Spatial-frequency tuning in the pooling of one- and two-dimensional motion signals

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ABSTRACT

Cortical neurons that initially extract motion signals have small receptive-fields, and narrow orientation- and bandpass-spatial-frequency tuning. Accurate extraction of the veridical motion of objects typically requires the global pooling of the output of multiple local-motion units across orientation and space. We examined whether the narrow spatial-frequency tuning present at the local-motion level is preserved at the global-motion-pooling stage. Stimuli consisted of numerous drifting Gabor or plaid elements that were either signal (carrier drift-speed consistent with a given global-motion vector) or noise (drift speed consistent with a random, noise vector). The carrier spatial-frequencies of the signal and noise elements were independently varied. Regardless of the frequency of the signal elements, broad low-pass masking functions were obtained for both Gabor (one-dimensional) and Plaid (two-dimensional) conditions when measuring the threshold signal ratio for identification of the global-motion direction. For the Gabor stimuli, this pattern of results was also independent of the relative orientations of the signal and noise elements. These results indicate that in the global-motion pooling of one-dimensional and two-dimensional signals, local-motion signals of all spatial frequencies are pooled into a single system that exhibits broadband, low-pass tuning.

1. Introduction

The processing of motion information in the human visual system occurs in a number of distinct stages (Born & Bradley, 2005; Britten, 2004; Movshon, Adelson, Gizzi, & Newsome, 1985; Newsome, Britten, & Movshon, 1989; Snowden, 1994). Initial detection of motion occurs via cells that have oriented and relatively small receptive-fields, which frequently leads to the well known aperture problem (Adelson & Movshon, 1982; Fennema & Thompson, 1979; Marr & Ullman, 1981). These cells can be thought of as extracting a one-dimensional (1D) component of an object's motion. The activity of these local-motion cells is then pooled across orientation and/or space to extract the veridical, two-dimensional (2D) motion of spatially extended objects (Amano, Edwards, Badcock, & Nishida, 2009).

Recent evidence has shown that the type of global pooling that occurs (i.e. the pooling of motion information across space) depends upon the amount of information contained in the stimulus at a local level (Amano, Edwards, et al., 2009). If local-motion signals are 1D, e.g. the moving carrier in a 1D Gabor, it is not possible to solve the aperture problem locally, and so the motion system pools these signals following the intersection-of-constraints (IOC) or a functionally similar rule (Adelson & Movshon, 1982; Simoncelli & Heeger, 1998; Weiss, Simoncelli, & Adelson, 2002). However, if the local-motion signals are 2D, e.g. dots or locally-defined plaid stimuli, it is possible to locally solve the aperture problem to generate 2D signals, and so the motion system pools these signals via a vector-averaging or functionally similar process (Mingolla, Todd, & Norman, 1992; Webb, Ledgeway, & McGraw, 2007). Additionally, previous studies have shown that local-motion cells are tuned for spatial-frequency (Anderson, Burr, & Morrone, 1991; Priebe, Lisberger, & Movshon, 2006). Given these earlier studies, two questions of interest arise. The first is whether spatial-frequency tuning is preserved in the global-motion pooling of these local signals, and secondly, whether the tuning is the same in the pooling of both 1D and 2D signals even though the pooling processes differ (Amano, Edwards, et al., 2009).

A number of previous studies have examined the issue of spatial-frequency tuning in global-motion pooling. Studies that have examined the pooling of 1D stimuli have typically used standard plaid-stimuli while those that have investigated the pooling of 2D stimuli have employed spatially-localised, moving envelope stimuli, such as dots. Plaid stimuli consist of two drifting, spa-

tially-overlapping 1D sine-wave gratings that have different orientations (Adelson & Movshon, 1982). A common response measure used is the type of percept elicited by the stimulus: transparent motion of the component sine-wave gratings or the coherent (plaid) motion that results from a rigid combination of the two sine-waves. Perception of transparency is interpreted as indicating that pooling of the 1D component sine-waves has not occurred and plaid motion as indicating that it has. Thus if two, different spatial-frequency sine-wave gratings are not perceived to cohere, it is taken as evidence of independent, spatial-frequency-tuned pooling systems. The results of studies that have employed plaid stimuli are somewhat complex. For angular differences between the component motions of 45° or less, coherence is typically perceived, regardless of the differences in the spatial-frequency content of the gratings (Kim & Wilson, 1993; Yo & Wilson, 1992). This finding has been taken as indicating the presence of broadband pooling. However, for angular differences greater than 45°, coherence is only perceived with gratings of a similar spatial frequency, i.e. narrow-band pooling (Kim & Wilson, 1993).

Yang and Blake (1994) and Bex and Dakin (2002) used stimuli that contained 2D local-motion cues. Yang and Blake used bandpass spatially-filtered dots while Bex and Dakin used circular-symmetric difference-of-Gaussian (DoG) stimuli. They investigated the extent to which randomly moving (noise) stimuli at one spatial-frequency affected the extraction of a global-motion signal carried by stimuli at a different spatial frequency. Both studies found broad-band tuning. Specifically, all spatial frequencies appeared to be combined into a common (vector-averaging) global-motion system.

