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A reevaluation of achromatic spatio-temporal vision: Nonoriented filters are monocular, they adapt, and can be used for decision making at high flicker speeds

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Abstract. Masking, adaptation, and summation paradigms have been used to investigate the characteristics of early spatio-temporal vision. Each has been taken to provide evidence for (i) oriented and (ii) nonoriented spatial-filtering mechanisms. However, subsequent findings suggest that the evidence for nonoriented mechanisms has been misinterpreted: those experiments might have revealed the characteristics of suppression (eg, gain control), not excitation, or merely the isotropic subunits of the oriented detecting mechanisms. To shed light on this, we used all three paradigms to focus on the 'high-speed' corner of spatio-temporal vision (low spatial frequency, high temporal frequency), where cross-oriented achromatic effects are greatest. We used flickering Gabor patches as targets and a 2IFC procedure for monocular, binocular, and dichoptic stimulus presentations. To account for our results, we devised a simple model involving an isotropic monocular filter-stage feeding orientation-tuned binocular filters. Both filter stages are adaptable, and their outputs are available to the decision stage following nonlinear contrast transduction. However, the monocular isotropic filters (i) adapt only to high-speed stimuli—consistent with a magnocellular subcortical substrate—and (ii) benefit decision making only for high-speed stimuli (ie, isotropic monocular outputs are available only for high-speed stimuli). According to this model, the visual processes revealed by masking, adaptation, and summation are related but not identical.

Keywords: masking, adaptation, subthreshold summation, contrast detection, human vision.

1 Introduction

Our visual perceptions of the world around us are derived from the dynamic retinal images on the backs of our eyes. These drive complex decision-making processes that control many of our interactions with the world. But how are the spatio-temporal retinal images encoded by our nervous system? Or put another way, what is the form of the neuronal representation that observers use for their decision making?

The textbook answer is that isotropic spatial filtering in the retina and lateral geniculate nucleus (LGN) is followed by orientation-tuned filtering in the primary visual cortex (V1). This view is supported by evidence from single-cell physiology, visual psychophysics, and various neural imaging techniques (Hubel and Wiesel 1962, 1968; Blakemore and Campbell 1969; Phillips and Wilson 1984; Bonhoeffer and Grinvald 1991). For example, from single-cell recordings we know that the receptive fields of cells in the retina and the LGN are approximately circular, having antagonistic centres and surrounds, or superimposed regions of antagonism in a push-pull arrangement. In contrast, cortical cells have elongated receptive fields that are well suited to detecting elongated image structures such as edges but that do not respond to edges, bars, or gratings that are oriented at right angles to their preferred orientations. The observer's decision making in behavioural tasks is presumably cortical and is thought to tap the outputs of these orientation-tuned cells, in simple contrast detection tasks at least. In other words, although the visual analysis *begins* with orientation-insensitive (isotropic) filtering (using circular receptive fields), the visual code upon which an observer's decision making is made is distributed across orientation-tuned filters.

1.1 Psychophysical evidence for the textbook model of early vision

Evidence from at least three psychophysical paradigms has been taken to support the textbook model above: (i) threshold elevation produced by contrast masking is orientation selective (Phillips and Wilson 1984; Meese and Holmes 2010), (ii) threshold elevation produced by contrast adaptation is orientation selective (Blakemore and Campbell 1969; Snowden 1992), and (iii) there is little or no subthreshold summation of contrast between pairs of superimposed gratings with very different orientations (Kulikowski et al 1973; Phillips and Wilson 1984; Georgeson and Shackleton 1994). None of these results would be expected if observers were to make their psychophysical decisions based on the outputs of mechanisms with nonoriented (eg, isotropic) receptive fields.

Intriguingly, though, the refinement in filtering (from isotropic to oriented) is counterproductive for the contrast detection of patterns containing image structure at more than one orientation. For example, consider a plaid made from a pair of superimposed sine-wave gratings with equal contrasts and oriented at right angles to each other. The Michelson contrast of this plaid is twice that of each of its components. Similarly, the responses of linear isotropic filter mechanisms situated at the peaks of the plaid are twice as high as the best response to just one of its components. Thus, the benefits to contrast detection that are available from isotropic filtering in the retina and LGN are lost to the decision-making processes, owing to the oriented cortical filtering—in the textbook model of vision, at least (figure 1a).

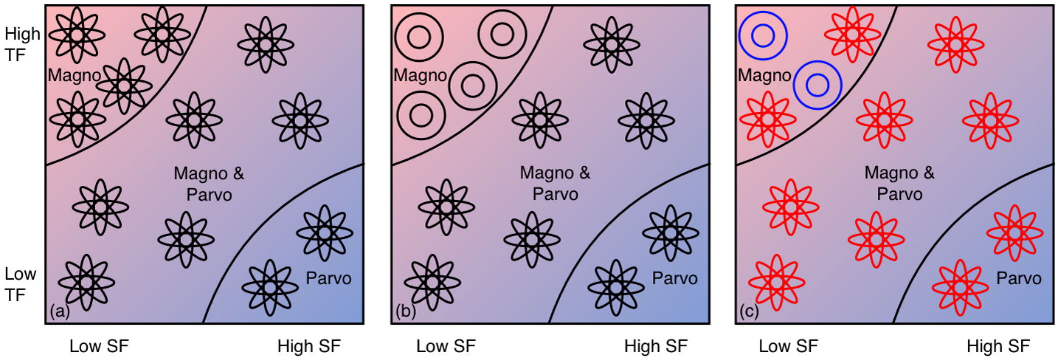

Figure 1. Three schematic models of achromatic spatio-temporal filtering in early vision. The filter outputs are available to the observer for decision making. The rose/lavender colour gradient indicates the linear speed gradient across spatio-temporal space from fast (top left) to slow (bottom right). In all cases, the filtering outside the high-speed corner is thought to be oriented (rosettes). The filtering in the high-speed corner might be (a) oriented, (b) nonoriented (here we suppose isotropic), or (c) a mixture of the two. Our results point to the scheme in (c). They also indicate that the oriented mechanisms are binocular (red), whereas the nonoriented mechanisms are monocular (blue). The allocation of the magnocellular and parvocellular labels is an idealised interpretation of Derrington and Lennie (1984) and Merigan and Maunsell (1993). Notes: SF: spatial frequency; TF: temporal frequency.

1.2 More masking, adaptation, and summation studies

The simple textbook picture outlined above (figure 1a) is a convenient one, but it has been complicated by subsequent experiments, which require a little untangling. Contrary to the textbook model, Burbeck and Kelly (1981) found that masks oriented at right angles to the target were able to raise threshold after all. However, this effect was limited to very low spatial frequencies (SF) and high temporal frequencies (TF): the high-speed corner of spatio-temporal frequency space (where speed = TF/SF; Burbeck and Kelly 1981; Meese and

Holmes 2007). A further study by Ferrera and Wilson (1985) found a similar result. The authors of both studies concluded that the detecting mechanisms for their oriented targets were nonoriented. (By 'detecting mechanism' we mean the mechanism whose output is used for decision making.) This conclusion follows from a 'within-channel' model of masking (Legge and Foley 1980; Wilson et al 1983), where masking is caused by a reduction in signal-to-noise ratio brought about by excitation of the detecting mechanism by the mask. As the masks and targets were at right angles to each other, the detecting mechanisms must be nonoriented, quite possibly isotropic. As it is unlikely that detecting mechanisms are subcortical, one obvious interpretation is that there is a set of isotropic detecting mechanisms in the cortex that can be accessed by the observer when performing a detection task (figure 1b).

Single-cell recordings also provide some support for the conclusion above. In addition to the well-known orientation-tuned cortical cells, several studies have reported subpopulations of layer 4 striate cells with isotropic receptive fields in cat (Hirsch et al 2003), in tree shrew (Mooser et al 2004), and in monkey (Hubel and Wiesel 1968; Blasdel and Fitzpatrick 1984), offering a potential cortical substrate for Burbeck and Kelly's (1981) masking results. However, there is at least one alternative interpretation of the cross-orientation masking results. Orientation-tuned cortical cells are thought to inhibit each other (Morrone et al 1982; Bonds 1989; Heeger 1992), producing cross-orientation suppression, and this could be the basis for the cross-orientation masking described above (Foley 1994; Meese and Holmes 2007, 2010; Cass et al 2009). A similar outcome might be achieved by the isotropic inhibitory neurons found by Hirsch et al (2003) in layer 4 of the primary visual cortex (Meese et al 2008; Roeber et al 2008). This general type of arrangement—involving suppressive interactions—is sometimes referred to as 'cross-channel' masking. There is also good psychophysical support for this model from a dual-masking paradigm (Ross et al 1993; Foley 1994; Holmes and Meese 2004), from contrast matching (Meese and Hess 2004), from experiments involving fine-pattern discriminations (Olzak and Thomas 1999), and from the analysis of the slope of the psychometric function (Meese and Holmes 2007; Meese et al 2008). See Meese and Holmes (2007, 2010) for details and reviews.

