

Double dissociation between first- and second-order processing

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Abstract

To study the difference of sensitivity to luminance- (LM) and contrast-modulated (CM) stimuli, we compared LM and CM detection thresholds in LM- and CM-noise conditions. The results showed a double dissociation (no or little inter-attribute interaction) between the processing of these stimuli, which implies that both stimuli must be processed, at least at some point, by separate mechanisms and that both stimuli are not merged after a rectification process. A second experiment showed that the internal equivalent noise limiting the CM sensitivity was greater than the one limiting the carrier sensitivity, which suggests that the internal noise occurring before the rectification process is not limiting the CM sensitivity. These results support the hypothesis that a suboptimal rectification process partially explains the difference of LM and CM sensitivity.

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1. Introduction

1.1. Luminance- and contrast-modulated sensitivity

We are less sensitive to contrast-modulated (CM) than to luminance-modulated (LM) stimuli (Fig. 1). Typically, first-order stimuli (ex: LM) are defined by luminance or color, and can be directly detected through Fourier analyses, while second-order stimuli (ex: CM) are defined by other attributes such as texture, orientation or spatial frequency, and cannot be directly detected through Fourier analyses (Baker, 1999; Cavanagh & Mather, 1989; Chubb & Sperling, 1988; Wilson, Ferrera, & Yo, 1992). There is no consensus on the type of nonlinearity enabling the system to process second-order stimuli and, more specifically, some researchers tried to determine whether the same mechanisms are involved in the detection of first- and second-order stimuli. Although this problem is debated in spatial and temporal vision, the present study will focus on the processing of static LM and CM stimuli (spatial

vision). As presented by Georgeson and Schofield (2002), the models illustrating the processing of these stimuli may be classified into three groups: Common mechanisms at all processing stages, completely separate mechanisms and initially separate but common late mechanisms.

1.1.1. Common mechanisms

In temporal vision (ex: direction discrimination of dynamic LM or CM stimuli), the common mechanism models suggest that motion detectors are sensitive to both types of stimuli. Although this hypothesis is not the most largely defended, some authors (Benton, 2002; Benton & Johnston, 2001; Benton, Johnston, McOwan, & Victor, 2001; Taub, Victor, & Conte, 1997) have shown that standard motion detection models processing first-order stimuli could also process second-order stimuli in certain conditions. For the detection of static LM or CM stimuli, the common mechanism hypothesis implies an early nonlinearity affecting the luminance profile of the stimulus enabling the LM processing system to also detect CM stimuli (illustrated by a compressive nonlinearity in the top row of Fig. 2 and first suggested in temporal vision by Henning, Hertz, & Broadbent (1975)). Although such nonlinearities

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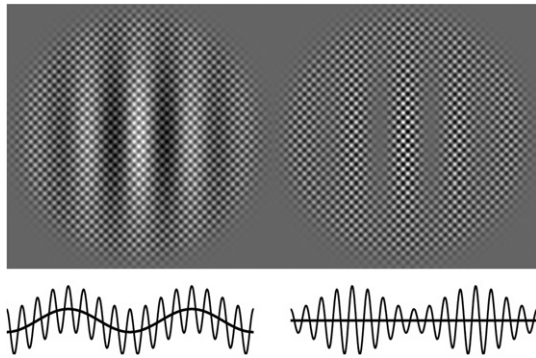


Fig. 1. A luminance- (left) and a contrast-modulated (right) stimuli, with their luminance profile (thin line). Thick lines represent the mean luminance variation at the signal spatial frequency.

are known to occur in the visual system (He & Macleod, 1998; Legge & Foley, 1980; MacLeod, Williams, & Makous, 1992), it is generally accepted that it cannot account for CM stimuli sensitivity in all conditions (Derrington & Badcock, 1985, 1986; Scott-Samuel & Georgeson, 1999; Smith & Ledgeway, 1997), which suggests the existence of another mechanism specialized in the detection of static CM stimuli.

1.1.2. Separate mechanisms

The second hypothesis suggests that separate mechanisms are processing both stimuli. Derrington and Badcock (1985, 1986) evaluated the processing of beat patterns (or CM stimuli) that are composed of two gratings defined at two different high spatial frequencies. The resulting stimulus appears to be one high spatial frequency grating periodically varying in contrast at a low spatial frequency. They found evidence that the processing of beat patterns has different qualitative processing behaviors from the processing of a low spatial frequency grating. For instance, they showed that increasing the temporal frequency reduced the detection threshold to low spatial frequency gratings but not to beat patterns. They also found that adaptation produced a motion aftereffect using low spatial frequency gratings but not using beat patterns. These results have led them to suggest that beat patterns (or CM stimuli) are processed by separated mechanisms evaluating the local contrast increment.

More recently in spatial vision, Georgeson and Schofield (Georgeson & Schofield, 2002; Schofield & Georgeson, 1999) found evidence supporting this hypothesis. They found that, although the processing of both stimuli induces similar responses (e.g. similar spatial (Schofield & Georgeson, 1999) and temporal (Schofield & Georgeson, 2000) integration, similar function shape relative to the spatial frequency (Schofield & Georgeson, 1999)), there is strong evidence suggesting that both stimuli are processed by separate mechanisms. To study this question, they used a facilitation paradigm in which observers were asked to identify a test modulation (LM or CM grating), in the presence of a background modulation (LM or CM grating). In one

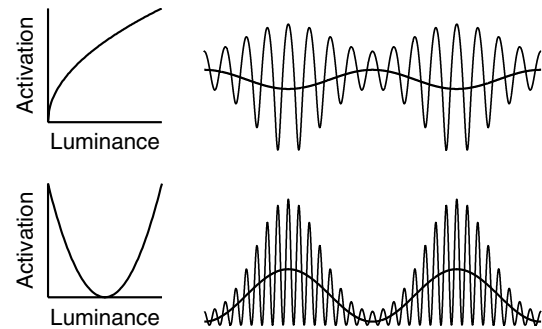


Fig. 2. The graphs on the left illustrate two types of nonlinearity that could enable the detection of CM stimuli. The top graph shows a compressive nonlinearity and the bottom one a rectification process. The resulting luminance profiles from passing the luminance profile of a CM stimulus (Fig. 1 on the right) through such functions are shown on the right using the thin lines. As we can observe, both nonlinearities introduce energy near the signal spatial frequency (illustrated by the thick lines showing the mean variation at the signal frequency).

interval, only the background grating was presented and in the other, the test grating was added to the background grating. The task consisted in identifying the interval containing the test grating. When the modulation depth of the background grating was near detection threshold, the detection of the test grating was facilitated in intra-attribute conditions (test and background gratings of the same modulation type), but not in inter-attribute conditions (gratings of different modulation types). In another experiment (Georgeson & Schofield, 2002), they found that the detection (LM vs noise and CM vs noise) and recognition (LM vs CM) thresholds were similar suggesting that both stimuli are not merged or confused. However, they also found evidence suggesting an interaction between the processing of the two stimuli. Adapting to one type of stimulus affected the perceived modulation depth (difference of luminance or contrast for LM and CM stimuli, respectively) of the other (Georgeson & Schofield, 2002). Based on these results, they concluded that separate mechanisms are processing both stimuli but share a common adaptation mechanism at a late processing stage. Since inter-attribute adaptation effects in high contrast conditions are not very pattern selective (Ross & Speed, 1996; Snowden & Hammett, 1992, 1996), they concluded that both stimuli are processed by separate mechanisms having similar properties with the exception of the common adaptation mechanism.