While these studies can be interpreted as indicating the degree of spatial-frequency tuning in the pooling of 1D (plaid) and 2D (dot and DoG) stimuli, there are a number of potential limitations with them that question the degree to which their findings actually reflect the spatial-frequency tuning of (first-order) motion pooling. Critically, previous studies have not examined spatial-frequency tuning in the pooling of 1D motion signals across space. In the studies that used standard-plaid stimuli, the pooling of the different 1D signals may have been performed at the same spatial-location and in those studies that used bandpass-dots and DoG stimuli, performance may have reflected the pooling of 2D, rather than 1D motion signals. In addition, a moving, spatially-localised stimulus, like a luminance-defined dot or DoG, drives both the first-order (luminance-based) and second-order (contrast-based) motion systems (Cavanagh & Mather, 1989; Chubb & Sperling, 1988; Edwards & Badcock, 1995). Given that there appears to exist both first-order and second-order global-motion systems (Badcock & Khuu, 2001; Edwards & Badcock, 1995), it is possible that the broad-band tuning observed in the studies that used the spatially-localised 2D stimuli may reflect the tuning of the second-order system to the stimulus envelope. Similarly, with plaid stimuli, the intersection of the two sine-wave components produces a second-order stimulus and it is possible that variations in the strength of this second-order component as a function of orientation difference between the component sine-waves may have influenced performance (Derrington, Badcock, & Holroyd, 1992; Wilson, Ferrera, & Yo, 1992).

In order to cleanly investigate spatial-frequency tuning of both the first-order 1D and 2D pooling processes, it is necessary to use stimuli that can selectively drive those systems, allow for fine manipulation of their spatial-frequency content and are not contaminated by second-order information. To achieve this, we used the global-Gabor and global-plaid stimuli developed by Amano, Edwards, et al. (2009). The 1D global-Gabor stimuli consist of numerous, spatially distributed, stationary Gabor elements with a drifting-carrier grating (Fig. 1a and c). While the orientation of the sine-wave carrier in each Gabor is randomly assigned, the drift rate of each carrier (i.e. its orthogonal motion) can be made consistent with a global, IOC-determined, 2D velocity. Under these conditions, observers see rigid-pattern motion. A subset of the Gabors can be made into noise elements by giving them drift rates that are incompatible with the global 2D motion. Since the envelopes of each Gabor patch remain stationary there is no informative second-order motion signal with these stimuli. The 2D global-plaid stimuli are similar to the global-Gabor stimuli except that the Gabor elements are replaced by local plaids, that is, two sine-wave gratings windowed by a stationary Gaussian (Fig. 1b).

2. Experiment 1: spatial-frequency tuning in the pooling of 1D stimuli

The first experiment examined spatial-frequency tuning in the pooling of 1D stimuli. This was achieved by using global-Gabor stimuli and determining how noise Gabors at one spatial-frequency affected the ability to extract the global-motion signal carried by Gabors at a different spatial frequency.
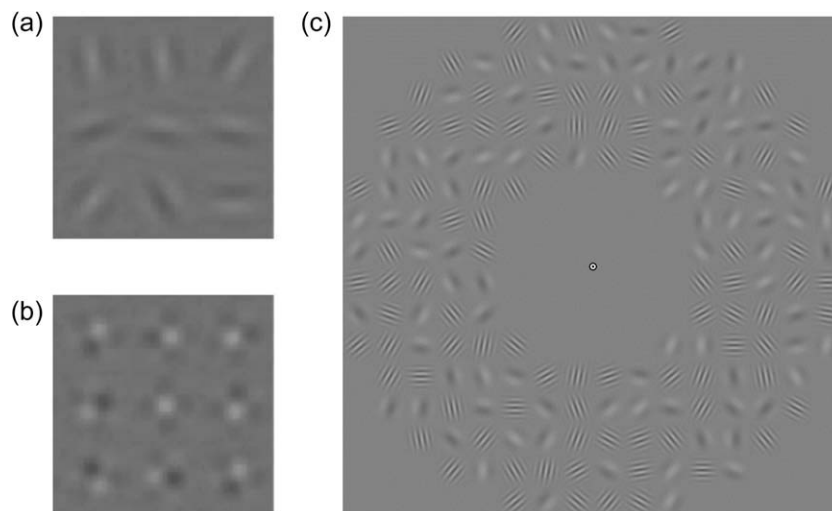

Fig. 1. Examples of the stimuli used in the current experiments: (a) A portion of the global-Gabor stimulus. (b) A portion of the global-plaid stimulus. (c) A depiction of the stimulus layout used for the current global-Gabor experiments in which the signal and noise Gabors had different spatial frequencies.

