



Multiple spatial frequency channels in human visual perceptual memory

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ABSTRACT

Current models of short-term visual perceptual memory invoke mechanisms that are closely allied to low-level perceptual discrimination mechanisms. The purpose of this study was to investigate the extent to which human visual perceptual memory for spatial frequency is based upon multiple, spatially tuned channels similar to those found in the earliest stages of visual processing. To this end we measured how performance on a delayed spatial frequency discrimination paradigm was affected by the introduction of interfering or 'memory masking' stimuli of variable spatial frequency during the delay period. Masking stimuli were shown to induce shifts in the points of subjective equality (PSE) when their spatial frequencies were within a bandwidth of 1.2 octaves of the reference spatial frequency. When mask spatial frequencies differed by more than this value, there was no change in the PSE from baseline levels. This selective pattern of masking was observed for different spatial frequencies and demonstrates the existence of multiple, spatially tuned mechanisms in visual perceptual memory. Memory masking effects were also found to occur for horizontal separations of up to 6 deg between the masking and test stimuli and lacked any orientation selectivity. These findings add further support to the view that low-level sensory processing mechanisms form the basis for the retention of spatial frequency information in perceptual memory. However, the broad range of transfer of memory masking effects across spatial location and other dimensions indicates more long range, long duration interactions between spatial frequency channels that are likely to rely contributions from neural processes located in higher visual areas.

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1. Introduction

Sensory perception and memory traditionally have been viewed as very different processes that are served by very different cortical networks within the brain. However, the ability to store basic sensory information forms an important means by which an organism can retain information about its surrounding environment which can subsequently be used to mediate and guide behaviour (Baddeley, 1983, 1986, 2003). This requirement, that sensory information has to be made readily available to memory systems, has led to the proposal that the neural mechanisms that underpin this kind of memory are closely allied to those that are involved in sensory processing and may even occur in the same sensory cortical areas (Bisley & Pasternak, 2000; Fuster, 1997; Gibson & Maunsell, 1997; Graham, Barense, & Lee, 2010; Pasternak & Greenlee, 2005).

In the visual domain, the retention of information relating to basic stimulus attributes, such as spatial frequency and contrast for example, has been shown to occur within what has been termed *visual perceptual memory* (Magnussen, 2009; Magnussen & Greenlee, 1999). This form of memory can be characterised as operating in a non-declarative, implicit fashion and constitutes a

pre-semantic level of storage for low-level sensory information (Magnussen, 2000, 2009). It has some (though not complete) overlap with related concepts such as: sensory working memory (Pasternak & Greenlee, 2005); the perceptual representation system (Schacter, Wagner, & Buckner, 2000; Tulving & Schacter, 1990) and visual short term memory (Magnussen & Greenlee, 1992). A key property of visual perceptual memory is that it is feature or dimension specific (Magnussen, 2000). It comprises a series of separate stores that are selective for the retention of specific visual attributes such as spatial frequency, orientation, motion, colour, and so forth (Greenlee, Magnussen, & Thomas, 1991; Magnussen & Greenlee, 1999; McKeefry, Burton, & Vakrou, 2007; Pasternak & Greenlee, 2005). This organisation mirrors that which is found right from the earliest stages in the visual pathway where the sensory processing of different stimulus attributes occurs in a similarly parallel fashion (e.g. Livingstone & Hubel, 1987). Evidence in favour of feature specificity in visual perceptual memory has emerged from psychophysical studies which, in many cases, have employed delayed discrimination paradigms. In these experiments the ability to retain information about a basic stimulus attribute is measured over a time delay or inter-stimulus interval (ISI) (e.g. Regan, 1985). The quality or fidelity of the retained information can then be indexed by any subsequent changes in performance. Using this approach, the retention of different stimulus features (contrast, orientation, spatial frequency, etc.) has been found to

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have different rates of decay with increasing ISI duration, suggesting that different perceptual memory mechanisms exist for different stimulus attributes or features (Fahle & Harris, 1992; Lee & Harris, 1996; Magnussen & Greenlee, 1999; Magnussen, Greenlee, & Thomas, 1996; Vogels & Orban, 1986). These findings are also consistent with results from 'dual-task' experiments in which observers are asked to retain information and make subsequent judgements about two stimulus features (e.g. contrast and spatial frequency). This can be done for multiple attributes virtually without impairment (Greenlee & Thomas, 1993; Magnussen & Greenlee, 1997; Magnussen, Greenlee, & Thomas, 1996; Vincent & Regan, 1995; Vogels, Eeckhout, & Orban, 1988). However, when observers are asked to make judgements about the same attribute (e.g. two spatial frequencies), then thresholds are significantly elevated (Magnussen & Greenlee, 1997). This indicates that for these tasks, interference occurs within, but not between different stimulus attributes.