1.1.3. Initially separate and common late mechanisms

In temporal vision, the model in which both stimuli are initially treated by separate mechanisms but are processed by common motion detection mechanisms at a later stage (usually referred as filter-rectify-filter model, (Wilson et al., 1992)) is the most largely defended (see Baker (1999) for a review). This model illustrated in Fig. 3 suggests that a rectification (or squaring as illustrated in the bottom row of Fig. 2) process locally evaluates the intensity of the carrier (in our case, the local contrast) over the entire

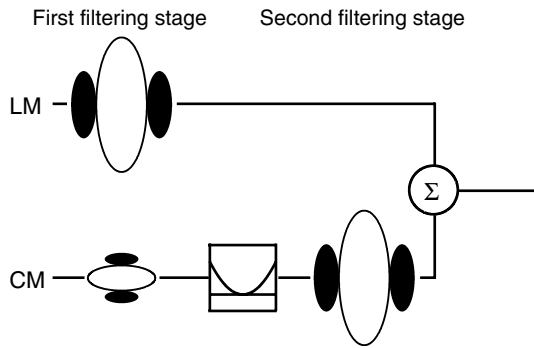


Fig. 3. The filter-rectify-filter model suggests that luminance- and contrast-modulated stimuli are initially processed by separate mechanisms and are combined after a rectification process occurring on the CM pathway. Adapted from (Baker, 1999).

stimulus making the second-order information similar to first-order information. This would then enable later mechanisms to process the combination of the first- and second-order information.

In a recent study on spatial vision (Allard & Faubert, 2006), we found additional evidence showing similar responses between the processing of LM and CM stimuli, which reinforce the hypothesis suggesting the existence of common post-rectification mechanisms other than an adaptation mechanism. Indeed, we decomposed both sensitivities into internal equivalent noise (IEN) and calculation efficiency (CE) (Pelli, 1981). The IEN may be defined as the noise contrast necessary to model the impact of the internal noise on the sensitivity. The CE is inversely proportional to the smallest signal-to-noise ratio (where the noise is composed of internal and external noise) the system needs to detect the signal. To derive the IEN and CE, we need to evaluate the detection threshold as a function of external noise contrast (the TvC function, Fig. 4). In high external noise conditions, the internal noise is not significant and the signal-to-noise ratio (or CE) can be measured since the signal and external noise contrast are known. Our results showed that the detection thresholds of both stimuli did not differ in high noise conditions, i.e. the CEs to these stimuli were similar. In other words, observers were just as efficient at detecting a LM signal embedded in LM noise as detecting a CM signal embedded in CM noise. Based on these similar efficiencies (and other responses such as the ones mentioned above) between the processing of both stimuli, we conclude that both stimuli are probably processed by common mechanisms after a rectification process converting the CM information (signal and noise) to an activation pattern similar to the LM information. In the general discussion below, we will explain more extensively how our conclusion can be compatible with Georgeson and Schofield's results mentioned above leading them to a different conclusion (separate mechanisms).

Since the difference of sensitivity between LM and CM stimuli is due to a difference of IEN and not to a difference of CE, studying the difference of sensitivity can be reduced

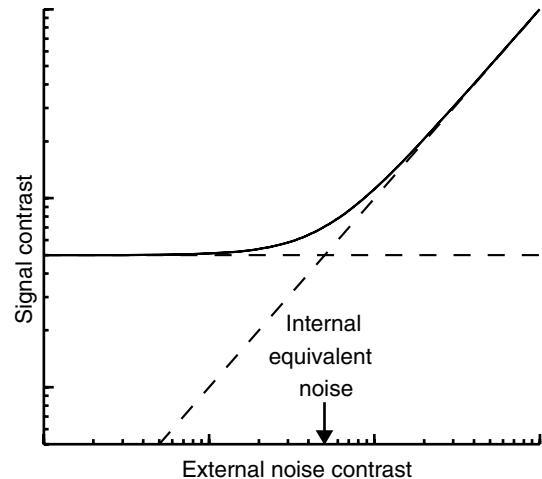


Fig. 4. Threshold versus contrast (TvC) function. The function shows the signal detection threshold as a function of the external noise contrast. Note that the two axes are scaled logarithmically.

to studying the difference of IEN, which is the aim of the present study.

1.2. Single internal noise source

An internal noise source may be defined as a signal deterioration occurring at any processing level such as photons transduction, signal transmission along the optical nerve, neuronal noise, etc. The IEN corresponds to the external noise quantity necessary to simulate the impact of the internal noise. Consequently, the IEN simulates the impact of the combination of all internal noise sources. Assuming that each noise source may be modeled by a Gaussian distribution centered on 0 with SD of σ_i and that the noise sources are not statistically related, the resulting standard deviation (σ_{total}) of their combination would be:

$$\sigma_{total} = \sqrt{\sum_i \sigma_i^2}$$

Therefore, the resulting SD of the combination of two uncorrelated patterns with SDs of σ_1 and σ_2 is $\sqrt{\sigma_1^2 + \sigma_2^2}$. Hence, if the difference between the two SDs is important, the resulting SD will not largely differ from the greater SD. The greater difference between the greater SD (σ_1 or σ_2) and the resulting SD (σ_{total}) occurs when $\sigma_1 = \sigma_2$. In such a case, the resulting SD will be $\sqrt{2}$ times greater.

The typical TvC function (Fig. 4), which may be used to decompose the sensitivity into IEN and CE, is a good example of the impact of the combination of two uncorrelated noise patterns. This function may be separated into three segments. If the external noise is small relative to the IEN, varying the external noise contrast does not significantly alter the effective noise (combination of internal and external noise) and the detection threshold remains relatively constant as a function of the external noise. However, in high noise conditions, the impact of the IEN is not significant and the effective noise contrast mainly

depends on the external noise. In such conditions, varying the external noise has a direct impact on the detection threshold, which is then proportional to the noise contrast (slope near 1 in log-log coordinates). The only segment in which the impact of both noise sources is noticeable is when the external noise contrast is near the IEN contrast.

Another example demonstrating that the impact of two noise sources generally behave as a winner-take-all rule is the absorbed-photon-noise occurring at the retinal level versus neural-noise occurring after luminance normalization that does not depend on the mean luminance. As presented by Pelli (1990), the IEN is greater in low than in high luminance conditions, he explains these results by two internal noise sources: one limiting the detection in low luminance conditions (absorbed-photon-noise) and another in high luminance conditions (neuronal-noise). The absorbed-photon-noise is not proportional to the stimulus luminance average but the neuronal-noise is since it occurs after luminance normalization. Consequently, if the luminance is sufficiently low, the resulting neuronal-noise is smaller than the absorbed-photon-noise, which does not vary according to the luminance average. As a result, the impact of the absorbed-photon-noise on the relative detection threshold (absolute minimum luminance variation detectable relative to the mean luminance background or Weber fraction) is then inversely proportional to the luminance average. However, in high luminance conditions, the internal noise measured (attributed to neuronal-noise) was proportional to the background luminance so the impact of such noise does not influence the relative detection threshold. Therefore, the visual system has at least two noise sources, one before the luminance normalization (absorbed-photon-noise) limiting the sensitivity in low luminance conditions and another after (neuronal-noise) limiting the sensitivity in high luminance conditions. These two examples show the interaction between two noise sources, where only the greater significantly affects the sensitivity and the smallest has no significant impact if their SDs largely differ.