2.1. Methods

2.1.1. Observers

Two of the authors (KA and SN) and one naïve observer (AM) participated in all of the experiments. All observers had normal, or corrected to normal spatial acuity and had no history of any visual disorders.

2.1.2. Apparatus

Stimuli were generated using a Cambridge Research System's ViSaGe graphics card and presented on a 21 in. CRT (Sony GDM-F500) at a frame rate of 100 Hz.

2.1.3. Stimuli and procedure

Global-Gabor stimuli, which consist of numerous Gabor elements, were used (Amano, Edwards, et al., 2009). Each Gabor element had a stationary Gaussian envelope (SD = 0.4°) and was drawn within a 2° square window. A total of 192 Gabors were presented in an annular viewing aperture that had an inner diameter of 6° and outer diameter of 32° (Fig 1c). Stimuli were presented for 200 ms and observers viewed the monitor at a distance of 52 cm, with their head stabilized by a chin rest.

Spatial-frequency tuning was examined by determining the masking effect that noise Gabors at one spatial frequency had on the extraction of a signal carried by Gabors at another spatial frequency. The signal Gabors were defined by having a carrier motion (direction and speed) that was consistent with a common, global 2D vector. X% of the Gabors were signal and the remaining Gabors $(100 - X$%) were noise, whose carrier drift speeds and directions were consistent with 2D vectors that were in random directions. The carrier orientation of each signal and noise Gabor was randomly selected from a range covering the full 180°, in 10° steps. Signal spatial frequencies were: 0.7, 1.4 and 2.8 c/deg, and noise spatial frequencies were 0.7, 1.0, 1.4, 2.0 and 2.8 c/deg. The Gabor contrast used was five times the direction-discrimination threshold for that particular spatial frequency (see below). The 2D speed for both the signal and noise Gabors was 2 deg/s and the signal

direction was randomly selected from eight directions (0, 45, ..., 315° from vertical) for each trial. The signal density was adaptively changed via a staircase procedure. Signal intensity started at 100%, two consecutive correct trials reduced the proportion of signal Gabors by $1/2^{0.25}$, and one incorrect trial increased the proportion of signal by $2^{0.25}$. A staircase terminated after six reversals and the threshold signal-intensity (X) for 71% correct performance was estimated from the average of the last four reversal points. For each observer, four staircases were run for each spatial frequency combination. Observers' responses were collected via a button box.

2.1.4. Establishing contrast thresholds for direction-discrimination

For the purpose of equating stimulus detectability across different spatial frequencies, the luminance contrast of the Gabors was matched in terms of their direction-discrimination thresholds. The procedure was the same as the main experiment described above except that staircase procedure varied the contrast level, while the proportion of signal Gabors was kept at 100%. The measured contrast thresholds for 71% correct direction-discrimination with [0.7, 1.0, 1.4, 2.0, 2.8] c/deg were [3.4%, 2.8%, 3.2%, 3.7%, 6.0%] for KA, [3.6%, 3.4%, 3.8%, 4.6%, 7.2%] for SN, and [4.3%, 3.9%, 3.7%, 3.3%, 5.0%] for AM, respectively.

2.2. Results and discussion

Fig. 2 shows the results of all individual observers. Threshold signal-intensities are plotted against the noise spatial-frequency for the various signal-spatial-frequency conditions. Higher thresholds indicate stronger masking. The pattern of results is the same for all three observers. Regardless of the spatial frequency of the signal, the effectiveness of the mask increased (thresholds increased) as the noise spatial-frequency was reduced (see also Supplementary movies). These results suggest broadband, low-pass tuning of 1D motion pooling. Note, however, that, the shape of the masking curves appears to vary slightly across the three signal spatial-frequencies. Specifically, masking strength appears to fall less steeply with increasing signal frequency. This interaction be-
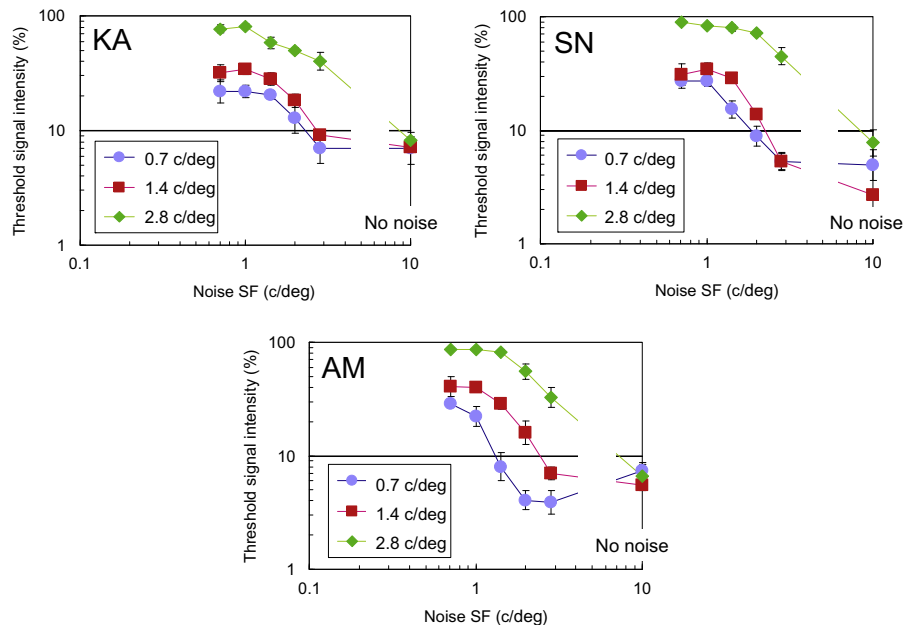