The conclusions above point back to the simple textbook model of early vision (figure 1a). Unfortunately, though, they do not resolve the issue because very different psychophysical results have been taken to suggest the contrary. Kelly and Burbeck (1987) performed cross-orientation adaptation experiments—where fast flickering adapters and targets had orthogonal orientations—and found substantial threshold elevation. For the detecting mechanisms to be desensitized by this type of adapter, the implication was that they were unselective for adapter orientation (figure 1b). However, more recent evidence that subcortical magnocellular (but not parvocellular) cells are prone to adaptation (Solomon et al, 2004) offers another interpretation: Perhaps the cross-orientation adaptation effects were the result of desensitization of the isotropic LGN cells (the subunits) that feed the oriented cortical mechanisms [but see Crowder et al (2006) for an alternative view]. The association of the magnocellular pathway with the high-speed corner of spatio-temporal vision (Derrington and Lennie 1984) is also consistent with this interpretation. Thus, a second thrust towards the arrangement in figure 1b turns out to remain consistent with that in figure 1a.

In a third strand of enquiry, Kelly and Burbeck (1987) also performed subthreshold summation experiments for cross-oriented gratings and found about 3 dB (a factor of $\sqrt{2}$) of summation between equally detectable components in the high-speed corner of spatio-temporal vision. This is more summation than expected for detection by independent oriented filter mechanisms (Phillips and Wilson 1984; Georgeson and Shackleton 1994), which is typically about 1.5 dB (a factor of ~ 1.2) according to several models of probability summation (Tyler and Chen 2000). This result takes us back again to the scheme in figure 1b, involving nonoriented detection mechanisms.

Kelly and Burbeck (1987) considered the results from their masking, adaptation, and summation experiments to provide good evidence for isotropic detecting mechanisms in the high-speed corner of spatio-temporal vision. However, the summation results were from just a single observer, and as we have seen, their interpretations of the masking and adaptation results are of questionable standing. Furthermore, there are some potential methodological problems with some of the experiments. For example, the main masking and adaptation experiments involved criterion-sensitive methods of assessment (method of adjustment and yes/no staircases). They also used a drifting adaptation stimulus, which added the potentially complicating factor of motion after-effects. Another potentially important factor is that Kelly and Burbeck (1987) performed their adaptation and subthreshold summation studies monocularly. No explanation was offered for this, and although cross-orientation masking effects have been found for binocular (Meese and Holmes 2007), monocular, and dichoptic mask and target arrangements (Baker et al 2007; Cass et al 2009; Meese and Baker 2009), the question of whether monocular stimulation was an important factor for obtaining cross-orientation adaptation and summation effects (Kelly and Burbeck 1987) remains open. This is potentially important because it could have implications for the ocularity of the filter mechanisms that are available for decision making.

1.3 Aims and outcomes

Our main aims here were three-fold. First, we wanted to make meaningful comparisons across the three contrast detection paradigms above (masking, adaptation, and subthreshold summation) by including common spatio-temporal conditions and observers within a single study. We used a jittering adaptation stimulus to avoid motion after-effects (see methods for details) and two-alterative forced-choice (2AFC) methodology to avoid the problems associated with criterion-sensitive methods. We also measured the slopes of the psychometric functions in the masking experiment to provide additional constraints on data interpretation. Second, we performed the experiments using monocular, binocular, and dichoptic presentations of stimulus components to assess the ocularity of the mechanisms involved. This was to extend our ongoing investigation of binocular interactions in early spatio-temporal vision (eg, Meese et al 2006; Baker et al 2007; Meese and Summers 2009). Third, we wanted to develop a model of early spatio-temporal vision, consistent with the results of Kelly and Burbeck (Burbeck and Kelly 1981; Kelly and Burbeck 1987) but also more recent findings, including those of the experiments performed here.

1.3.1 *The value of masking, adaptation, and summation paradigms.* Of the three psychophysical paradigms used here we consider subthreshold summation to be the most valuable, since it does not require detailed models or assumptions about suprathreshold interactions. Models of the interactions involved in masking are fairly well developed, and we do not aim to extend them here. The main purpose of our masking experiment was to provide the additional constraint [over that in the Burbeck and Kelly (1981) study] that comes from measuring the slope of the psychometric function. Owing to the potential complexity of the processes involved in adaptation—the arrangement and interactions between filter mechanisms and the form and loci of desensitization (Tolhurst et al 1973; Foley and Chen 1997; Langley and Bex 2007; Crowder et al 2006)—we view this as a fairly blunt instrument and urge caution when interpreting results. Nevertheless, the simple model that we propose does a good job in accounting for most of our results.

1.3.2 *Possible filtering schemes for achromatic spatio-temporal vision.* The general hypotheses that we wished to test are summarised in figure 1. In all cases, contrast detection is by oriented mechanisms for most of spatio-temporal space; the focus of interest is the high-speed corner (top left in each panel).(1) In figure 1a this is purely oriented (the 'textbook' model), in figure 1b it is purely nonoriented (Kelly and Burbeck 1987), and in figure 1c both types of mechanism exist. In each case the different mechanisms could be monocular and/or binocular. Our results favour the model in figure 1c, with the new insight that nonoriented high-speed achromatic mechanisms are strictly monocular (blue) whereas the others are binocular (red). We elaborate on the details of this scheme in the general discussion.

2 Methods

2.1 Overview of the experiments

We ran five experiments in total. We refer to monocular masking, adaptation, and summation experiments as experiments 1, 2a, and 3a, respectively. We refer to the adaptation and summation experiments in which we manipulated ocularity (monocular, binocular, dichoptic) as experiments 2b and 3b, respectively. We did not manipulate ocularity for the masking experiment here, but we have done so elsewhere (eg, Meese and Baker 2009).

2.2 Apparatus and stimuli

Stimuli were presented using either a ViSaGe (experiments 1, 2a, and 3a) or a VSG2/5 (experiments 2b and 3b) stimulus generator (both from Cambridge Research Systems Ltd, Kent, UK), controlled by a PC. Each setup used a Clinton Monoray monitor (CRS) running at 120 Hz, with a maximum luminance output of 250 cd/m^2. The monitors were gamma corrected using standard techniques. In all experiments observers viewed the display through ferro-electric shutter goggles (CRS, model FE-1) to enable independent images to be shown to each eye using a frame interleaving technique. The goggles act as a neutral density filter of 0.9 log units, which reduced the effective mean luminance of the display to 16 cd/m^2.

Target stimuli were circular sine-phase Gabor patches, oriented at ±45 deg. from vertical, depending on the experimental conditions. The Gaussian spatial envelope had a full-width-at-half-height of 1.67 carrier cycles and the patch size scaled with spatial frequency. Our main spatial frequency was 0.5c/deg. (all experiments), but some conditions were also run at 2c/deg. (experiments 2a and 3a) and 0.25 c/deg. (reported in the general discussion). Stimuli were temporally modulated using either a 15 Hz biphasic pulse for 0.25 c/deg. ('fast') and 0.5 c/deg. stimuli (see figure 2c) or a single cycle of a 2 Hz sinusoidal modulation for 2c/deg. stimuli ('slow') (figure 2f). This produced stimulus durations of 67ms and 500ms, respectively.

In the adaptation paradigm (experiments 2a and 2b), the adapter was a large circular patch of sinusoidal grating, oriented at −45 deg. from vertical and with contrast of 80%. The total diameter of the adapter was 18 deg., with raised cosine blur the width of half a carrier cycle around the boundary (see figure 2d-e). If, instead, we had used an adapter matched to the size of the target, then small eye-movements during adaptation could result in the target region being underadapted. This is less likely to be a problem with our large adapting field.

The adapter was phase-jittered to prevent local luminance adaptation. This was done by incrementing the phase angle by 90 deg. + x, where x is a random value in the range 0:180 deg. The jitter was constructed to be consistent with the temporal properties of the appropriate target stimulus: for 15 Hz conditions a phase shift occurred every 33 ms, and for the 2 Hz conditions it occurred every 250 ms. A control experiment confirmed that this produced similar results to the more conventional counter-phase flickering adapter.

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(1) By 'speed' we mean the ratio of temporal frequency to spatial frequency (TF/SF). All of the stimuli in this study were flickering gratings. They did not drift.

Stimulus contrast is reported as Michelson contrast in percent $(100(L_{\max} - L_{\min})/(L_{\max} + L_{\min}))$.