1.3. Different IENs

Assuming the existence of different internal noise sources and that the greater one is significantly greater than the combination of the others, then the IEN measured models the impact of a single noise source. Consequently, when decomposing the sensitivity into IEN and CE, the former probably represents the impact of a single internal noise source. As mentioned above, the difference of LM and CM sensitivity can be attributed to a difference of IEN. Since the IEN probably models the impact of a single internal noise source for each stimulus type, comparing the sensitivity between LM and CM stimuli can be reduced to comparing the impact of their main internal noise sources (MINSs) limiting their sensitivities.

The fact that different IENs were measured for both types of stimuli does not necessarily imply that both

MINSs are distinct. Indeed, a low contrast gain (stimulus attenuation, which mathematically corresponds to reducing the contrast of the signal) prior to the MINS increases the impact of the internal noise and, thereby, increases the IEN measured. In high external noise conditions, a low contrast gain does not affect the observer's performance since it reduces both the signal and main noise source (external noise), which does not affect the signal-to-noise ratio. Consequently, a low contrast gain does not affect the CE. Stimulus attenuation prior to the MINS increases the impact of this internal noise source and thereby directly affects the IEN measured without affecting the CE. Therefore, the IEN measured represents the combination of the MINS with the contrast gains prior to it. However, these two parameters have the same impact on the TvC function (more specifically on the IEN), which led many authors (Bennett, Sekuler, & Ozin, 1999; Lu & Dosher, 1998) to state that both are mathematically equivalent and therefore cannot be segregated.

Since the IEN depends on the MINS and the contrast gain prior to it, the difference of IEN observed does not necessarily imply that separate mechanisms are processing LM and CM. The difference of IEN could be due to different contrast gains prior to a common noise source. For instance, an early nonlinearity enabling the detection of CM stimuli by the mechanisms processing LM stimuli could explain these results. In such a model, the local variation of luminance (local contrast) introduces an alteration in the local mean luminance. Consequently, the early nonlinearity would introduce a LM grating into the CM grating with a smaller modulation depth than the modulation depth of the CM grating. In other words, both stimuli would be processed by the same mechanisms but would have different contrast gains prior to their MINS. In high external noise conditions, the signal-to-noise ratio would be the same for both types of stimuli since the contrast gain would affect both the signal and the main noise source being the external noise. However, in low external noise conditions, only the signal would be affected by the contrast gain (not the MINS occurring after the nonlinearity) resulting in different signal-to-noise ratios (different detection thresholds). Consequently, we would observe different IENs for both types of stimuli even though they would be processed by the same mechanisms and share a common MINS.

1.4. Different types of external noise

Two spatial frequencies are relevant to define CM stimuli, the ones relevant to the carrier and the ones to the signal. The present study evaluates the impact of three different external noise types: LM noise near the signal spatial frequency, CM noise near the signal spatial frequency and LM noise near the carrier spatial frequency (which we will refer to as LM-noise, CM-noise and carrier-noise respectively, Fig. 5). Note that since CM information can only be defined at lower spatial frequencies relative to the



Fig. 5. LM- (left), CM- (center) and carrier-noise (right), all three in the presence of a carrier.

carrier, it is not possible to have CM noise near the carrier spatial frequency. Before the nonlinearity enabling the detection of CM stimuli (early nonlinearity or rectification process), the energy of the CM signal is near the carrier spatial frequency and energy near the signal spatial frequency only occurs after the nonlinearity making the CM information (signal and/or external noise) visible. Consequently, the CM detection threshold of an ideal observer is affected by CM- or carrier-noise, but not by LM-noise. LM-noise only affects the mean local luminance without affecting the local contrast defining the CM stimulus.¹ Oppositely, CM- and carrier-noise affects the local contrast without affecting the mean local luminance.

1.5. Purpose of the present study

The objective of the first experiment was to evaluate inter-attribute interactions between both types of modulations. If an early nonlinearity converts CM information into LM information or if both types of information are merged after a rectification process, we should expect inter-attribute interactions: CM-noise should affect LM signal detection and LM-noise should affect CM signal detection. However, if both attributes are initially processed by separate mechanisms (suggesting that a rectification process evaluates the local contrast of CM stimuli to enable its processing) and they are not merged after the rectification process, then we should observe no or little inter-attribute interaction: noise of one attribute should have little impact on the signal detection of the other.

After showing that both stimuli are initially processed by separate mechanisms (CM detection is due to a rectification process evaluating the carrier contrast and not to an early nonlinearity converting CM information into LM information, see Fig. 2), the second objective was to determine if the MINS limiting CM sensitivity occurs before the rectification or not. Before the rectification process making CM information visible, the processing can be reduced to

¹ If the local contrast is defined as the local difference of luminance relative to the local mean luminance (as opposed to the local difference of luminance relative to the background mean luminance of the entire stimulus), then altering the mean local luminance would affect the local contrast. As a result, it may be argued that the LM component is “leaking” in the CM component. However, the results obtained in the present study showed that, if such interaction exists, it had no significant impact.

treating the carrier. The second experiment was aimed at evaluating if the MINS limiting the detection of the carrier also limits the CM detection. To do so, this experiment evaluated the impact of carrier-noise on the carrier and CM detection.

2. Experiment 1: Inter-attribute interactions

In a previous study (Allard & Faubert, 2006), we showed that observers were just as efficient at detecting LM signal embedded in LM-noise as to detect CM signal embedded in CM-noise. The first objective of the present study was to evaluate if LM and CM stimuli are processed, at least at some point, by separate mechanisms. To do so, the interactions between the processing of LM and CM stimuli were evaluated by measuring LM and CM stimuli detection threshold embedded in LM- and CM-noise (intra- and inter-attribute conditions). The absence of inter-attribute facilitation found by Schofield and Georgeson (1999) using a near threshold signal as background suggests that separate mechanisms are processing these stimuli. We could therefore expect to find no inter-attribute masking effect using noise as a background. Such double dissociation between LM and CM stimuli processing (i.e. LM-noise affecting more LM than CM stimuli detection and CM-noise affecting more CM than LM stimuli detection) would support the hypothesis suggesting the existence of a separate rectification mechanism processing CM stimuli, i.e. separate mechanisms are initially processing both stimuli. It would also imply that both stimuli are not merged to form a single activation pattern after the rectification. On the other hand, if an early nonlinearity in the visual system enables the detection of CM stimuli or if both attributes are merged after a rectification process, then LM- and CM-noise would affect both LM and CM signal detection, since CM information (signal and noise) would be converted into LM information.

2.1. Method

2.1.1. Observers

Three subjects aged 26, 27 and 27 years participated to the study. They had normal or corrected to normal vision. One of them (ra) was an author and the others were naive to the purpose of the experiment.

2.1.2. Apparatus

The stimuli were presented using a 19 in ViewSonic E90FB .25 CRT monitor with a mean luminance of 43 cd/m² and a refresh rate of 100 Hz, which was powered by a Pentium 4 computer. The 10-bit Matrox Parhelia512 graphic card could produce 1024 gray levels that could all be presented simultaneously. The monitor was the only light source in the room. A Minolta CS100 photometer interfaced with a homemade program calibrated the output intensity of each gun. At the viewing distance of 1.14 m, the

width and height of each pixel were 1/64 deg of visual angle.