Fig. 2. The results for Experiment 1, which examined spatial-frequency tuning in the pooling of 1D local-motions using a global-Gabor stimuli. For each observer, the threshold signal-intensities for identification of the global-motion direction are plotted as a function of the spatial-frequency of the noise for the three signal-frequencies. The rightmost points are the thresholds obtained without noise. Error bars indicate ±1 standard error of the mean. The pattern of results indicates broad, low-pass spatial-frequency tuning.

tween the frequencies of the signal and noise could indicate that the frequency tuning of the underlying mechanism cannot be simply described by a single tuning function. However, the relatively flat function for the highest signal frequency can be ascribed, at least partially, to a ceiling effect. The signal intensity had an upper-bound of 100%, and the observers performed the task perfectly without noise. As a result, a potential difference between effective noise maskers could be underestimated at the high signal-level region. This ceiling effect cannot account for the difference between the two lower signal-frequencies, however another factor could account for that difference. This issue was addressed in Experiment 4 below.

The observed broadband masking effect for 1D motion pooling is qualitatively consistent with those previously obtained with bandpass-dot and DoG patterns (Bex & Dakin, 2002; Yang & Blake, 1994) that presumably tapped 2D motion pooling. To make a more direct comparison of spatial-frequency tuning between 1D and 2D pooling processes, the next experiment investigated masking effects with 2D stimuli, that are comparable to those used in Experiment 1, by using global-plaid stimuli.

3. Experiment 2: noise masking in 2D pooling

While the first experiment investigated spatial-frequency tuning in the pooling of 1D motion stimuli, this experiment investigated spatial-frequency tuning with 2D stimuli (i.e. those that provide a 2D solution locally) by using global-plaid stimuli.

3.1. Methods

Experimental procedures were exactly the same as for Experiment 1 except that global-plaid stimuli were presented (Fig. 1b). Within each plaid patch, two orthogonal sinusoidal gratings of the same spatial frequency were linearly added, and windowed by a Gaussian. The contrast of each grating in a plaid patch was identical to the grating contrast of the corresponding Gabor patch used in Experiment 1 (i.e., five times the direction identification threshold).

3.2. Results

Fig. 3 shows the results for each observer individually. The masking effect had broad, low-pass tuning. Except for a general improvement in performance that may flow from local-motion unambiguity and the higher Michelson contrast of the compound plaid elements, the pattern of results were very similar to that obtained with global-Gabor stimuli.

4. Experiment 3: noise masking in 1D pooling: effect of orientation

Previous studies that used standard-plaid stimuli found that apparent spatial-frequency tuning depended upon the orientation difference between the component sine-waves that made up the plaid (Kim & Wilson, 1993). To account for this finding, Kim and Wilson proposed a model in which motion signals are integrated within each spatial scale, with facilitative across-scale interactions within similar directions (which implies within similar orientations in the case of the plaid). The aim of the current experiment was to determine whether the spatial-frequency tuning of the masking observed with the global-Gabor stimuli in Experiment 1, i.e. without the use of plaids, also depends upon the relative orientations of the sine-wave gratings of the Gabors.

