuned but not selective for LM/CM (because of a common adaptation process, Fig. 7) and approximately multiplicative (a gain control) then this could (a) explain the transfer of aftereffects between LM and CM, (b) enable aftereffects for large (suprathreshold) signals, and (c) explain why transfer is not revealed by threshold elevation. This last point hinges on the (reasonable) assumption that the noise source(s) that limit detection arise before the gain control. A subsequent change in gain (stage 2) that attenuates signal and noise equally does not change the signal-noise ratio and therefore will not affect detectability. Hence only the early (subtractive) adaptation process will be revealed by threshold measurements, while the later (multiplicative) adaptation process will be revealed only by suprathreshold tasks.

An analogous distinction between selective and non-selective adaptation processes was previously suggested by Snowden and Hammett (1992). They found that contrast threshold elevation was orientation-selective (Snowden, 1991), while the suprathreshold, contrast-reduction aftereffect was not clearly orientation-specific and (when the adapt and test gratings were orthogonal) it behaved like a multiplicative contrast gain control. Ross & Speed (1996) confirmed that the orientation selectivity of contrast adaptation disappears at high contrasts. They found that at low test contrasts, adapting to the same orientation ('parallel') gave a greater loss of perceived contrast than adapting to the orthogonal orientation, while at high test and high adapt contrasts the loss of perceived contrast was the same for parallel and orthogonal adapters, implying little or no orientation selectivity for contrast adaptation at high contrasts. Snowden & Hammett (1996) also found a lack of spatial frequency selectivity in these high contrast cases. Any evidence for a multiplicative (gain control) form of contrast adaptation was, however, weak in Ross & Speed's data. Thus contrast adaptation shows a lack of pattern selectivity at higher contrasts, analogous to the lack of LM/CM selectivity that we observed in the suprathreshold aftereffects (experiments 1 and 2). The selectivity of aftereffects may, however, also depend on the perceptual code that is required for the task in hand. To account for the tilt aftereffect, adaptation within the system coding orientation must surely be orientation-specific, even though it appears not to be so for contrast coding, as we have just seen. These two aftereffects may thus depend in part on different coding systems, and an analysis of their very different dependence on contrast leads to similar conclusions (Georgeson, 2000). In our

current proposal (Fig. 7) both stages of adaptation must be orientation-selective, but the second stage of adaptation is not selective for type of modulation (LM/CM).

Our findings and others are thus broadly consistent with the 2-stage scheme of Fig. 7, and appear to rule out the single-channel integration model (Fig. 1b). Fig. 7 adopts the parallel channels of Fig. 1c, and confines integration to the adaptation process alone, rather than supposing that LM and CM signals are combined in the representation of information. This scheme seems the simplest that can accommodate all the findings discussed here, but strictly speaking it does not rule out the possibility of multi-channel LM/CM integration, perhaps at even later stages of processing. For example, twin outputs that carried the sum (LM+CM) and difference (LM-CM) signals might be consistent with our data. During many hours of looking at the compound gratings we have been struck not only by the ease of discrimination (Fig. 6b) but also by their very different perceived structure. Above threshold, the in-phase (LM+CM) compound creates a vivid impression of an illuminated, 3-D corrugated surface, while the anti-phase compound (LM-CM) does not; instead it tends to look like a flat textured surface (the noise) viewed through transparent strips of frosted tape. It is easy to show that when a corrugated, textured surface is illuminated from above by an extended light source (e.g. the sky) then this results in shading (LM) and amplitude modulation of the texture (CM) that are indeed in-phase. This occurs simply because the higher points on the surface ‘see’ more sky, and so have higher illumination which produces higher local mean luminance (LM) and higher luminance variation in the texture (CM) than at lower points on the surface. Thus the LM/CM phase relation could be a powerful cue to the conjoint interpretation of 3D surface shape and illumination. When they are in-phase the likelihood of an illuminated corrugated surface is high, but in anti-phase the LM component could not have arisen from the shading of a 3D surface with lighting from above, and so demands a different interpretation such as transparency or reflectance change. Langley, Fleet & Hibbard (1999) have made an interesting start on such issues by investigating interactions between LM, CM and stereo disparity cues in the perception of transparency and depth. We leave further consideration of this high-level coding to future work, and conclude that Fig. 7 offers a well-supported outline for the early stages of shading and texture vision.