2.1.3. Stimuli

All the stimuli used in the present experiment are the sum of two terms: a luminance modulation ($M_{LM}(x,y)$) and the multiplication of a contrast modulation ($M_{CM}(x,y)$) with a texture ($T(x,y)$):

$$L(x,y) = L_0[M_{LM}(x,y) + M_{CM}(x,y)T(x,y)]$$

where L_0 represents the luminance average of the stimulus and the background luminance. Both modulations ($M_{LM}(x,y)$ and $M_{CM}(x,y)$) may be defined as

$$M(x,y) = 1 + S(x,y) + N(x,y)$$

where $S(x,y)$ and $N(x,y)$ are the signal and external noise functions respectively.

2.1.3.1. Signal function. The signal function ($S(x,y)$) was a Gabor patch (Fig. 6 left) with a center spatial frequency of 1 cpd, a SD of 1 deg, a phase randomized at each stimulus presentation and a Michelson contrast (C_{LM} or C_{CM} depending on the type of modulation) that varied depending on the task (see below).

2.1.3.2. External noise. The noise function ($N(x,y)$) generated a matrix of 320 times 320 pixels (5 times 5 deg), each element being randomly selected from a Gaussian distribution centered on 0. Each noise template was bandpass filtered by applying an ideal circular filter in the Fourier domain to keep all the orientations and only the frequencies within one octave below and above the relevant spatial frequency (1 cpd for the first experiment (Fig. 6 right) and 8 cpd for the second experiment). The SD of the Gaussian distribution before the filtering corresponded to the noise contrast in modulation depth (N_{ExtLM} or N_{ExtCM} depending on the type of modulation), which varied from one task to another.

2.1.3.3. Carrier. The carrier ($T(x,y)$, Fig. 6 center) was a plaid, i.e. the sum of two sinusoidal gratings. The spatial frequency of the gratings was 8 cpd and their orientations were oblique and perpendicular from one another (± 45 deg). Such a carrier has the advantage of being defined within a narrow band spectral frequency. Conse-

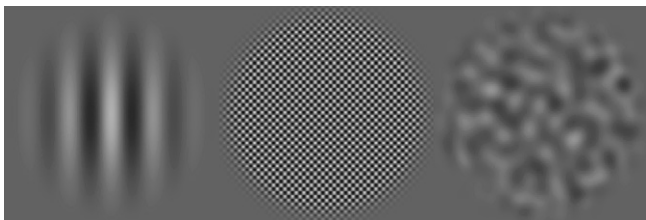


Fig. 6. Signal (Gabor patch, left), carrier (plaid, center) and filtered noise near the signal spatial frequency (right).

quently, the carrier had a limited impact on the sensitivity to LM stimuli defined at a lower spectral frequency. Using noise as a carrier does not have this advantage since it introduces noise at the signal frequency, which may mask the MINS. Another advantage of using a narrow band carrier is that it is easier to introduce noise that will selectively affect the carrier frequencies without affecting the signal frequency as was done in the second experiment. The phases of the two oblique sinusoidal gratings forming the carrier were randomized at each stimulus presentation and the contrast was set so that, in the absence of signal and noise, the luminance peaks were $0.25L_0$ and $0.75L_0$ (i.e. $-0.5 \leq T(x,y) \leq 0.5$).

2.1.4. Procedure

In all the conditions, a 2-interval-forced-choice method was used: one interval contained a carrier modulated by a signal and noise, and the other contained only a carrier modulated by noise. The task was to identify which interval contained the signal (LM or CM Gabor patch). Different noise templates with the same contrast were used in the two intervals. For a given task (detection of a LM or CM signal in LM or CM noise), the signal and noise modulation types were fixed and known to the observer. The stimuli were presented for 500 ms with stimuli intervals of the same duration. The spatial window was circular with a full contrast plateau of 4 deg width and soft edges following a Gaussian distribution with a SD of 0.25 deg. After each trial, a feedback sound indicated to the observer if his response was correct. To evaluate thresholds, a 2-down-1-up procedure was used (Levitt, 1971), that is, after two consecutive correct responses the dependant variable, which varied depending on the task, was decreased (or increased when the dependant variable was a noise contrast) by 10% and increased (or decreased) by the same proportion after each incorrect response resulting in a threshold criterion of 70.7%. For each threshold measured, 100 trials were performed and the threshold was defined as the geometric mean of the last 6 inversions (peaks) of the dependant variable values.

The experiment was conducted in three consecutive steps. The objective of the present experiment (the last step) was to evaluate LM and CM sensitivity in LM- and CM-noise conditions (see Fig. 7 for stimuli examples). Prior to evaluating the impact of different noise types on LM and CM signal detection, we had to determine the noise contrast of the two noise types (second step), which were arbitrarily set to the noise contrast increasing the detection thresholds of their respective stimulus by 0.5 log units. Thus, the first step consisted in measuring the detection thresholds of their respective stimulus, i.e. LM and CM stimulus, in noiseless conditions.

Hence, for the first step, the noise contrasts (N_{ExtLM} and N_{ExtCM}) were set to 0. For each modulation signal detection, the signal contrast of the relevant modulation (C_{LM} or C_{CM}) was the dependant variable while the other was set to 0.

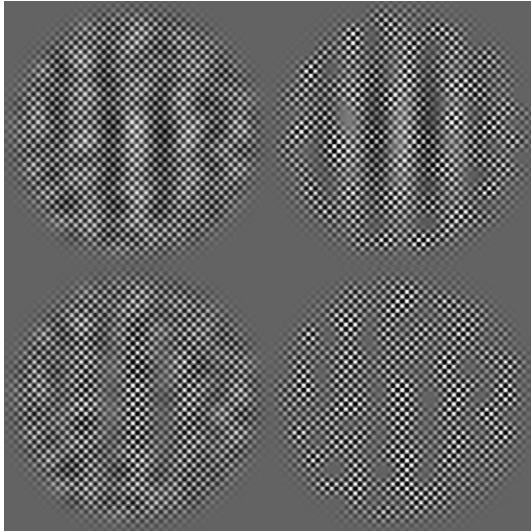


Fig. 7. LM signal (top row) and CM signal (bottom row) embedded in LM- (left column) and CM-noise (right column).

The second task consisted in defining the noise contrast for each noise modulation. Therefore, for each modulation signal detection, the dependant variable in the previous task (C_{LM} or C_{CM}) was fixed to 0.5 log units above the threshold found for each subject and the noise contrast (N_{ExtLM} or N_{ExtCM}) became the dependant variables. Note that the noise contrast increasing the CM detection threshold was so high that the contrast modulation function had to be truncated ($0 < M_{CM}(x,y) < 2$). Near threshold, this truncation reduced the RMS of the contrast modulation function by less than 1%. We therefore assumed that it had no significant impact on the results.

After fixing the two noise contrasts, the final step consisted in detecting the LM and CM stimuli in these noise contrasts resulting in 4 staircases (2 signal \times 2 noise types). For each noise type, the noise contrast was set to the one measured in the previous step while the other was kept to 0. One signal contrast (C_{LM} or C_{CM}) was the dependant variable while the other was fixed to 0.