4.1. Methods

Two conditions were used to investigate the effect of orientation on the spatial-frequency tuning of masking. In one condition the signal and noise Gabors had the same range of orientations while in the other they were selected from different orientation-ranges. In same-orientation condition, the orientations of both the signal ($X\%$) and noise Gabors ($100 - X\%$) were randomly chosen from a uniform distribution covering 0 (horizontal)±20°. In the different-orientation condition, the signal orientations were randomly chosen from $0 \pm 20°$ and the noise orientations from 90 (vertical) ±20°. The minimum orientation difference between signal and noise Gabors in this condition was 50°. The spatial-fre-
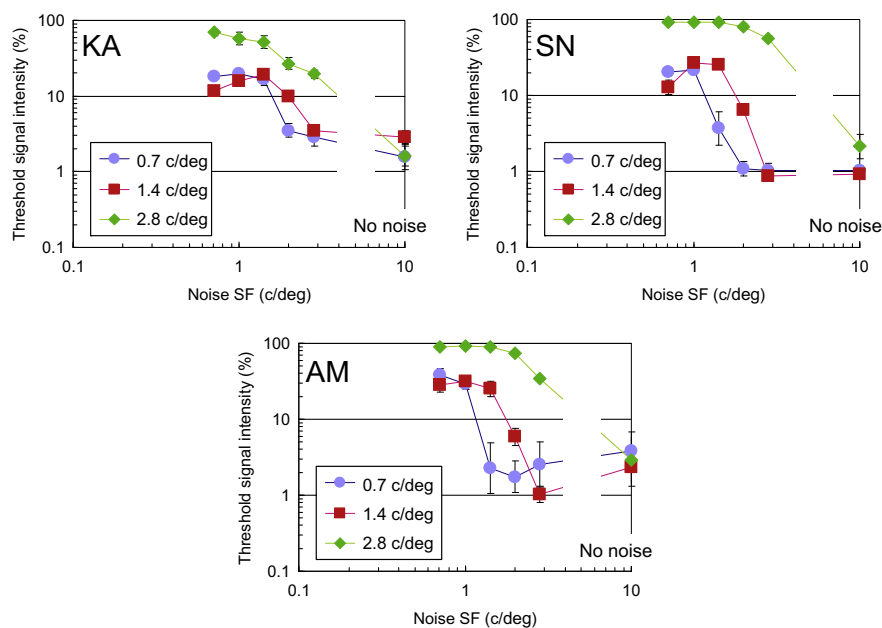

Fig. 3. The results for Experiment 2, which examined spatial-frequency tuning in the pooling of 2D local-motions using global-plaid stimuli. For each observer, the threshold signal-intensities for identification of the global-motion direction are plotted as a function of the spatial-frequency of the noise for the three signal-frequencies. The rightmost points are the thresholds obtained without noise. The pattern of results indicates broad, low-pass spatial-frequency tuning.

quency combinations tested were the same as in Experiment 1. The signal direction was randomly chosen from four directions: 90 (right) ± 20° and 270 (left) ± 20°. This more limited range of signal directions, compared to the previous experiments, was used because signal directions beyond this range, in combination with the narrow orientation distribution of the signal Gabors, resulted in a stimulus with a similar orientation relationship to Type II plaids (Wilson & Kim, 1994). Under these conditions, the perceived global-motion direction tended to deviate from the intended physical value (IOC direction) towards the mean orthogonal direction of the Gabor orientations, as we have previously shown with Type II global-Gabor motion (Amano, Edwards, et al., 2009). All other aspects of the methods were the same as those used in Experiment 1.

4.2. Results and discussion

The results are shown in Fig. 4. The patterns of spatial-frequency tuning of the masking effect obtained under the two orientation conditions were very similar to each other (compare upper and lower sub-plots for each observer), and to that obtained in random-orientation condition (Experiment 1). Since relative orientation seems unimportant to the outcome, these results do not support the model of Kim and Wilson (1993) at least as an account of global spatial pooling of 1D motion signals.

5. Experiment 4: spatial range of 1D pooling

Our results indicate that low-spatial-frequency local-motion signals contribute to global-motion pooling more strongly than high-spatial-frequency signals. One possible reason for this low-pass tuning is that the spatial pooling area is scaled with the carrier-frequency content, being larger for low- than for high-frequency motion signals (Anderson & Burr, 1987). It is important

to test this hypothesis, since it assumes a system structure more complex than assumed by the single-pooling system idea. The last experiment therefore examined whether the spatial pooling range of global-Gabor motion varied with carrier spatial frequency.

5.1. Methods

We examined how the detectability of global-motion direction was affected by the inter-patch separation. To increase the patch separation to N, we presented only one Gabor every N lines both horizontally and vertically. In other words, we erased $(N - 1)$ lines for every N lines without changing the original regular Gabor grid structure. This reduced the density to $1/N^2$. N varied from 1 to 5, corresponding to 2–10° separation. The spatial position of the presentation lines was changed randomly for every trial. All the Gabor elements were signal, giving a common 2D vector chosen from eight directions. The proportion of correct direction identification was measured for 0.7 and 2.8 c/deg at each patch separation.

5.2. Results and discussion

The results are shown in Fig. 5. The performance of direction identification gradually declined with increasing patch separation. The curves for frequencies between 0.7 and 2.8 c/deg were very similar. This suggests that the range of spatial pooling does not change with stimulus carrier-frequency, at least for the spatial frequencies used in the current study.