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Figure Legends

Fig 1. Three views of LM/CM information processing. (a) Common channel, no specificity at any stage; (b) initially separate channels, followed by signal combination with a single output; this is the 'single-channel integration' discussed in the text; (c) separate channels at early and late stages.

Fig.2. Examples of LM and CM adapting gratings tilted 20° clockwise (CW) from vertical.

Fig.3. Experiment 1. Tilt aftereffect for the 3 individual Ss, and their mean, averaged over contrast conditions 1-3.

Fig. 4. Experiment 2. (a) example of CM adapting display. (b) example of LM test display

Fig. 5. Experiment 2. Mean (± 1 s.e.) reductions in perceived contrast or modulation for LM and CM gratings.

Fig.6 (a) Experiment 3; mean performance of 3Ss detecting and recognizing single LM and CM gratings. (b) Experiment 4; mean performance of 3Ss detecting and recognizing compound (LM+CM, LM-CM) gratings. Note that absolute levels of LM and CM modulation were not the same in (a) and (b).

Fig. 7. A parallel processing scheme for LM and CM signals consistent with our results and others. Adaptation (filled circles) at the first stage would be orientation-tuned, spatial frequency-tuned, and selective for LM or CM. It would be responsible for selective threshold elevations. For the TAE, adaptation at the second stage has to be orientation-tuned, but not selective for LM or CM because each channel affects the other through a common gain control that mediates the observed transfer of suprathreshold aftereffects.

Table 1

Experiment 1: Noise contrasts, LM/CM modulation depths and orientations for the 6 adapting conditions

Condition name	Noise adapt	Noise test	LM adapt	LM test	CM adapt	CM test	Adapt orient
1. LowAllCon	0.2	0.2	0.2	0.2	0.8	0.8	$\pm 20^0$
2. Standard	0.4	0.4	0.4	0.4	0.8	0.8	$\pm 20^0$
3. LowTestCon	0.4	0.2	0.4	0.2	0.8	0.8	$\pm 20^0$
4. LowTestMod	0.4	0.4	0.4	0.2	0.8	0.4	$\pm 20^0$
5. LowAdaptMod	0.4	0.4	0.2	0.4	0.4	0.8	$\pm 20^0$
6. ± 70 Standard	0.4	0.4	0.4	0.4	0.8	0.8	$\pm 70^0$

Table 2.Experiment 1: Tilt aftereffects ($^{\circ}$) for the 3 observers in 6 conditions of adapting contrast

	Test same		Test different		% transfer
	Ad LM	Ad CM	Ad LM	Ad CM	
1. LowAllCon					
MVJS	1.96	3.26	1.80	1.21	57.7
SJG	4.15	2.96	2.46	2.73	72.9
ZLC	3.81	5.00	4.69	2.70	83.8
Mean	3.31	3.74	2.98	2.21	73.7
2. Standard					
MVJS	2.74	3.58	2.26	1.90	65.9
SJG	4.23	2.86	2.60	2.74	75.3
ZLC	4.74	5.29	5.48	3.05	85.0
Mean	3.90	3.91	3.45	2.56	76.9
3. LowTestCon					
MVJS	1.61	2.98	1.90	2.04	85.8
SJG	4.06	3.50	2.81	2.80	74.2
ZLC	4.19	4.69	4.54	2.98	84.6
Mean	3.29	3.72	3.08	2.60	81.2
4. LowTestMod					
MVJS	4.70	2.93	3.74	4.26	104.9
SJG	5.21	3.85	3.46	5.38	97.5
ZLC	<i>not tested</i>				
Mean	4.96	3.39	3.60	4.82	100.9
5. LowAdaptMod					
MVJS	1.54	1.34	1.69	0.51	76.5
SJG	2.95	2.38	1.78	2.28	76.1
ZLC	2.75	2.03	2.71	1.66	91.6
Mean	2.41	1.91	2.06	1.48	81.9
6. ± 70 Standard					
MVJS	0.43	0.46	0.34	0.04	
SJG	-0.29	-0.46	-0.73	-0.31	
ZLC	<i>not tested</i>				
Mean	0.07	0.00	-0.19	-0.14	n/a

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