2.2. Results

Table 1 shows the LM and CM detection thresholds in noise free conditions (first step) and the noise contrasts necessary to increase each detection threshold by 0.5 log units, respectively (second step) for each subject. In the absence

of noise, observers were more sensitive to LM than CM stimuli by a factor of 15, 14 and 11 for subjects *il*, *jmh* and *ra* respectively. In similar proportions (factors of 11, 15 and 10 respectively), greater external noise contrasts were required to affect the CM signal detection because of a greater IEN for CM detection (Allard & Faubert, 2006).

2.2.1. Double dissociation between LM and CM stimuli detection

Fig. 8 shows the LM and CM signal detection thresholds measured in LM- and CM-noise. As expected, thresholds in intra-attribute noise conditions (LM and CM signals embedded in LM- and CM-noises respectively) were near 0.5 log units above the ones obtained in noiseless conditions (or close to, learning or measurement errors may explain the small differences). Oppositely, in the inter-attribute conditions, thresholds were similar or slightly above the ones in noiseless conditions. The important results are that, for all three observers, intra-attribute noise had a greater impact than inter-attribute noise for both types of modulation. Consequently, the detection threshold of LM stimuli increased more in LM- than in CM-noise conditions and the detection of CM stimuli was more affected by CM- than LM-noise. These results show a clear double dissociation between LM and CM stimuli processing. It is therefore possible to define a condition that selectively impairs the processing of one attribute while keeping the processing of the other relatively intact.

2.3. Discussion

2.3.1. Initially separate mechanisms

This double dissociation between LM and CM stimuli processing implies that both stimuli are, at least at some point, processed by separate mechanisms. Therefore, in agreement with the general consensus in the literature, the detection of static CM stimuli is not due to early nonlinearities (at least not in all conditions) in the visual system making the stimulus detectable through the same mechanisms processing LM stimuli. If this was the case, CM-noise would interfere with LM processing and *vice versa*, and a double dissociation would not be observed. By rejecting the common mechanisms hypothesis, the present data support the existence of a rectification mechanism independent of the mechanisms processing LM stimuli enabling the

Table 1

The first two columns show the detection thresholds for both types of modulations. The last two columns show the noise contrast (prior to the bandpass filtering) that was necessary to increase the respective detection threshold by 0.5 log units. The data are expressed as the geometric mean \times/\div geometric standard error

Subjects	Detection threshold		Noise threshold	
	LM	CM	LM	CM
<i>il</i>	0.0074 \times/\div 1.039	0.11 \times/\div 1.042	0.59 \times/\div 1.157	6.2 \times/\div 1.071
<i>jmh</i>	0.0070 \times/\div 1.057	0.10 \times/\div 1.035	0.42 \times/\div 1.042	6.4 \times/\div 1.032
<i>ra</i>	0.0034 \times/\div 1.050	0.039 \times/\div 1.144	0.33 \times/\div 1.062	3.4 \times/\div 1.030

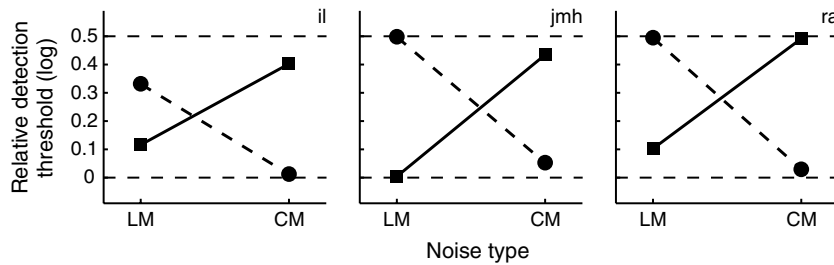


Fig. 8. LM and CM signal detection in LM and CM noise. Y-axis shows the elevation detection threshold relative to the detection threshold in the absence of noise. The X-axis shows the two noise conditions: LM- and CM-noise. The circles show the relative detection thresholds for LM signals and the squares for CM signals.

detection of CM stimuli. In such a model, CM stimuli processing would require an extra processing stage converting CM information into an activation pattern analogous to LM information by evaluating the local contrast over the entire stimulus. Afterwards, both stimuli would be similar and could be processed by common mechanisms (initially separate but common late mechanisms hypothesis) explaining the similarities between the processing of both stimuli or could still be treated by separate post-rectification mechanisms (separate mechanisms hypothesis).

It is worth noting that Schofield and Georgeson (1999) found that a high contrast LM background signal masked the detection of CM signal but not vice-versa. These results differ from ours in which no inter-attribute interaction was observed. However, our results are not necessarily inconsistent with theirs since, as opposed to their methodology, we evaluated the impact of a mask at only one contrast level. Consequently, it is possible that greater noise contrasts would also cause an asymmetrical inter-attribute interaction.

2.3.2. No post-rectification merging

The double dissociation between LM and CM stimuli processing also implies that, after a second-order rectification, both stimuli are not merged to form a single activation pattern. If both stimuli were merged and then processed by common mechanisms, inter-attribute noise would also impair the detection. Consequently, our results reinforce the conclusion emitted by Georgeson and Schofield (2002) that both stimuli are not merged or combined after a second-order rectification process. However, as defended in the general discussion below, we do not agree with their interpretation that the absence of post-rectification merging implies separate post-rectification mechanisms.

3. Experiment 2: Pre-rectification internal noise

The first experiment suggested that CM detection is due to the existence of a rectification mechanism evaluating the carrier contrast and not to an early nonlinearity converting CM information into LM information. Since the CM detection initially requires the processing of the carrier, the aim of the present experiment was to evaluate whether

the MINS limiting the CM sensitivity occurs before the rectification process or later.

As mentioned above, prior to the rectification process, the energy of a CM stimulus is near the carrier spatial frequency. Locally, a CM stimulus affects the local contrast of the carrier and therefore does not affect its spatial frequency. Globally, however, modifying the local contrast of a carrier gives rise to energy slightly off the central spatial frequency of the carrier (side-band components). Since the receptive fields in V1 respond to frequencies one octave above and below their central spatial frequency (Campbell & Robson, 1968), it is generally accepted that the detection of CM stimuli cannot be reduced to the processing of side-band components (Derrington & Badcock, 1985, 1986). Therefore, we will assume that the carrier central spectral frequency and its side-bands components stimulate the same receptive fields (and thereby the same receptive fields as an unmodulated carrier) and that observers detect CM stimuli by evaluating the local contrast increment rather than by detecting the presence of side-band components.

We can also reasonably assume that an unmodulated carrier and a CM stimulus both stimulating the same receptive fields, are detected using the same receptive fields. Indeed, for efficiency reasons, it would be unlikely to have similar receptive fields using some for the carrier detection and others for the first filtering stage of the CM detection. Based on these assumptions, the processing of an unmodulated carrier and a CM stimulus share the same initial pathways (the first filtering stage of the CM pathway shown in Fig. 3). Thus, the MINS limiting the carrier sensitivity may also be the MINS limiting the CM sensitivity. If this was the case, an external noise greater than the impact of this common MINS should significantly affect the detection thresholds to both stimuli (carrier and CM stimuli). Otherwise, if the external noise is greater than the MINS limiting the sensitivity to the carrier but smaller than the one limiting the CM sensitivity, then the carrier sensitivity would be affected but not the CM sensitivity.