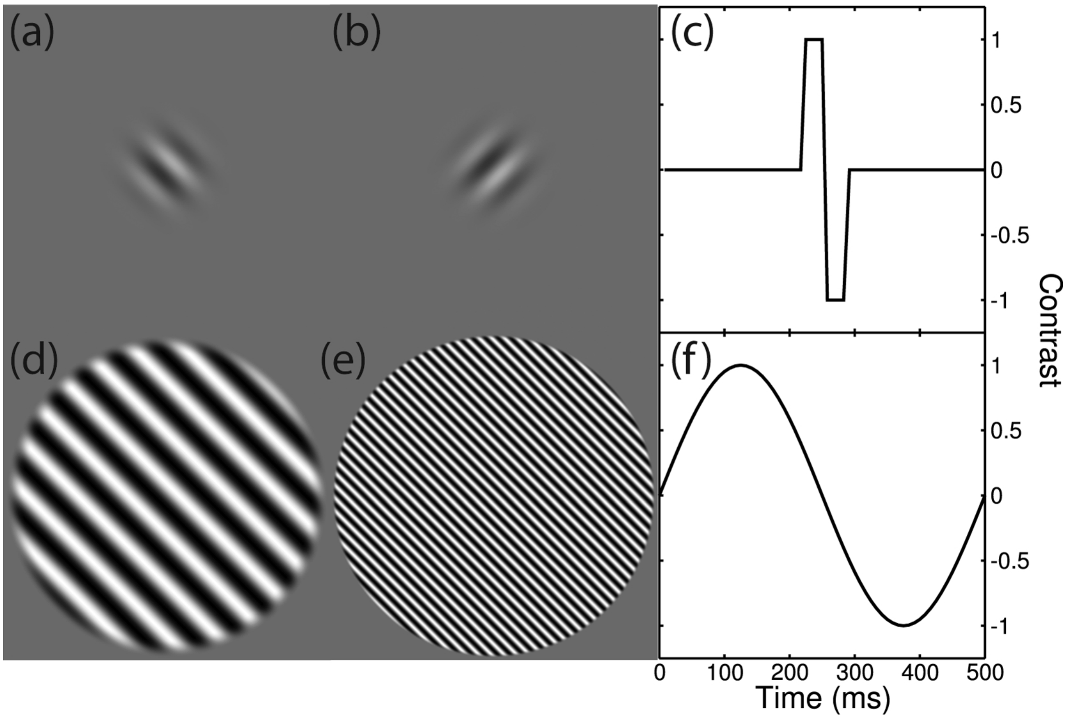

Figure 2. Spatial and temporal properties of the jittering or flickering (adapter) stimuli used in this study. None of our stimuli drifted. (a, b) Left- and right-oblique Gabor patches (±45 deg.), used as targets in all experiments. In experiment 1 they were also used as masks. (d, e) Adapter stimuli at the two main spatial frequencies (0.5c/deg. and 2c/deg.). Temporal waveforms were a ('fast') 15 Hz biphasic pulse (c) and a ('slow') single cycle of 2 Hz sinusoidal modulation (f).

2.3 Procedures

In all experiments we measured contrast-detection thresholds for oriented Gabor patches, sometimes in the presence of a mask. Observers were seated in a darkened room with their head in a chin support to which the shutter goggles were attached. The viewing distance was 57cm. All experiments used a temporal two-interval forced-choice (2IFC) paradigm, with an interstimulus interval of either 400ms (DHB) or 500ms (all other observers). The stimulus location was indicated by a quad of fixation points placed on a virtual circle with a radius of 1.41 carrier cycles of the target stimulus (Summers and Meese 2009).

Psychometric functions were fitted using a 3-parameter Weibull function to estimate threshold (81.6% correct after correcting for lapsing), slope, and lapse rate (Wichmann and Hill 2001a, 2001b). Data from each experimental block were fitted independently, and the thresholds and slopes were averaged across multiple blocks, and then across observers. A bootstrapping technique was used to resample the original fits to each individual psychometric function to produce threshold and slope distributions for statistical analyses. Significance testing was always two-tailed.

Specific procedures for each experiment were as described below.

2.4 Experiment 1: monocular masking

There were five conditions: (i) no mask, (ii, iii) co-oriented masks at 2% and 30% contrast, and (iv, v) cross-oriented masks at 2% and 30% contrast. The target was always a 0.5c/deg. right oblique Gabor patch. All stimuli were presented monocularly to the right eye and the left eye viewed mean luminance. Preliminary staircases were run to determine the approximate sensitivity in each condition, in order to set target contrast levels for the main experiment. To achieve detailed measures of the psychometric functions, we used the method of constant stimuli, with six target contrast levels per condition. Each block consisted of 40 trials per contrast level presented in a random order for a given condition. Each observer completed four blocks, giving 960 trials per psychometric function.

2.5 Experiment 2a: monocular adaptation

The adaptation regimen consisted of two minutes of continuous adaptation at the start of a block, and 5 seconds of top-up adaptation before each trial. Between the top-up adaptation and the first 2IFC interval there was a gap of 400 ms. The adapter was always left oblique (−45 deg.), and the target was either left oblique (co-oriented) or right oblique (cross-oriented), with conditions blocked by target orientation. All stimuli were presented monocularly to the right eye, and the left eye viewed mean luminance. Baseline thresholds (involving no adaptation phase) were measured for both orientations in the right (target) eye in blocks at the beginning and end of the entire experimental series and on different days from the adaptation. Adaptation was performed for the 0.5c/deg. and the 2c/deg. stimuli on different days. Target contrast was determined by a pair of 3-down–1-up staircases, with a step size of 3 dB (where contrast in dB is twenty times the $\log_{10}$ of the Michelson contrast). Each adaptation block lasted around 15 minutes, and there were four blocks of trials for each condition.

2.6 Experiment 2b: multiple ocular adaptation conditions

The methods were similar to those for experiment 2a, except that only one spatial frequency (0.5c/deg.) was used, and there were three ocular arrangements of target and adapter. In the monocular condition the target and adapter were both presented to the right eye. This condition was identical to its equivalent from experiment 2a. In the dichoptic condition the adapter was presented to the left eye, and the target was presented to the right eye. In the binocular condition both adapter and target were presented to both eyes. Only one ocular condition was performed on any given day. Baseline thresholds were measured for the relevant binocular and monocular targets in the same way as above.

2.7 Experiment 3a: monocular cross-orientation summation

We measured subthreshold summation for orthogonally (cross-)oriented Gabor patches in the right eye using the method of constant stimuli. The range of target contrasts was determined by the results from experiments 1 and 2a. Thresholds were measured for the left- and right-oblique component stimuli (ie, Gabor orientations of −45 deg. and 45 deg.), and their sum (the compound), for both spatial frequencies. Preliminary analysis showed that the sensitivity for the two orientations was very similar and so results were averaged across component orientations for comparison with the compound stimulus when calculating the summation ratio (see Results).

2.8 Experiment 3b: multiple ocular summation conditions

This experiment was similar to experiment 3a, except that there were three ocular conditions, each performed with the 0.5c/deg. stimulus. The monocular condition was as described for experiment 3a, and the binocular condition was the same except that the stimuli were presented to both eyes. In the dichoptic condition one target component (left oblique) was presented to the right eye, and the other target component (right oblique) was presented to the left eye. Thus, in the compound condition different eyes saw different stimuli.

2.9 Observers and preliminary analysis

Three undergraduate optometry students participated in experiments 1, 2a, and 3a as part of their course requirements (AJ, KB, SS). Experiments 2b and 3b were completed by one author

(DHB) and four undergraduate students (JC, MD, RP, SB), one of whom was paid (SB), the others participating for course credit. All observers wore their required optical correction during testing and had normal stereopsis (ie, they were able to see depth in stereograms containing crossed and uncrossed disparities).

Preliminary analysis of the results led us to exclude the data from two of the undergraduate observers in experiments 2b and 3b. For one observer (MD), the psychometric functions were remarkably unreliable as revealed by their unusually high standard errors (SE > 3 dB for more than half of the psychometric functions). For the other (JC) there was a marked instability in the baseline measures: contrast detection thresholds were 3 dB higher in the block of baselines measured at the end of the experiment compared with the first. This made it impractical to evaluate the after-effects of adaptation for this observer. Observers DHB and SB were subsequently recruited to replace the discarded datasets.

3 Results and discussion

3.1 Experiment 1: monocular masking

The stimulus conditions for the monocular masking experiment are summarised in figure 3a. Example psychometric functions are shown for one observer (AJ) in figure 3b for each of the five mask conditions (see legend of figure 3b). Note that relative to baseline (black), these are shifted rightwards for the 30% contrast masks (dark blue), regardless of whether the mask was co-oriented or cross-oriented relative to the target, but that the slope of the psychometric function becomes very shallow only in the co-oriented condition (solid dark blue).

Threshold elevation (TE) was calculated in the conventional way as follows: TE = $20\log_{10}(C_{MASK}/C_{NO\_MASK})$, where C_{MASK} and C_{NO_MASK} are the contrast detection thresholds with and without the mask, respectively. Figure 3c shows threshold elevation averaged across the three observers (AJ, KB, and SS). (In this, and other bar charts, results for individual observers are shown by the coloured dots.) Average slopes of the psychometric functions are shown in figure 3d.

For threshold elevation statistical significance was evaluated by assessing the difference between the averaged bootstrapped populations for baseline and masked thresholds. For psychometric slopes we compared the bootstrapped populations for each condition to a value of $\beta = 1.3$, which is the characteristic of a linear psychometric function(2) (Foley and Legge 1981; Pelli 1985; Tyler and Chen 2000). Statistical significance is indicated in figure 3 (and other figures) by one asterisk for $p < 0.05$ and two asterisks for $p < 0.01$.

The co-oriented mask produced threshold elevation of around 12 dB (a factor of 4) at high contrasts (30%), but produced a threshold reduction at low contrasts (2%) of around 7 dB (a factor of> 2). These statistically significant effects are consistent with the well-known dipper function for pedestal masking (Legge and Foley 1980). The co-oriented mask reduced the slope of the psychometric function (Weibull β) substantially, from $\beta > 5$ with no mask to $\beta = 1.8$ for the low contrast mask, and $\beta = 1.1$ for the high contrast mask. The latter value is not significantly different from the prediction of $\beta = 1.3$, as anticipated by the linearizing effect of pedestal contrast for small signal increments (Foley and Legge 1981; Bird et al 2002; Meese et al 2006).

The high-contrast cross-oriented mask produced significant threshold elevation of around 8 dB (ie, it was about 4 dB less potent than the co-oriented mask), whereas the

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(2) By this we mean the sigmoidal psychometric function produced by a linear system (ie, the psychometric function produced by a linear contrast transducer). When expressed as d’ (ie, d’ as a function of target contrast), the psychometric function for a linear system is linear and has a slope of unity.

low-contrast cross-oriented mask did not affect threshold significantly. Although slopes for these conditions were shallower than for the baseline, they were both significantly steeper than $\beta = 1.3$, with values around $\beta = 3$.