6. General discussion

The present study examined spatial-frequency tuning of global-motion pooling of 1D and 2D local-motion signals by using a noise-masking paradigm. The results indicate that all spatial frequencies
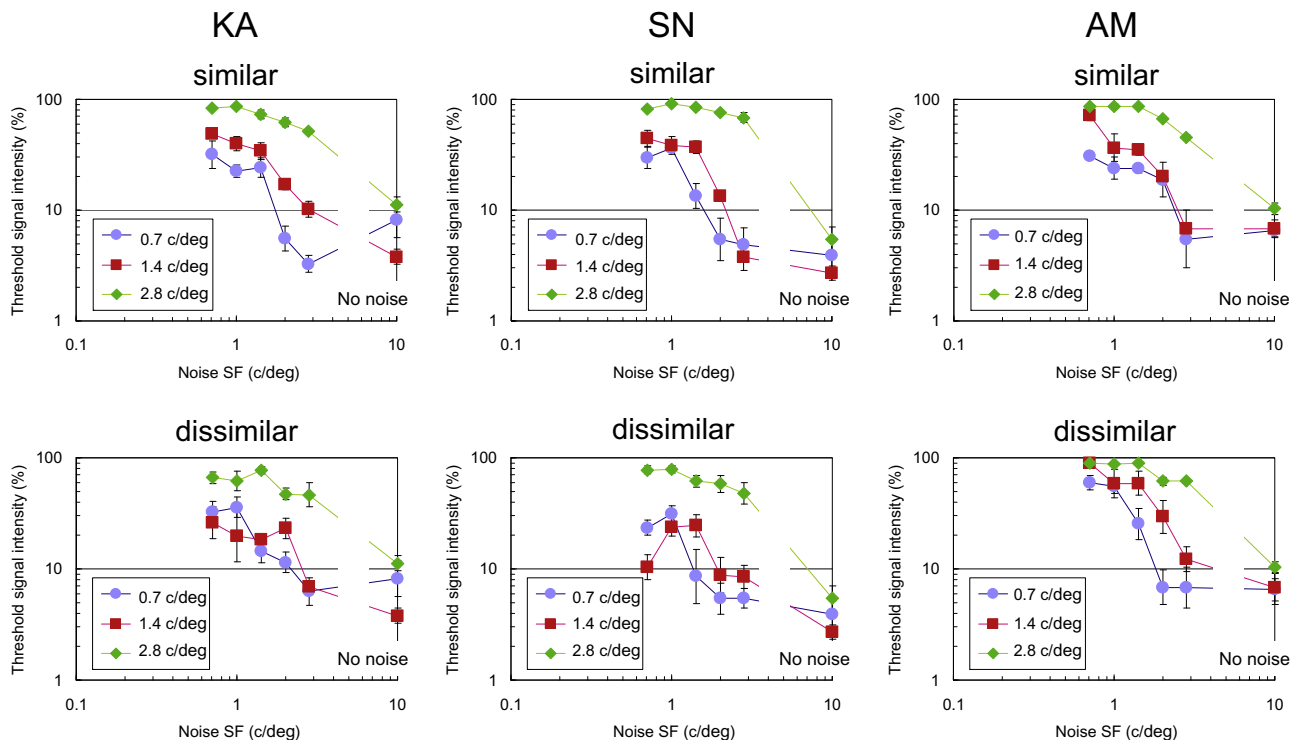

Fig. 4. The results for Experiment 3. Two orientation conditions were used. In the similar condition (top row) the narrow orientation-ranges of signal and noise Gabors were the same and in the dissimilar condition (bottom row) they were orthogonal to each other. Threshold signal-intensities for identification of the global-motion direction are plotted as a function of noise spatial-frequency for the three signal-frequencies. The pattern of results is the same for both orientation conditions, indicating that orientation difference had no effect on the broad low-pass spatial-frequency tuning of the masking.
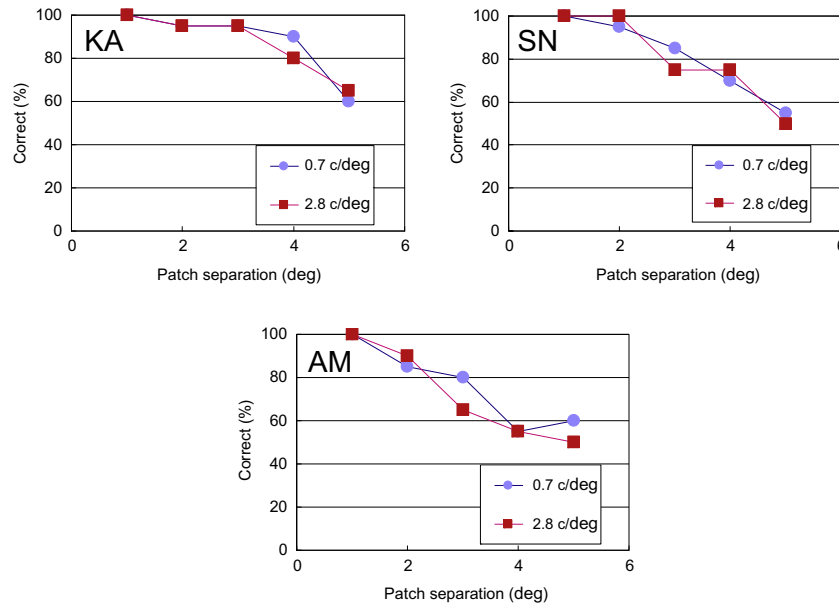
Fig. 5. The results for Experiment 4, which determined the spatial pooling range of global-Gabor motion. Performance, percentage of correct identifications of the global-motion direction at 100% signal level, is plotted as a function of patch separation (centre-to-centre distance) for two global-Gabor carrier frequencies. Results indicate similar spatial ranges of 1D motion pooling despite the two-octave difference in carrier-frequency.

are pooled into a single system that exhibits broadband, low-pass tuning. This is true for both 1D and 2D pooling for the stimuli employed here. We found low-pass tuning even though the stimulus contrast was set to equal multiples of the direction-discrimination threshold for each spatial frequency. Since the physical contrast was greatest for the highest spatial-frequency, the low-pass tuning would be retained even if we had used the same physical contrast for each spatial frequency.