3.1. Method

Since the method was very similar to the one used in the previous experiment, the present section only mentions their differences. Two tasks were performed in different

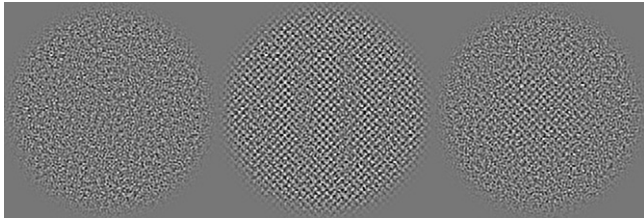


Fig. 9. Carrier-noise without a carrier (left), CM signal embedded in carrier-noise (center) and carrier with a Gaussian envelope with standard deviation of 1 deg in carrier-noise (right). In all three stimuli, the carrier-noise contrast (N_{ExtLM}) is 0.5.

noise contrasts: detection of the CM signal and detection of the carrier. Compared to the previous experiment, the noise was filtered near the carrier spatial frequency (carrier-noise, >4 and <16 cpd, Fig. 9) instead of the signal spatial frequency. No CM-noise was used ($N_{CM} = 0$) and five noise contrasts (SD of the Gaussian distribution before applying the bandpass filter) were used for the LM noise function (which now represents the carrier-noise): $N_{LM} = 0, 0.0625, 0.125, 0.25$ and 0.5 modulation depths. The task consisting in detecting the CM stimuli was identical to the one in the previous experiment with the exception of the noise: the dependant variable was the signal contrast (C_{CM}) and the task consisted in discriminating the interval containing the CM signal from two intervals containing a carrier embedded in noise. For the detection of the carrier, the Michelson contrast of the texture was the dependant variable and the contrasts of both envelopes (C_{LM} and C_{CM}) were fixed to 0. Consequently, one interval contained the carrier embedded in noise and the other contained only noise. Since we were interested in the detection of the carrier near the signal, which was a Gabor patch with a spatial window of 1 deg of standard deviation, the same Gaussian window was used for the carrier detection. The order of the ten staircases (2 tasks \times 5 noise levels) was randomized.

To separate the sensitivity into IEN and CE, the typical TvC function fitted to the data was (Legge, Kersten, & Burgess, 1987; Pelli, 1981; Pelli, 1990):

$$C(N_{ext}) = k\sqrt{N_{eq}^2 + N_{ext}^2}$$

where $C(N_{ext})$ represents the detection threshold in the noise contrast N_{ext} . The two parameters fitted were k and N_{eq} . k is inversely proportional to the CE and N_{eq} repre-

sents the IEN. The fit consisted in minimizing the sum of the differences in log units between the evaluated thresholds and the ones estimated by the fit ($C(N_{ext})$).

3.2. Results

For the carrier detection task, the IENs were 0.085, 0.051 and 0.063 noise contrast for the observers il, jmh and ra respectively. For CM detection task, the IENs were 0.32, 0.56 and 0.15, respectively, although we should consider that the IEN evaluated for observers il and jmh is likely to be inaccurate because of the absence of detection threshold in high noise conditions (considerably above the IEN). However, as it can be observed in Fig. 10, the IEN for CM stimuli detection for these two observers was near the maximum noise contrast used (0.5) or greater since the detection threshold difference between the greater noise contrast condition and the absence of noise is relatively small. The IEN for the detection of CM stimuli was consistently greater than the IEN for the detection of the carrier by a factor of 3.8, 10.1 and 2.4, respectively.

3.3. Discussion

3.3.1. Pre-rectification noise not a limiting factor

Since the IEN for the detection of the carrier was smaller than the IEN measured for the detection of CM stimuli, it is possible to find a given noise condition (carrier-noise with a contrast level between the two IENs) affecting the detection of the carrier without significantly affecting the detection of the CM stimuli. In other words, such a noise level would be greater than the MINS limiting the carrier sensitivity, but smaller than the one limiting the CM sensitivity. We therefore conclude that the MINS limiting the CM sensitivity cannot occur at a processing level common with the carrier detection and must occur after the carrier and CM detection pathways have separated. Since the only processing prior to the rectification is related to the carrier, the present results suggest that the MINS limiting the CM sensitivity does not occur before the rectification but at or after the rectification.

3.3.2. Inter-subject difference

The IENs measured for the carrier sensitivities of the observers were very similar between all three subjects.

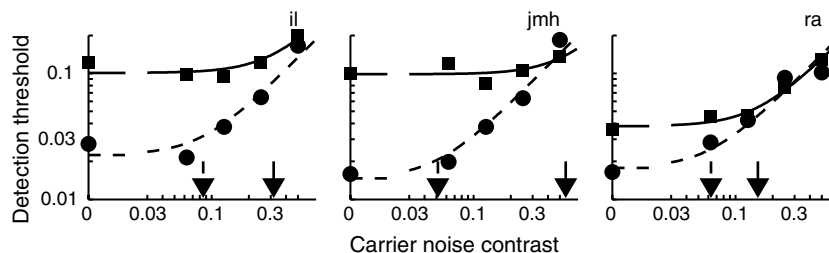


Fig. 10. CM (squares) and carrier (circles) detection thresholds in carrier-noise. Full- and dash-lines show best TvC function fits for CM and carrier detections respectively and arrows corresponds to the IENs.

However, this was not the case for the IENs limiting the CM sensitivity, in which the observer ra (one of the authors) had considerably smaller IEN compared to the two other observers. A possible explanation is that this observer had participated in a greater amount of psychophysical testing using CM stimuli. As shown by Doshier and Lu (2006), learning may reduce the IEN without affecting the CE for CM sensitivity. As a result, the contrast of the carrier-noise necessary to be greater than the MINS would be smaller resulting into a smaller difference between the two IENs for this observer. Note that this observation does not change the fact that, for all three observers, pre-rectification internal noise cannot explain the IEN measured.

4. General discussion

4.1. Common post-rectification mechanisms

Although we agree with Georgeson and Schofield's (2002) conclusion that LM and CM stimuli are not merged after a second-order rectification process applied to a CM stimulus (which thereby rejects, at least for static stimuli, the filter-rectify-filter model illustrated in Fig. 3), we do not agree that this implies that both stimuli are processed by separate post-rectification mechanisms. Post-rectification mechanisms could be able to process both attributes (luminance or contrast) without merging them. Separate processing does not imply separate mechanisms. As illustrated by a modified filter-rectify-filter model in Fig. 11, late mechanisms could process one attribute while ignoring the other. In other words, attentional selection could allow late mechanisms to focus on a single attribute. This modified filter-rectify-filter model can explain the similar responses, such as spatial and temporal integration and CEs, observed during the processing of either attribute and can also explain the lack of interaction between both types of stimuli since ignoring one attribute would limit its impact on the processing of the other.