3.1.1 *Interpretation of masking results.* For a conventional within-channel model of masking—where masking derives from direct excitation of the target mechanism by the mask (Wilson et al 1983; see also Meese and Holmes 2010) —the effects of cross-orientation masking might be taken to indicate nonoriented detecting mechanisms (Ferrera and Wilson 1985). However, in contradistinction from co-oriented masking: (i) the slope of the psychometric function was not linearized (it was not reduced to $\beta = 1.3$) (Meese and Holmes 2007), and (ii) there was no facilitation (Foley 1994). This shows that different processes were involved for the two mask orientations. These results are consistent with previous studies of binocular cross-orientation masking (Ross and Speed 1991; Foley 1994; Meese 2004; Meese and Holmes 2007) and stand against a within-channel account, suggesting that our high-speed targets (low spatial frequency, high temporal frequency) were detected by oriented detection mechanisms subject to suppressive interactions from the mask. We consider the nature of these interactions in the general discussion.

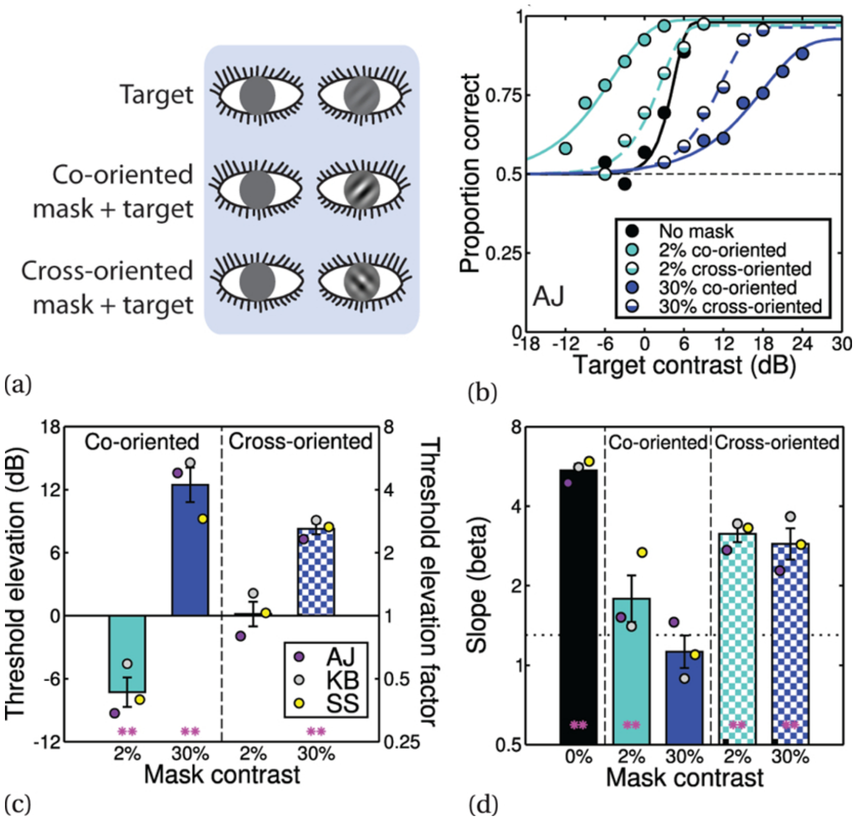

Figure 3. Masking experiment (experiment 1). (a) Stimulus configurations (mask plus lower contrast target) for co-oriented and cross-oriented conditions). The stimuli had a spatial frequency of 0.5 c/deg. and a temporal frequency of 15 Hz (‘fast’). (b) Example psychometric functions for observer AJ. (c) Threshold elevation for contrast detection. (d) Slopes of the psychometric function (β). Note the logarithmic ordinate. In this figure and others bars show results (±1 SE) averaged across three observers (here: AJ, KB, and SS), and the coloured circles are for individual observers. Asterisks indicate statistical significance, as described in the text. The dotted horizontal line indicates $\beta = 1.3$, which is the psychometric slope expected for a linear system.

3.2 Experiment 2a: monocular adaptation

The stimulus conditions for the adaptation experiments are summarised in figure 4a. Threshold elevation (TE) from adaptation was calculated in the conventional way as follows: $\mathrm{TE} = 20\log_{10} C_{ADAPT}/C_{BASELINE})$, where C_{ADAPT} and $C_{BASELINE}$ are the contrast detection thresholds with and without adaptation, respectively. This is shown for the two adaptation conditions and two spatial frequencies in figure 4b, averaged across three observers (AJ, KB, and SS). The co-oriented adapter raised thresholds significantly—by around 6 dB (a factor of 2)—at both spatial frequencies. When the adapter was cross-oriented, threshold elevation was weaker (2.2 dB), but significant in the fast condition (0.5 c/deg., 15 Hz flicker). There was no significant threshold elevation in the slow condition (2 c/deg., 2 Hz flicker) for the cross-oriented adapter.

3.2.1 *Interpretation of monocular adaptation results.* The standard view of adaptation is that the adapter desensitizes the visual mechanisms that respond to the adapter, with the caveat that some visual mechanisms do not adapt (eg, parvocellular cells in the LGN; Movshon and Lennie 1979; Solomon et al 2004). Therefore, these results provide evidence for a nonoriented component to the detection process in the high-speed corner of spatio-temporal vision. We will elaborate on what that might be in the general discussion.

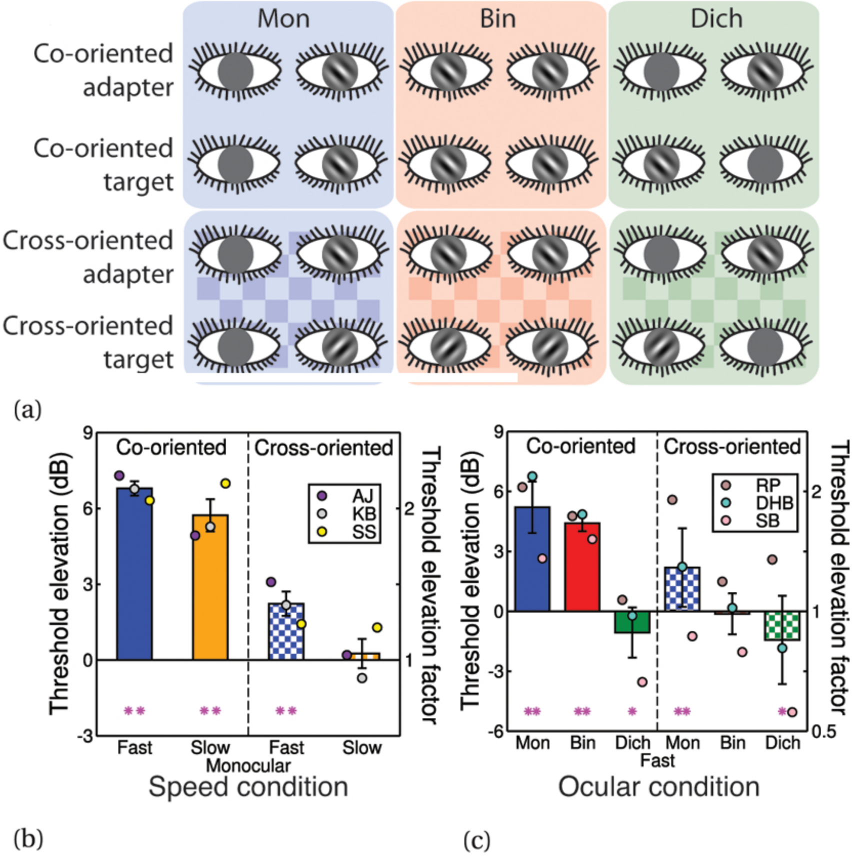

Figure 4. Adaptation experiments. Stimulus configurations (a) are shown for the two orientation conditions in experiments 2a and 2b (b and c, respectively) and for each of the three ocular conditions in experiment 2b (c). The 'fast' stimuli had a spatial frequency of 0.5 c/deg. and temporal frequency of 15 Hz. The 'slow' stimuli had a spatial frequency of 2 c/deg. and a temporal frequency of 2 Hz (see figure 2 for details). In (b) and (c) asterisks denote the conditions where threshold elevation for contrast detection was significantly different from 0 dB.

3.3 Experiment 2b: Multiple ocular adaptation conditions

We repeated the fast stimulus condition from experiment 2a in three ocular arrangements. The monocular condition was an exact replication of the condition from experiment 2a, but for three different observers (RP, DHB, and SB). The results were very similar to before, with significant adaptation after-effects of around 5.2 dB and 2.2 dB for the co-oriented and cross-oriented targets, respectively (figure 4, blue). When the adapter and target were presented binocularly (figure 4c, red), the adaptation after-effect was weaker than in the monocular case for each of the adapter orientations. For the co-oriented target the effect dropped marginally (to 4.4 dB), and for the cross-oriented target the effect was abolished (there was no significant effect). When the adapter and target were presented to different eyes (dichoptic condition), there was a small negative adaptation after-effect of around 1 dB (ie, detection performance was slightly improved by adaptation). This was statistically significant ($p < 0.05$) for both orientations (figure 4c, green).