Although we interpret the current findings as indicating that the motion-pooling mechanism has a low-frequency preference, that cannot be ascribed to contrast sensitivity, we should acknowledge that another factor might enhance this apparent low-pass tuning. Since the Gabor or plaid patches were presented at eccentricities that ranged between 3° and 16°, and 100% signal-intensities were used to establish the contrast thresholds, it is possible that stimulus visibility was equated only at relatively small eccentricities, and hence the low-frequency Gabors were more visible at large eccentricities.

In Experiments 1–3, the obtained noise-masking functions were fairly low-pass when the signal frequency was low, while more broadly tuned when the signal frequency was high. We suggest that this interaction could be ascribed to a ceiling effect with high-spatial-frequency targets and thus does not contradict the single mechanism hypothesis.

In Experiments 1–3, all of the signal elements were one spatial frequency and all of the noise elements a different, common, spatial frequency. It is theoretically possible, therefore that observers may have been able to, at least in part, attentively segment the signal and noise elements, and track the signal elements. Such a potential strategy is expected to make masking functions apparently more bandpass, since frequency similarity controls the difficulty of segmentation. Therefore, frequency-based segregation is unlikely to have had any significant effect on the main results – given the broad-band tuning of the observed masking. However, to further check for any potential influence of frequency-based segregation, we ran a control study based upon the method employed previously by Edwards and Badcock (1994, 1995, 1996) in which 50% of the Gabors were given the signal spatial frequency and 50% the mask (additional noise-group) spatial

frequency. To render signal and noise segmentation based on spatial frequency unhelpful, the signal spatial frequency group was divided into signal and noise directions as before and the staircase procedure varied this proportion while observers performed the direction discrimination task. The outcome still revealed broadband low-pass tuning, consistent with a single channel (see Fig. 6) at least for the low- and middle-frequency signal-group conditions. For the highest spatial-frequency signal-group condition (2.8 c/deg), even at the maximum signal-intensity (50%), all three observers were unable to identify the signal direction when the spatial frequency of the additional noise-group was low to intermediate. This was the main reason we did not use this technique in the main experiments. Interestingly, it could be argued that the tuning functions obtained here are more similar to each other than those obtained in Experiments 1 and 3. If so, then this suggests that the spatial-frequency interactions observed in those experiments may have been influenced by attention-based factors, meaning that the tuning may be more low-pass than those tuning curves indicate.

The present finding of broad spatial-frequency-tuning of motion-pooling mechanisms is consistent with previous studies that have used dot-type stimuli (Bex & Dakin, 2002; Yang & Blake, 1994). The major novelty of our study in relation to these studies is to reveal broad spatial-frequency-tuning of 1D motion pooling, in addition to 2D pooling. The existence of broadband motion mechanisms is also suggested by motion adaptation effects induced by 1D grating stimuli and measured with suprathreshold dynamic test stimuli (Ashida & Osaka, 1994; Thompson, 1981).