This model could also explain that adapting to one attribute could affect the processing of the other since the adap-

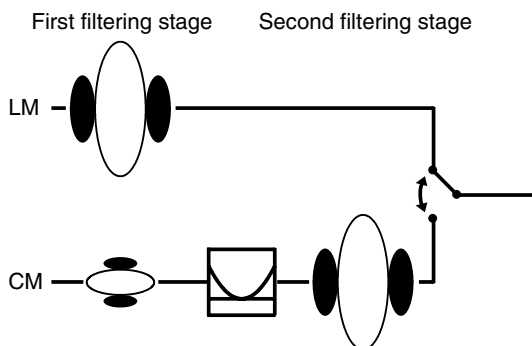


Fig. 11. A modified filter-rectify-filter model in which the late mechanisms can focus on either attribute (LM or CM) and ignore the other compared to the original filter-rectify-filter model (Fig. 3) suggesting that both attributes are combined.

tation could affect the mechanisms that are common to both pathways. As mentioned in the introduction, some data found by Georgeson and Schofield suggest that common late mechanisms could process both stimuli. They found an important inter-attribute tilt after-effect and an almost complete adaptation transfer effect on the perceived contrast to the cross-attribute stimulus. However, since they found that both stimuli are not merged (because of no sub-threshold summation), they concluded that they must be processed by separate mechanisms with the exception of a common adaptive mechanism. We argue that they share more than adaptive mechanisms and that it is because they share common mechanisms that it is possible to observe cross-type adaptation.

As an analogy demonstrating that common late mechanisms processing two stimuli do not imply merging them, consider a visual search task in which the target is either a red or a green vertical bar within distracters composed of blue vertical bars. We can reasonably assume that the observer's performance will be similar for either target. Now suppose that red horizontal bars are also added as distracters. Based on Treisman and Gelade's (1980) study on visual search, the search of the green target would now require the processing of a single attribute (color) while the search of the red target would require the conjunction of two (color and orientation). As a result, the presence of these two distracters (blue vertical and red horizontal bars) would affect more the observer's ability of searching the red than the green vertical bar. In the presence of green instead of red horizontal bars added as distracters, the opposite results would be obtained. This double dissociation (red horizontal bars affecting the search of the red vertical bar but not the search of the green vertical bar and *vice versa*) would lead to the correct conclusion that green and red bars are processed, at least at some point, by separate mechanisms. This is true because at the retinal level red and green are not absorbed by the same cones. However, it is highly improbable that we have a distinct searching mechanism for each color. Even though the same searching mechanism is used for searching both targets, we will certainly be able to show, using other tasks, that both colors are not merged or confused. Consequently, the visual search mechanism would be common to both colors even though these colors are not merged. Thus, the processing of these stimuli would invoke similar responses without, or with few, interactions. Red and green targets would not be confused, the presence of one would not affect the detection of the other and it would be possible to find two conditions (presence of blue vertical bars combined with the presence of either red or green horizontal bars) that would result in a double dissociation showing that they are processed, at least at some point, by separate mechanisms. Consequently, the fact that a higher-level mechanism is processing two stimuli regardless of their attributes does not imply that these attributes are lost and that the presence of one affects the processing of the other or that we should confuse one with the other.

This analogy shows that the fact that LM and CM stimuli are not merged or confused (lack of inter-attribute interaction) and the presence of a double dissociation does not imply that separate post-rectification mechanisms are processing both stimuli. Oppositely, we argue that processing similarities and inter-attribute adaptation effects suggest that both stimuli are processed by common post-rectification mechanisms able to select either attribute. We find more parsimonious the conclusion that both attributes are processed by common post-rectification mechanisms than the conclusion that they are processed by separate similar mechanisms sharing only an adaptation mechanism.

4.2. No impact of pre-rectification internal noise on CM sensitivity

As mentioned in the introduction, the CM detection threshold of an ideal observer would be affected by CM-noise or carrier-noise but not by LM-noise. For human observers, the first experiment showed that LM-noise also had no or little impact on the CM detection threshold. Consequently, pre-rectification internal noise at the signal spatial frequency cannot be a limiting factor, since such noise does not affect the CM sensitivity. The second experiment showed that the MINS limiting the CM sensitivity was greater than the one limiting the detection of the carrier, which implies that the MINS limiting the CM sensitivity must occur once the two pathways have separated. Consequently, pre-rectification internal noise at the carrier spatial frequency cannot be a limiting factor, since it is possible to add external noise greater than this internal noise (which affects the carrier detection) without affecting the CM sensitivity. Since the CM stimuli used in the present study were defined near two spatial frequencies (carrier and signal) and that pre-rectification noise (analogous to LM noise) at either spatial frequency cannot be limiting the CM sensitivity, we conclude that the internal noise occurring before the rectification process does not, in the present conditions, limit the CM sensitivity.

4.3. Impact of the first filtering stage

In a previous study, we decomposed the sensitivity to LM and CM stimuli into IEN and CE, and found similar CEs using both stimuli (Allard & Faubert, 2006). Consequently, although the CE is a factor affecting the CM sensitivity, it does not explain the difference of sensitivity between LM and CM stimuli processing. The present study therefore focused on the difference of IEN. In the introduction, we showed that the IEN may also be separated into two factors: the MINS and a contrast gain prior to the MINS, which affects the signal strength and therefore affects the impact of the MINS.

The last experiment showed that the MINS limiting the CM sensitivity is not analogous to (or cannot be modeled by) adding LM noise to the stimulus either at the signal

or carrier spatial frequency. We conclude that the MINS limiting the CM sensitivity must occur either at or after the rectification process. The fact that the MINS occurs after the first filtering stage does not imply that the processing at this filtering stage does not have an impact on the IEN. It rather implies that the internal noise occurring at the first filtering stage does not have a significant impact on the IEN and thereby on the sensitivity. However, contrast gain (signal attenuation or enhancement) prior to the MINS would affect the impact of the MINS and thereby affect the IEN measured. Therefore, the contrast gain occurring at the first filtering stage is a factor determining the IEN and should be considered when comparing LM and CM sensitivity.

For instance, Schofield and Georgeson (1999) have shown that the CM sensitivity is affected by the carrier contrast probably because of a compressive nonlinearity affecting the carrier. A compressive nonlinearity would affect the carrier contrast unevenly depending on the local contrast (defined by the CM signal) and would thereby affect the signal strength of the CM signal. As a result, the CM sensitivity would depend on the carrier contrast and stimulus attenuation prior to the compressive nonlinearity (analogous to lowering the carrier contrast) would influence the signal strength. As stated in the introduction, reducing the signal strength would increase the impact of the MINS without affecting the CE. Consequently, the IEN is not entirely due to second-order processing and, although first-order noise is not a limiting factor, first-order factors such as stimulus attenuation prior to the compressive nonlinearity and the compressive nonlinearity itself also affects the IEN.

4.4. Suboptimal second-order processing?

If pre-rectification noise near the carrier spatial frequency would have been the MINS for CM sensitivity, then the difference of IEN (thereby the difference of sensitivity) between LM and CM processing would have been entirely due to first-order limitations since the IEN (the MINS and the contrast gain prior to it) would have occurred at the first filtering stage. We would have been less sensitive to CM than LM stimuli not because they are more complex or require more computation, but simply because CM processing initially requires the processing of the carrier, which introduces noise. Excluding first-order factors is specially important when evaluating clinical populations such as aging (Faubert, 2002; Habak & Faubert, 2000) and autism (Bertone, Mottron, Jelenic, & Faubert, 2003, 2005) in which reduced CM sensitivity has been attributed to second-order processing.