3.3.1 *Interpretation of adaptation within and between the eyes.* If the nonoriented component of adaptation identified in experiment 2 arose after binocular combination, then it should have been evident in the dichoptic condition. The fact that it was not suggests that the effect arises within purely monocular mechanisms. Similar conclusions follow from preliminary reports of a related adaptation study by Cass (2010).

The finding of facilitation in the dichoptic condition (and its inconsistency across observers) replicates an earlier finding by Baker et al (2007) and preliminary reports by others (Bex et al 2007; Cass 2010). As Baker et al (2007) pointed out, this might derive from the release of standing inhibition between cross-oriented mechanisms in different eyes. That is, the cross-oriented adaptation causes disinhibition across orientation and eye. Similarly, the release of standing inhibition between co-oriented mechanisms in different eyes would explain the co-oriented facilitation.(3) This type of inhibitory interaction between the eyes and its release by adaptation in the fellow eye might also explain why the after-effects were smaller in the binocular condition than in the monocular condition (figure 4c).

3.4 Experiment 3a: Monocular cross-orientation summation

Summation ratios (SR) were calculated in the conventional way as follows: SR = $20\log_{10}(C_{LR}/C_{L+R})$, where C_{LR} is the average detection threshold for the individual components and C_{L+R} is the detection threshold for the compound stimulus (the sum of the two components). With this arrangement, SR = 6 dB (a factor of 2) would indicate perfect linear summation, and SR = 0 dB (a factor of 1) would indicate no summation (ie, no benefit of adding a second component to the first). Summation ratios are plotted in figure 5b averaged across three observers (AJ, KB, and SS). Only modest levels of summation were found at each spatio-temporal frequency, but were greater in the fast condition (0.5 c/deg., 15 Hz flicker) than in the slow condition (2 c/deg., 2 Hz flicker) ($p = 0.016$).

3.4.1 *Types of summation.* Probability summation [sometimes called 'signal selection'; Meese and Baker (2011)] is usually taken to be the minimal combination rule (Tyler and Chen 2000). When this occurs between two sets of independent noisy linear mechanisms, the SR is about 1.5 dB (Tyler and Chen 2000). Nonlinearities prior to probability summation would reduce this value further. For example, a square-law transducer produces SR ≈ 0.75 dB in conjunction with probability summation. A distinct alternative to probability summation is *signal combination*, where signals are summed within a single mechanism. Most analyses

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(3) Only one of the three observers here (SB) shows good evidence of the co-oriented dichoptic facilitatory effect. Preliminary analysis of work to be published elsewhere found only weak evidence for this in 3 of the 5 observers (up to 1.4 dB of facilitation). Clearly, even if real, the facilitatory effect is typically small and inconsistent across observers. We consider this effect to be a minor observation and one that is peripheral to the main conclusions and motivations in this paper.

find that this is a more potent form of summation than probability summation (eg, see Meese 2010; Meese and Summers 2009; Meese and Baker 2011). However, predictions are complicated by the potential effects of spatial pooling (eg, Georgeson and Shackleton 1994; Bergen et al 1979) and integration of early noise (Meese 2010), each of which can dilute the predicted level of summation across orientation. For example, for our sine-phase Gabor patches linear summation across orientation followed by peak-picking (a MAX operator) across space and late additive noise predicts SR = 5.6 dB (nearly a factor of 2). But it is easy to show that this drops to 3.9 dB, 3.0 dB (a factor of $\sqrt{2}$), and 2.1 dB for Minkowski summation over space using Minkowski exponents of 4 (fourth-root), 2 (quadratic; Meese 2010), and 1 (linear), respectively.(4)

To establish evidence for signal combination across orthogonal orientations, we required that summation were significantly greater than the probability summation level of SR = 1.5 dB. This criterion was met in the fast condition, with empirical summation levels just more than 2 dB. For the slow condition summation was actually a little less than 1.5 dB (see figure 5b).

3.4.2 *Interpretation of summation results.* These results (figure 5b) suggest there are mechanisms in the high-speed corner of spatio-temporal vision that can perform signal combination of luminance contrast across orthogonal orientations and that the observer can use these mechanisms in contrast detection tasks. Isotropic cortical mechanisms (cells with circular receptive fields) are plausible candidates for this because they sum luminance modulations at all orientations.

3.5 Experiment 3b: Multiple ocular summation conditions

We also extended the cross-orientation summation experiment to multiple ocular conditions using the fast stimuli (0.5 c/deg., 15 Hz flicker). The results are shown in figure 5c. The monocular condition produced 3.1 dB of summation—a little more than the equivalent condition from the different observers in experiment 3a—and as before, was significantly greater than the probability summation prediction of 1.5 dB. (The average level of monocular summation across experiments 3a and 3b was 2.6 dB; $n = 6$ observers). When the stimuli

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(4) These standard computations are fairly simple, but it is not easy to provide intuitions for the results, and the equations involved do little to help (not shown). There are one or two points that we can make, though. First, the usual intuition for linear summation between two equally detectable components (for which the response to each is one arbitrary unit) with late additive noise (ie, limiting noise that arises at the final stage, just before the decision variable) is that the summation ratio is 2 (6 dB), because $1 + 1 = 2$. For sine-wave gratings this intuition holds if a MAX operator is used over space so that the computation is not affected by spatial pooling. For the sine-phase Gabor stimuli used here the contrast modulation at right angles to the orientation of the bars means that the spatial peak in the compound stimulus is the sum of two local contrasts, each of which is slightly less than the Michelson contrast of each component. Therefore, the summation ratio is slightly less than 2 (here, 5.6 dB), assuming the spatial MAX operator again. Second, it is well-known (eg, Bergen et al 1979) that when pairs of differently oriented 1D luminance modulations (eg, gratings or Gabor patches) are summed, the constructive and destructive interference across two-dimensional space (the beats) means that when spatial pooling (ie, the combination of responses over space) is more potent than a MAX operator, there is a reduction in the benefit of the second component. As the spatial pooling exponent (ie, Minkowski exponent) is increased (ie, spatial pooling becomes more nonlinear) this effect decreases. For example, a large Minkowski exponent (eg, ≥ 10) represents highly nonlinear spatial pooling and is a good approximation to the spatial MAX operator (above), which preserves the intuitive summation ratio of 2 (6 dB) across grating orientation. [Note that the comments here are for the situation where the limiting noise is late. When limiting noise is placed before the MAX operation, the effects of pooling are often approximated by a Minkowski exponent of about 4, assuming a linear transducer (Tyler and Chen 2000).]

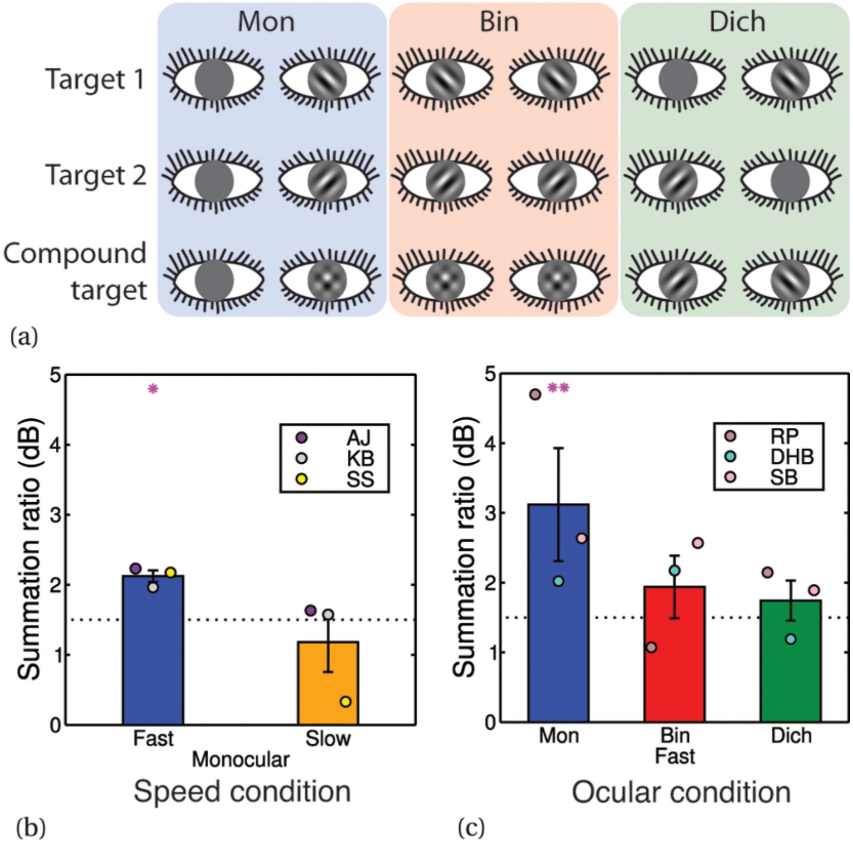

Figure 5. Cross-orientation summation experiments (experiments 3a and 3b). Stimulus configurations are shown in (a) and results for experiments 3a and 3b in (b) and (c), respectively. The 'fast' stimuli had a spatial frequency of 0.5 c/deg. and temporal frequency of 15 Hz. The 'slow' stimuli had a spatial frequency of 2 c/deg. and a temporal frequency of 2 Hz (see figure 2 for details). The horizontal dotted lines in the results panels indicate SR = 1.5 dB: the prediction for the canonical model of probability summation. Statistical tests were performed against this criterion, and significant results are denoted by the asterisks at the top of the figures.

were presented either binocularly or dichoptically, summation was weaker (~ 1.8 dB) and not significantly greater than 1.5 dB.