However, the observed tuning of 1D motion pooling does not agree with results previously obtained with standard-plaid stimuli (Kim & Wilson, 1993). While the previous study found broad-band tuning when there was a small angular difference between the component directions, narrow-band tuning was obtained for large angular differences. One might suspect that the dissociation can be ascribed to the presence of second-order components (contrast modulations) in the standard plaid-stimuli and the effect that changing the relative orientation of the components has on the effectiveness of those components (Derrington et al., 1992). Note that these second-order components are absent in our global-Ga-
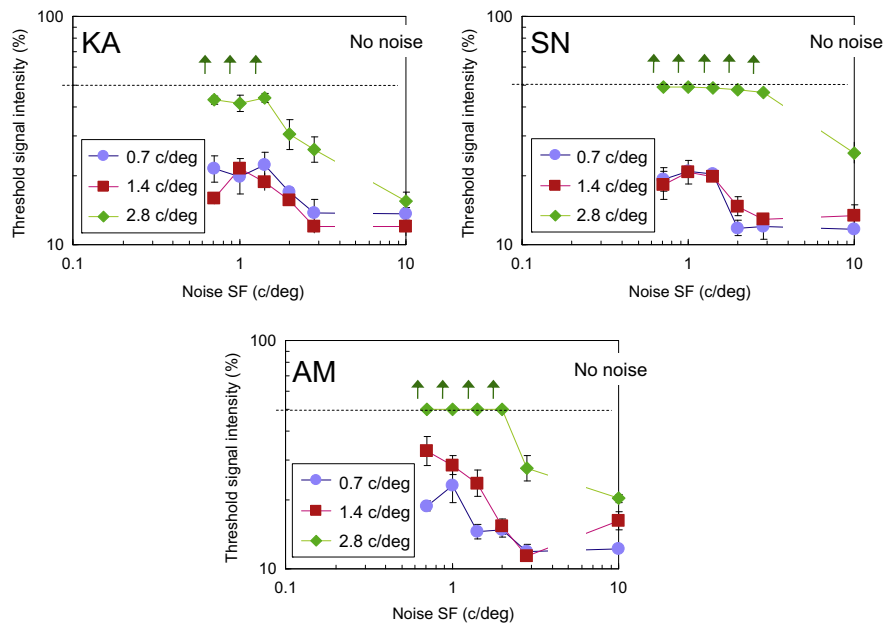
Fig. 6. The results indicate the spatial frequency dependence of the noise masking effect on 1D motion pooling revealed when secondary noise elements with the same spatial frequency as the signal frequency are also added to the display. Threshold signal-intensities for identification of the global-motion direction are plotted as a function of the noise spatial-frequency for the three signal-frequencies. The dotted lines indicate the upper limit of the signal-intensity (50%), and the upward arrows indicate that the observer made at least one incorrect response at that maximum signal level. The pattern of results indicates broad, low-pass spatial-frequency tuning of the masking.

bor stimuli since the individual Gabors do not overlap and the envelopes do not move. However, it is debatable whether strong second-order signals are generated by the addition of two gratings that have markedly different spatial frequencies (Wilson, 1994). In addition, the expected effect of adding second-order components would be to increase the bandwidth of the spatial tuning (Sutter, Sperling, & Chubb, 1995), however the present dissociation is in the opposite direction.

Instead, we suspect the apparent dissociation may be due to differences in the task requirements in the two studies. While the present study evaluated spatial tuning by using noise masking, Kim and Wilson used a motion coherency/transparency judgment. To create a situation similar to the plaid case, we made informal observations with a global-Gabor motion stimulus consisting only of two orientations. When the spatial frequency was the same between the two orientations, coherent motion was perceived (cross-orientation pooling). However, when the frequency was different, i.e., 0.7 c/deg and 2.8 c/deg for the two orientations, coherent motion was not perceived (i.e. a lack of cross-orientation/frequency pooling) regardless of the orientation difference. This observation is consistent with the transparent perception with plaid stimuli, but inconsistent with the present conclusion of a single broadband global-motion system. It seems that 1D motion pooling across spatial frequency for the perception of motion coherency/transparency cannot be simply predicted from the results obtained from masking studies. It remains unclear whether this is because the global-motion system has certain multi-scale low-pass subsystems that are not somehow cleanly visible using noise masking (Nishida, Ohtani, & Ejima, 1992), or because the single broadband global-motion system accomplishes frequency-based motion segmentation through interactions with pattern processing mechanisms (Stoner & Albright, 1993). Systematic study on this issue is underway.

Finally, while our psychophysical study does not indicate where in the cortex 1D motion signals are spatially pooled, the notion of broadband integration of motion signals is consistent with one model of MT neurons (Simoncelli & Heeger, 1998). However, monkey physiology has not revealed empirical evidence of across-space

integration of 1D motion signals in MT (Majaj, Carandini, & Movshon, 2007). Although the spatial-frequency tuning measured by single gratings does not seem to be obviously wider for MT than for V1, MT neurons, but not V1 neurons, show a nonlinear cross-frequency interaction (Priebe, Cassanello, & Lisberger, 2003; Priebe & Lisberger, 2004; Priebe et al., 2006), which one might be able to connect with the broadband interaction observed in the present study. Human brain imaging studies show that the overall spatial-frequency tuning of hMT+ is more low-pass than earlier visual areas are (Amano, Kimura, Nishida, Takeda, & Gomi, 2009; Anderson, Holliday, Singh, & Harding, 1996; Henriksson, Nurminen, Hyvärinen, & Vanni, 2008; Korth, Rix, & Sembritzki, 2000; Singh, Smith, & Greenlee, 2000), apparently in agreement with a low-frequency dominance in motion pooling.

Appendix A. Supplementary material

Movies 1 and 2: Both stimuli show global-Gabor motion at 50% signal-intensity moving vertically downwards. In movie 1, the carrier spatial-frequency of the signal is lower than that of the noise resulting in the signal direction being clearly visible. The frequencies of the signal and noise elements are swapped in movie 2, making it difficult, if not impossible, to perceive the signal direction. The frequency difference is two octaves. QuickTime movies saved in H.264 format. Play with QuickTime 7 or later. The image sequences were made using the original programme, but the movie playing speed is slower than the original stimuli for demonstration purpose. Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2009.08.026.

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