The results of the present study suggest that the MINS limiting the CM sensitivity occurs after the first filtering stage. As we have previously shown (Allard & Faubert, 2006), a suboptimal rectification process evaluating the local contrast would affect the IEN without affecting the CE. In other words, the rectification process could be suboptimal and thereby limit the CM sensitivity by signifi-

cantly introducing noise (that is, by being the MINS) and/or by attenuating the signal strength. Consequently, the rectification process (half-wave rectification, full-wave rectification or any other type of rectification) evaluating the carrier contrast over the entire stimulus is a potential candidate for the MINS. Further investigations are required to determine the proportion of the IEN due to the signal attenuation at the first filtering stage and the one due to the suboptimal rectification process.

5. Conclusion

In a previous study, we evaluated the detection of LM and CM stimuli embedded in LM and CM noises, and found that observers had the same sensitivity to both stimuli in high noise conditions. The present study evaluated the detection of LM and CM stimuli embedded in three different noise types: LM-, CM- and carrier-noise. We found a double dissociation between LM and CM stimuli detection in the presence of LM- and CM-noise. LM-noise had a greater impact on LM processing than on CM processing, while CM-noise had a greater impact on CM processing than on LM processing. This double dissociation implies that both stimuli are, at least at some point, processed by separate mechanisms. Combining these results to the ones found in a previous study where similar CEs were observed for LM and CM stimuli detection, we conclude that the processing of CM stimuli requires an extra rectification process but that both stimuli are processed by common post-rectification mechanisms.

Our results also demonstrate that the IEN limiting the sensitivity to the carrier was smaller than the one limiting the sensitivity to CM stimuli. We conclude that pre-rectification noise is small relative to the total amount of internal noise and therefore does not limit the CM sensitivity. We suggest that the internal noise limiting the sensitivity to CM stimuli is caused by a suboptimal rectification.

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References

- Allard, R., & Faubert, J. (2006). Same calculation efficiency but different internal noise for luminance- and contrast-modulated stimuli detection. *Journal of Vision*, 6(4), 322–334.
- Baker, C. L. Jr., (1999). Central neural mechanisms for detecting second-order motion. *Current Opinion in Neurobiology*, 9(4), 461–466.
- Bennett, P. J., Sekuler, A. B., & Ozin, L. (1999). Effects of aging on calculation efficiency and equivalent noise. *Journal of the Optical Society of America, A, Optics, Image Science, and Vision*, 16(3), 654–668.
- Benton, C. P. (2002). Gradient-based analysis of non-Fourier motion. *Vision Research*, 42(26), 2869–2877.
- Benton, C. P., & Johnston, A. (2001). A new approach to analysing texture-defined motion. *Proceedings of the Biological Science*, 268(1484), 2435–2443.
- Benton, C. P., Johnston, A., McOwan, P. W., & Victor, J. D. (2001). Computational modeling of non-Fourier motion: further evidence for a single luminance-based mechanism. *Journal of the Optical Society of America, A, Optics, Image Science, and Vision*, 18(9), 2204–2208.
- Bertone, A., Mottron, L., Jelenic, P., & Faubert, J. (2003). Motion perception in autism: a “complex” issue. *Journal of Cognitive Neuroscience*, 15(2), 218–225.
- Bertone, A., Mottron, L., Jelenic, P., & Faubert, J. (2005). Enhanced and diminished visuo-spatial information processing in autism depends on stimulus complexity. *Brain*, 128(Pt 10), 2430–2441.
- Campbell, F. W., & Robson, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *Journal of Physiology*, 197(3), 551–566.
- Cavanagh, P., & Mather, G. (1989). Motion: the long and short of it. *Spatial Vision*, 4(2-3), 103–129.
- Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A*, 5(11), 1986–2007.
- Derrington, A. M., & Badcock, D. R. (1985). Separate detectors for simple and complex grating patterns? *Vision Research*, 25(12), 1869–1878.
- Derrington, A. M., & Badcock, D. R. (1986). Detection of spatial beats: non-linearity or contrast increment detection? *Vision Research*, 26(2), 343–348.
- Dosher, B. A., & Lu, Z.-L. (2006). Level and mechanisms of perceptual learning: learning first-order luminance and second-order texture objects. *Vision Research*, 46(12), 1996–2007.
- Faubert, J. (2002). Visual perception and aging. *Canadian Journal of Experimental Psychology*, 56(3), 164–176.
- Georgeson, M. A., & Schofield, A. J. (2002). Shading and texture: separate information channels with a common adaptation mechanism? *Spatial Vision*, 16(1), 59–76.
- Habak, C., & Faubert, J. (2000). Larger effect of aging on the perception of higher-order stimuli. *Vision Research*, 40(8), 943–950.
- He, S., & Macleod, D. I. (1998). Contrast-modulation flicker: dynamics and spatial resolution of the light adaptation process. *Vision Research*, 38(7), 985–1000.
- Henning, G. B., Hertz, B. G., & Broadbent, D. E. (1975). Some experiments bearing on the hypothesis that the visual system analyses spatial patterns in independent bands of spatial frequency. *Vision Research*, 15, 887–897.
- Legge, G. E., & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the Optical Society of America*, 70(12), 1458–1471.
- Legge, G. E., Kersten, D., & Burgess, A. E. (1987). Contrast discrimination in noise. *Journal of the Optical Society of America A*, 4(2), 391–404.
- Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *Journal of the Acoustical Society of America*, 49 (2), Suppl 2:467+.
- Lu, Z. L., & Dosher, B. A. (1998). External noise distinguishes attention mechanisms. *Vision Research*, 38(9), 1183–1198.
- MacLeod, D. I., Williams, D. R., & Makous, W. (1992). A visual nonlinearity fed by single cones. *Vision Research*, 32(2), 347–363.
- Pelli, D. G. (1981). *The effects of visual noise*. Department of Physiology, Ph.D. Cambridge: Cambridge University.
- Pelli, D. G. (1990). The quantum efficiency of vision. In C. Blakemore (Ed.), *Visual coding and efficiency*. Cambridge: Cambridge University Press.
- Ross, J., & Speed, H. D. (1996). Perceived contrast following adaptation to gratings of different orientations. *Vision Research*, 36(12), 1811–1818.
- Schofield, A. J., & Georgeson, M. A. (1999). Sensitivity to modulations of luminance and contrast in visual white noise: separate mechanisms with similar behaviour. *Vision Research*, 39(16), 2697–2716.
- Schofield, A. J., & Georgeson, M. A. (2000). The temporal properties of first- and second-order vision. *Vision Research*, 40(18), 2475–2487.
- Scott-Samuel, N. E., & Georgeson, M. A. (1999). Does early non-linearity account for second-order motion? *Vision Research*, 39(17), 2853–2865.

- Smith, A. T., & Ledgeway, T. (1997). Separate detection of moving luminance and contrast modulations: fact or artifact? *Vision Research*, 37(1), 45–62.
- Snowden, R. J., & Hammett, S. T. (1992). Subtractive and divisive adaptation in the human visual system. *Nature*, 355(6357), 248–250.
- Snowden, R. J., & Hammett, S. T. (1996). Spatial frequency adaptation: threshold elevation and perceived contrast. *Vision Research*, 36(12), 1797–1809.
- Taub, E., Victor, J. D., & Conte, M. M. (1997). Nonlinear preprocessing in short-range motion. *Vision Research*, 37(11), 1459–1477.
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12(1), 97–136.
- Wilson, H. R., Ferrera, V. P., & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience*, 9(1), 79–97.