3.5.1 *Interpretation of summation within and between the eyes.* If the nonoriented detecting mechanism identified in experiment 3 were binocular, then the levels of dichoptic and monocular cross-orientation summation should have been the same because the binocular response would be the same for each of these conditions. The fact that the SR was less in the dichoptic condition suggests that the isotropic detecting mechanisms are purely monocular. But why should there be less summation for binocular stimuli than monocular stimuli? In fact, the scheme we are to propose does predict that this should happen, but we withhold explanation until after describing the model details in the general discussion.

4 General discussion

We performed masking, adaptation, and summation experiments for the contrast detection of achromatic flickering Gabor patches. We found interactions across orientation in all three paradigms. For adaptation and summation the effects were greater for the fast condition (0.5 c/deg., 15 Hz flicker; 30 deg./s) than the slow condition (2 c/deg., 2 Hz flicker; 1 deg./s), confirming previous reports of a departure from scale invariance (Kelly and Burbeck 1987).

Elsewhere this departure has also been reported for cross-orientation masking (Burbeck and Kelly 1981; Meese and Holmes 2007, 2010).

The summation results provide good evidence for nonoriented detecting mechanisms in the high-speed corner of spatio-temporal vision and reject the 'textbook' scheme involving only oriented detectors (figure 1a). However, although the results of our masking experiment confirm the existence of cross-orientation interactions, we doubt these derive from within-channel activity in isotropic detecting mechanisms because of the steep psychometric function and the lack of facilitation (see results section). It is more likely that the target was detected by an oriented mechanism that was suppressed by the cross-oriented mask than that the high-speed corner of spatio-temporal vision was dominated by nonoriented mechanisms (figure 1b). This leaves the hypothesis in figure 1c: there are both nonoriented *and* oriented mechanisms in the high-speed corner of spatio-temporal vision.

For the adaptation and summation experiments we also found greater cross-orientation effects for monocular conditions than dichoptic conditions. The summation result is new and suggests that the nonoriented detection mechanisms that we have investigated are purely monocular. We have denoted this with the dark blue colouring in figure 1c. The adaptation result confirms some previous observations (Kelly and Burbeck 1987; Meese et al 2007; Bex et al 2007; Cass 2010) and is also consistent with the conclusion above.

In the study here we were able to calculate a binocular summation ratio (not shown) for co-oriented components from the monocular and binocular thresholds measured in experiments 2b and 3b. On average, this was 3.9 dB for the fast target ($n = 3$ observers). This is similar to previous studies (eg, Meese et al 2006) and confirms the existence of conventional (co-oriented) binocular summation in the study here. Furthermore, in a preliminary report by Georgeson and Meese (2007) binocular summation ratios were derived for a wide range of spatio-temporal frequencies. Signal combination was found in all cases providing firm evidence for binocular mechanisms throughout spatio-temporal vision (red symbols in figure 1c).

We present a summary of the full set of our current results in table 1. This is in anticipation of the qualitative assessment of our model in the following sections, where we cross reference the effect numbers in this table.

4.1 A specific proposal

How might early vision be wired to be consistent with our results? Figure 6 shows a simple neural hierarchy designed to achieve this, where figure 6a is for the high-speed corner of spatio-temporal vision, assessed by our 'fast' stimulus condition, and figure 6b is for everywhere else, assessed by our 'slow' stimulus condition (we discuss this generalization below). In figure 6a a pair of isotropic monocular filters at level 1 feed into an oriented binocular filter at level 2. The green dashed boxes indicate that all three mechanisms are susceptible to adaptation. For simplicity, we have shown binocular summation, orientation filtering, and adaptation at a single stage in level 2, though several sub-stages might be involved. The addressable outputs of all three filters pass through sigmoidal transducers (Legge and Foley 1980) before reaching the decision stage. [We note that detailed models of more elaborate datasets might involve multiple stages of contrast transduction (Meese and Summers 2009; Meese and Baker 2011)]. In principle, this contrast transduction could derive from accelerating square-law energy mechanisms (Duong and Freeman 2008; Meese 2010) and dynamic contrast gain control (Foley 1994). Figure 6b is identical to figure 6a except that (i) there are no monocular outputs from the isotropic mechanisms and (ii) the desensitizing effect of adaptation is limited to the orientation-tuned mechanism (green dashed box).

Table 1. Summary of the 18 effects (including 5 null effects) reported in this study. Two other relevant effects (3 and 4) are reported from other studies (eg, Burbeck and Kelly 1981; Meese and Holmes 2007). The coloured text in the final column indicates the relative success of the model in figure 6: green = good; blue = simple refinements needed (these are omitted from figure 6 to simplify the presentation); red = further work needed. 'Yes, with some elaboration' means that the model's behaviour requires some explanation beyond that evident in the pictorial presentation. Two-tailed significance testing of the experimental results was done using a bootstrapping technique. *Although this result appears significant, the result is in the opposite direction from the effect that is described. See effect 15 and the green checked bar in figure 4c.

Effect number	Paradigm	Effect	Data figure	Significance level	Accounted for by the model in figure 6
1	**Masking**	Pedestal masking	Figure 3c	< 0.001	Yes
2		Cross-orientation monocular masking	Figure 3c	< 0.001	Yes, with some elaboration
3		Cross-orientation dichoptic masking	*Not in this study*	N/A	No, but easily fixed
4		More cross-orientation masking at higher stimulus speeds	*Not in this study*	N/A	No, but easily fixed
5		Facilitation for low contrast pedestals	Figure 3c	< 0.001	Yes
6		No facilitation for low contrast cross-oriented masks	Figure 3c	0.986	Yes
7		Shallow psychometric function for pedestal masking	Figure 3d	0.249	Yes
8		Steep psychometric function for baseline	Figure 3d	< 0.001	Yes
9		Steep psychometric function for cross-oriented masking	Figure 3d	< 0.001	Yes, with some elaboration
10	**Adaptation**	Threshold elevation for monocular cross-orientation adaptation	Figure 4b, c	< 0.001 < 0.001	Yes
11		No threshold elevation for dichoptic cross-orientation adaptation	Figure 4c	0.014*	Yes
12		No threshold elevation for binocular cross-orientation adaptation	Figure 4c	0.474	No. Not easily assessed qualitatively
13		More monocular threshold elevation for co-oriented adapters than cross-oriented adapters	Figure 4b, c	< 0.001 < 0.001	Yes, with some elaboration
14		More threshold elevation at higher stimulus speeds	Figure 4b	0.004	Yes
15		Facilitation for dichoptic adaptation (co-oriented and cross-oriented)	Figure 4c	0.036 0.014	No, but easily fixed
16	**Summation**	Monocular signal combination	Figure 5b, c	0.040 < 0.001	Yes
17		No dichoptic signal combination	Figure 5c	0.527	Yes
18		No binocular signal combination	Figure 5c	0.182	Yes
19		Signal combination only at high speeds	Figure 5b	0.016	Yes
20		Binocular summation of co-oriented components	Not shown	< 0.001	Yes

4.2 A successful model

The model in figure 6a has six elements (all from the notional catalogue of standard psychophysical model parts), which reduces to three by symmetry (adaptable isotropic monocular filters, adaptable binocular oriented filter, output nonlinearities). Four changes to figure 6a are needed to produce figure 6b, which reduces to two by symmetry (remove monocular outputs, remove monocular adaptability). Arguably then, a total of five design decisions were required to construct the model. Without elaboration or extension, this simple model is consistent with 13 of the 18 effects reported here (as we shall soon describe). A further four of these effects (effects 2, 9, 13, and 15) are easily explained with simple elaborations and refinements, as are another two relevant effects from other studies (3 and 4). Only one (effect 12) is not easily explained within the framework we propose and probably requires detailed quantitative modelling to be properly understood. This is beyond the scope of this study and the constraints of our data. In what follows we provide a brief overview of the qualitative relation between our model and all 20 effects in table 1 (18 from this study, including 5 null effects, and 2 from elsewhere), starting with adaptation, then summation, and finally masking.

4.2.1 *Adaptation in the model and in humans.* Threshold elevation occurs for monocular cross-oriented adapters (effect 10) owing to the adaptable isotropic filters at level 1 in figure 6a (Ohzawa et al 1985; Solomon et al 2004; Mante et al 2005; Duong and Freeman 2007). It does not happen in the dichoptic case (effect 11) because there is no adaptable node (green dashed box) that is common to orthogonal orientations in different eyes. However, why should monocular adaptation be orientation tuned (effect 13)? (That is, why is threshold elevation greater for co-oriented adapters than for cross-oriented adapters?) As the only adaptable monocular route is isotropic, the implication is that the oriented binocular filter is

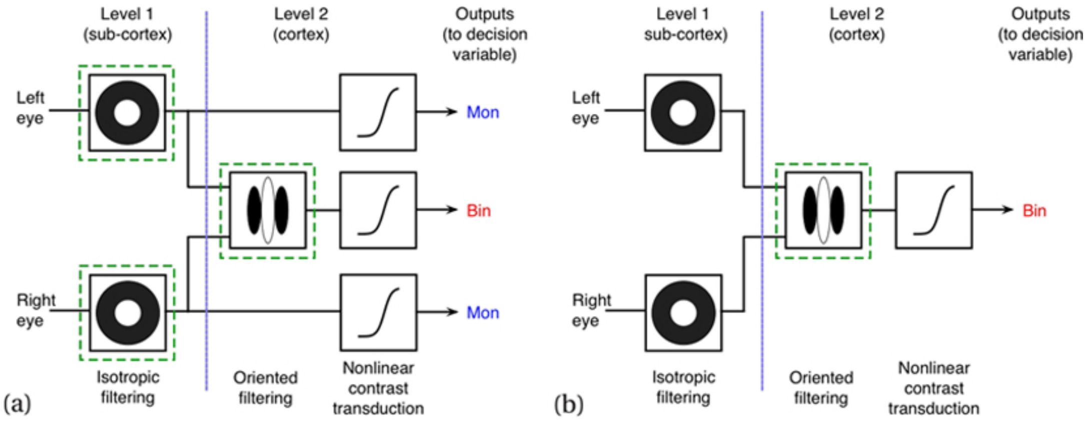

Figure 6. Proposed circuit diagrams for the mechanisms of achromatic spatio-temporal vision. (a) Arrangement for isotropic monocular mechanisms and oriented binocular mechanisms in the high-speed corner of figure 1c. (b) Arrangement for the oriented binocular mechanisms outside the high-speed corner of figure 1c. The green dashed squares indicate the various loci of adaptation. The assignment of levels 1 and 2 to subcortex and cortex is based on known physiology and is not constrained by the results here. The implication is that the outputs of adaptable isotropic filters are available for decision-making in the high-speed corner of spatiotemporal vision, but not elsewhere. (The various pathways that might be involved in cross-channel suppression and interocular suppression are omitted for clarity but have been shown in previous publications: Meese et al 2006; Baker et al 2007, Baker and Meese 2007; Meese and Baker 2009, 2011).

used for the detection. But why should this happen, given that this route takes a double hit from adaptation? We suggest that the orientation tuning derives, in part, from linear spatial summation across an array of isotropic filter elements (Hubel and Wiesel 1962; Mooser et al 2004). Thus, the oriented filter elements are more sensitive than their nonoriented subunits because of the benefit of spatial summation within their elongated receptive fields (Meese 2010). Instead, we might have pursued a more complex argument (and model) involving oriented monocular filters. Indeed, we cannot rule out the possibility that such mechanisms exist, but we were not compelled to appeal to them here. But we do need the monocular isotropic outputs in figure 6a to account for the summation results, as we describe in the next section.

Threshold elevation is greater at higher stimulus speeds (effect 14) because in this corner of spatio-temporal vision there are two stages of adaptation (figure 6a), compared with the single stage elsewhere (figure 6b).

As explained above, there is no threshold elevation for cross-oriented dichoptic masking (effect 11), but there is a facilitatory after-effect, and this is found for both orientations of the dichoptic adapter (effect 15). This is not explained by the model in figure 6, but it can be achieved by the simple extension described in the results: if the model were to include suppressive interactions across eyes and orientation (Sengpiel et al 1995; Walker et al 1998; Li et al 2005; Sengpiel and Vorobyov 2005; Ding and Sperling 2006; Meese et al 2006; Baker et al 2007; Moradi and Heeger 2009), then when adapted, these could result in disinhibition and facilitation (see Meese et al 2007).

In figure 6a we would expect binocular cross-orientation adaptation to be just as potent as its monocular counterpart. The fact that it was not (effect 12) points to a potential weakness in the model. It is possible that this might have something to do with interocular suppression between the binocular adapters, which is not explicit in the simple scheme sketched out in figure 6. For example, we have found that when a mask in one eye is matched to a mask in the other eye, this can reduce the potency of the original mask. We say that the binocular match of the masks gates the level of masking (Meese and Hess 2005; Baker et al 2007). Similar effects have been found for binocular rivalry (Nichols and Wilson 2009). We now see that a binocular match of a cross-oriented adapter also reduces the potency of cross-orientation adaptation (effects 10 and 12). Another possibility is that there is disinhibition from the interocular component of the binocular adapter (see our explanation of effect 15 above), which cancels out the adaptation effect of desensitization. However, the variability in our data (across observers) dissuaded us from attempting to develop a detailed quantitative model of this effect.

4.2.2 *Summation in the model and in humans.* Cross-oriented signal combination is seen for pairs of monocular components (effect 16) because contrast is linearly summed across orientation by the isotropic filters at level 1 (figure 6a) and this output is available to the decision stage. We have argued above that the oriented filter elements are more sensitive than the isotropic filter elements, but presumably, the extra stimulus component that is visible to the isotropic filter overcomes this setback. This does not happen for binocular stimuli, however (effect 18), because in that case the more sensitive oriented binocular filter also benefits from summing a pair of parallel components from the two eyes. Summing a pair of monocular components across orientation within the less sensitive isotropic filters cannot beat this binocular benefit.

There is no cross-orientation signal combination for dichoptic presentation (effect 17) because the two components do not stimulate a common isotropic filter.

Cross-orientation signal combination occurs only at high speeds (effect 19) because there are no outputs from isotropic filters at lower speeds (figure 6b).

Finally, there is binocular summation of co-oriented components (effect 20) because the model contains oriented binocular mechanisms at all spatio-temporal frequencies.

4.2.3 *Masking in the model and in humans.* Pedestal masking (effect 1) in the model derives from the compressive region of the sigmoidal contrast nonlinearity at high contrasts (Legge and Foley 1980).

Monocular cross-orientation masking (effect 2) could arise from either of two routes. First, it could arise from cross-orientation inhibition between oriented mechanisms in the cortex (Albrecht and Giesler 1991; Heeger 1992; Foley 1994; Haun and Essock 2010; Spratling 2011), an approach that could also accommodate cross-oriented dichoptic masking (effect 3) (Ding and Sperling 2006; Baker and Meese 2007; Baker et al 2007; Meese and Baker 2009). This is not shown in figure 6, but the scheme is easily extended to do this, and we have made explicit proposals elsewhere (Baker et al 2007; Baker and Meese 2007). The simplest method here would be to replace the sigmoidal output nonlinearities with dynamic contrast gain control with a broadly tuned suppression field (Foley 1994; Meese and Holmes 2010). This would involve inhibitory interactions amongst differently oriented mechanisms at level 2 in figure 6.(5) A second explanation of effect 2 is that masking arises within the isotropic filters at level 1 (Klein et al 1997; Meese and Holmes 2010). If the output characteristic of these cells were such that the cross-oriented mask reduced the effective contrast available to the subsequent stage of orientation filtering, then this would produce suppression while retaining the characteristics of the output nonlinearity at the decision stage. One way that this could be achieved would be from an isotropic suppression field, such as that identified in the retina (Shapley and Victor 1978) and LGN (Bonin et al 2005) of cats [see Meese and Holmes (2010) for further discussion, but also see Spratling (2011)].

The fact that cross-orientation masking is more potent at high stimulus speeds (effect 4) is not an emergent property of our model here, but it could be easily accommodated by the

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(5) The details are more complicated than this. Elsewhere (Baker et al 2007; Meese and Baker 2009) we have argued that the suppressive interactions arise after orientation tuning but before binocular summation. This implies an additional stage between stages 1 and 2 in figure 6.

appropriate setting of suppression weights in the contrast gain control at either level 1 or level 2 (Meese and Holmes 2007; Meese and Baker 2009).

The pedestal facilitation (effect 5) is explained in the conventional way (Legge and Foley 1980)—by arranging that the output nonlinearity accelerates at low contrasts, similar to the square-law process needed for energy (or power) detection (Meese 2010). This also produces a steep psychometric function at detection threshold (effect 8) (Foley and Legge 1981). Since none of our proposals for cross-orientation masking attribute the effect to within-channel excitation of isotropic detecting mechanisms (ie, we do not require that the observer is able to access the outputs of the isotropic filters in the masking experiment), the cross-oriented mask does not drive the sigmoidal output nonlinearity at the decision stage. Therefore, there is no facilitation (effect 6), and the psychometric function is steep for cross-orientation masking (effect 9) (Holmes and Meese 2004). However, it is shallow for pedestal masking (effect 7) because of the linearizing effect for small signal increments caused by the drive up the transducer (Foley and Legge 1981; Meese et al 2006).

4.2.4 *Model summary and interpretation.* For the purposes of this paper the important features of our model are illustrated in figures 1c and 6. As with previous proposals (Hubel and Wiesel 1962; Mooser et al 2004), oriented filters are fed by (arrays of) isotropic filters. However, the isotropic filters are also available for decision making, but only within monocular channels selective for low spatial frequencies and high temporal frequencies. Isotropic filters are also prone to adaptation in this corner of spatio-temporal vision. Taken together with results from neurophysiology (Solomon et al 2004), our model of achromatic vision might be interpreted as follows: the observer can tap into an image-representation at an earlier stage in the (transient) magnocellular stream than in the (sustained) parvocellular stream (the situation for *chromatic* vision is probably different, as we discuss below). However, the purpose of this monocular privilege remains unclear.

4.3 Comparisons with Kelly and Burbeck (1987)

The results of the adaptation and summation experiments here (experiments 2b and 3b) suggest that Kelly and Burbeck (1987) were wise (or fortuitous) to conduct their experiments monocularly. Indeed, for the experimental conditions used here this type of presentation is essential for revealing each type of cross-orientation interaction. This also follows from preliminary observations of adaptation recently reported by Cass (2010).

4.3.1 *Monocular summation.* In the high-speed corner of spatio-temporal vision the average level of cross-orientation summation found by us (2.6 dB) was only a little less than that found by Kelly and Burbeck (1987) (~ 3 dB). We note that Kelly and Burbeck reported results for only a single observer and that one of our six observers (RP) produced summation levels that were in excess of this (figure 5c). We have presented quantitative arguments (see the results section for experiment 3a) to suggest we might expect only modest effects of cross-orientation summation from isotropic mechanisms (2 to 3 dB) if spatial summation were a significant factor (see also Bergen et al 1979), consistent with our average results.

4.3.2 *Monocular adaptation.* A comparison between our monocular cross-adaptation results and those of Kelly and Burbeck reveals notable differences. We have replicated their finding that thresholds are elevated in the high-speed corner of spatio-temporal vision by adapting to an orientation at right angles to the target, but our effects (typically a little less than 3 dB) are notably smaller than theirs (typically a little greater than 6 dB). Why might this be? We wondered whether we might get larger effects at faster speeds, so DHB performed cross-orientation adaptation for 0.25 c/deg. adapter and target stimuli at 15 Hz (60 deg./s). This increased the after-effect of adaptation a little for this observer (from 2.2 dB at 0.5 c/deg.

to 4.6 dB at 0.25 c/deg.),(6) confirming that 'speed' is important (Kelly and Burbeck 1987) but still not achieving the higher levels found by Kelly and Burbeck. Furthermore, our main spatio-temporal conditions were comparable to some of those used by Kelly and Burbeck, so the question of why their effects were larger remains. Kelly and Burbeck used a slightly higher contrast adapter than us (95% versus 80%), a higher mean luminance (90cd/m^2 versus 16cd/m^2), and drifting adapters rather than our jittering adapters. Another factor is that the method used for monocular stimulation might be important. We used shutter goggles to present uniform mean luminance to the irrelevant eye. Unfortunately, Kelly and Burbeck (1987) do not report how they achieved monocularity, though an occluder is a likely possibility. It is also possible that the difference owes to the criterion sensitive (yes/no) methods used by Kelly and Burbeck (1987) compared with the criterion free 2IFC method used here.

Another factor relates to the method used for measuring the baselines for contrast detection thresholds. Previous studies have adopted two different approaches. In one (eg, Baker et al 2007) the baseline blocks of trials are identical to the experimental blocks, except that the adapter contrast is set to 0% (ie, observers adapt to a blank screen). This has the benefit of using consistent experimental protocols across the measures being compared but means that the baseline involves adaptation to mean luminance. This is a questionable comparison, since the visual system is normally 'adapted' to the natural images encountered in the real world (Elliot et al 2011). In the other approach (eg, Langley and Bex 2007) the adaptation periods (both pre and top-up) are removed from the experimental sequence. This avoids the artificial process of blank adaptation but has the disadvantage that the experimental sequence is not identical for the baseline and experimental measures that are to be compared. We used the second of these methods here, but it is not clear which method Kelly and Burbeck (1987) used. To check whether the method might be important, we ran a control experiment to compare baselines measured each way. For DHB and SB and a fast stimulus (0.5 c/deg., 15 Hz flicker) the baselines were 1.9 dB and 2.2 dB lower, respectively, when blank adaptation was used (typical standard error was 0.27 dB and 0.85 dB for DHB and SB, respectively). For the slow stimulus (2 c/deg, 2 Hz flicker) the effects were smaller (average difference of 0.5 dB) and in opposite directions for the two observers. Thus, a case could be made that we have underestimated the magnitude of the adaptation after-effects in our fast conditions by about 2 dB. Fortunately, this does not change any of our main conclusions or the model architecture that we propose in figure 6.

Whether any one or some combination of the factors above is responsible for the different levels of cross-orientation adaptation reported across studies remains unclear.

4.4 Further considerations

4.4.1 *Cascading stages of adaptation and spatial selectivity.* One feature of our model is the cascading stages of adaptation (levels 1 and 2 in figure 6a). We note that similar cascades have been suggested before (Georgeson and Schofield 2002; Shady et al 2004; Langley and Bex 2007). For example, Georgeson and Schofield (2002) used the tilt after-effect to reveal a cascade of orientation tuned stages (beyond the scope of the present study), whereas Langley and Bex (2007) identified an initial adaptable transient stage followed by a parallel pair of adaptable temporal channels. Whether our stage 1 filter is related to the initial temporal filter of Langley and Bex (2007) is not clear and would require a better understanding of the spatial selectivity of the filters in each case. For example, we have represented our initial stage (level 1) with a familiar icon for a spatially opponent receptive field (figure 6). However,

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(6) Facilitation from a dichoptic adapter (co-oriented and cross-oriented) was also confirmed for the 0.25 c/deg. adapter and target.

there is nothing in our data to demand that our level 1 filter is pattern selective (as we discuss further in the next section). It could be that its primary function is that of temporal selectivity.

4.4.2 *Generalization of spatio-temporal conditions.* The study here has concentrated on the high-speed corner of achromatic spatio-temporal vision. Burbeck and Kelly (1981), Meese and Holmes (2007), and Meese and Baker (2009) surveyed the entire spatio-temporal space using a cross-orientation masking paradigm for binocular, monocular, and dichoptic masks and targets. No similarly extensive study has been performed for adaptation or summation using criterion free methods, but the yes/no adaptation study of Kelly and Burbeck (1987) covered a substantial spatio-temporal region. In sum, it is possible that our results and conclusions from the 2 c/deg., 2 Hz Gabor stimuli do not generalize to the entire achromatic space outside the high-speed corner. Nonetheless, we are aware of no results to suggest that they might not, and the Kelly and Burbeck study suggests that they do, at least for adaptation.

4.4.3 *Chromaticity versus achromaticity.* In stark contrast to above, we do not generalize our conclusions (figure 1a and figure 6) to *chromatic* spatio-temporal space. In a preliminary report Mullen et al (2010) used the summation paradigm to reveal nonoriented chromatic (red/green) mechanisms—but not achromatic mechanisms—at low spatial frequency and *low* temporal frequency. Like their achromatic counterparts here, these mechanisms appeared to be strictly monocular. Intriguingly, the nonoriented monocularity is consistent with single-cell recordings in layer $4C\alpha$ and layer $4C\beta$ of primary visual cortex (Hubel and Wiesel 1968, 1977; Blasdel and Fitzpatrick 1984) for the achromatic and chromatic studies, respectively. The implication is that these cells not only provide convergent inputs to orientation-tuned filters (Mooser et al 2004), but their outputs (or similar) are also available to the observer for decision making.

4.4.4 *Our conclusions derive from the simplest model arrangement.* Our model in figure 6 is the simplest one we could devise to account for the majority of our data. As always, more complex models might be derived that can also account for the results, and these might change our interpretations and conclusions. For example, our claim that observers are able to access the outputs of a monocular stage of processing (for the high-speed stimuli) follows from the diminution of cross-orientation summation when the components were presented to different eyes (experiment 3b). However, another possibility is that this arises from interocular suppression across orientation between the targets in the different eyes. Indeed, we have proposed such pathways to account for the minor adaptation aftereffects of dichoptic cross-orientation facilitation that we observed, attributing that effect to disinhibition. However, the problem here is to devise a model in which cross-orientation suppression could arise from components that are themselves only at threshold. Indeed, studies where the relevant masking measures have been made (eg, Baker et al 2007; Meese and Baker 2009) suggest that suppression is not found until the mask component is above its own detection threshold.

4.4.5 *Further considerations.* Notwithstanding our comments above, our conclusions regarding perceptual access to an adaptable isotropic mechanism might require some elaboration. Using uniform flicker (ie, no spatial pattern) as adapt and test patterns, Shady et al (2004) report that flicker frequencies that are too high to be seen can serve as effective adapters. Meier and Carandini (2002) found a similar result for cross-orientation masking. In other words, each of these studies points to what is presumably an isotropic mechanism that can influence visual perception but for which the observer *cannot* access the output. These results can be reconciled with our account if a low pass temporal frequency filter (Langley and Bex 2007) were inserted between our level 1 filter and the output to the decision variable.

As it seems likely that this is subcortical [eg, see Meier and Carandini (2002) for a brief review], this temporal filtering is presumably positioned before binocular convergence in our scheme.

5 Summary

Our criterion-free psychophysical experiments confirm earlier findings of Kelly and Burbeck (Burbeck and Kelly 1981; Kelly and Burbeck 1987): cross-orientation interactions can be found in the high-speed corner of spatio-temporal vision but are diminished or absent elsewhere. However, Kelly and Burbeck attributed the results from all three paradigms (masking, adaptation, and summation) to a common explanation: that the detecting mechanisms are isotropic. In the light of a greater number of experimental conditions and analyses, we interpret these results rather differently, arguing that only the summation paradigm reveals nonoriented detecting mechanisms directly. Adaptation possibly reveals adaptable isotropic subunits of oriented filters, and masking reveals cross-orientation interactions from either oriented or isotropic mechanisms onto oriented detectors. We also conclude that the high-speed corner of spatio-temporal vision contains both oriented and nonoriented filters, but that the nonoriented variety is strictly monocular (figure 1c). We have argued that 16 of the 18 psychophysical effects reported here are consistent with a simple model of these processes involving only five design decisions and some simple elaborations. One further effect and two other relevant results in the literature are easily accommodated with simple extensions to our model. A notable property of our model (figure 6) is that if a filter is available for decision making, it is also adaptable.

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