The idea that perceptual memory is made up of a number of limited capacity sub-systems that independently store information relating to different stimulus attributes has also been demonstrated by the selective effects of interference or masking stimuli presented during the ISI of delayed discrimination tasks (Magnussen et al., 1991). In these so called 'memory masking' experiments increases in discrimination thresholds, induced by the introduction of masking stimuli, point to the ability of certain stimuli to disrupt the retention of information about specific stimulus features. However, these disruptions to stored representations of visual stimuli only occur when the interfering or masking stimuli differ from the remembered stimulus in some key aspect, when the mask is identical to the reference there is no disruption of performance (Magnussen & Greenlee, 1992; Magnussen et al., 1991; McKeefry, Burton, & Vakrou, 2007). An important property of memory masking is that the effects are specific to changes only along certain relevant stimulus dimensions with discrimination thresholds being unaffected by changes along other irrelevant dimensions. Furthermore, the effects are also tuned for finite ranges of these features (Magnussen et al., 1991).

In this study we employed a memory masking paradigm in order to investigate how spatial frequency information is organised within visual perceptual memory. Perhaps one of the most enduring models of low-level visual processing describes the analysis of spatial patterns in terms of the parallel operation of multiple spatial frequency filters or channels (Campbell & Robson, 1968). Experiments using pattern or contrast adaptation have played a major role in characterising these low-level sensory filters which are responsive to specific bandwidths of frequency and orientation and operate in discrete spatial locations within the visual field (e.g. Blakemore & Campbell, 1969; Blakemore & Nachmias, 1971; Georgeson & Harris, 1984). Memory masking experiments have made an analogous contribution in revealing the organisation of perceptual memory for spatial frequency. Magnussen et al. (1991), for example, have demonstrated that visual perceptual memory does exhibit spatial frequency tuning which mirrors that found in low-level vision. This finding has been central to the proposition that such memory stores are closely linked to the mechanisms that operate at the earliest stages of sensory processing (Magnussen, 2009; Magnussen et al., 1991; Pasternak & Greenlee, 2005). In this study we wanted to explore this link in more detail. One issue centres around the fact that contrast adaptation, in addition to generating increases in detection thresholds for stimuli of spatial frequency that are close (within 2 octaves) to the adapting frequency, also generate shifts in the perceived spatial frequency of subsequently viewed supra-threshold grating stimuli (Blakemore, Nachmias, & Sutton, 1970). In these experiments Blakemore and colleagues demonstrated that following a period of adaptation to grating stimuli of specific spatial frequencies, patterns with higher

spatial frequencies appeared to be of higher frequency than they actually were. Conversely, subsequently presented patterns of lower spatial frequencies than the adapting frequency, appeared even coarser than they were in actuality. Thus perceived spatial frequency can be altered by prior adaptation. We wanted to examine whether a similar spatial frequency shift phenomenon exists in the domain of low level perceptual memory. Previous 'memory masking' paradigms have been largely concerned as to how discrimination thresholds are affected by the introduction of a masking stimulus during the delay period (e.g. Magnussen et al., 1991). In this study we were interested in ascertaining whether an interfering stimulus can induce a change in the 'remembered' spatial frequency. If this is the case then over what spatial frequency range is the mask effective in interfering with the retained information? If low level perceptual memory is indeed based upon spatial frequency channels similar to those found in the sensory domain then the prediction would be that these spatial frequency shifts would only occur for masking stimuli within 2 octaves of any chosen reference stimulus. Such a finding would further strengthen the case for visual perceptual memory being closely allied to low-level visual processing.

2. Methods

2.1. Stimuli

Sinusoidal luminance contrast grating stimuli were presented on a colour graphics monitor (GDM500; Sony, Tokyo, Japan; frame rate 120 Hz) controlled via a video graphics card (VSG 2/5; Cambridge Research Systems, Rochester, UK). The reference, mask and test stimuli were presented in circular windows of diameter equal to 2.5 deg, with a contrast equal to 50% on a grey (illuminant C) background of the same mean luminance (12.5 cd/m²) (see Fig. 1). In terms of the spatial configuration of the stimuli, two versions of the experiment were performed: in the first, *spatially coincident version*, the reference, mask and test stimuli were all presented at the same retinal location centred on the fixation point. In the second, *spatially non-coincident version*, the reference stimulus was presented with a horizontal displacement to the right of the central fixation mark; the mask stimulus was presented at the fixation mark and the test stimulus was placed horizontally displaced to the left of fixation. The magnitude of the displacements from the fixation point varied up to a maximum of 6 deg. During the presentation cycle fixation was maintained on a central fixation cross.

2.2. Procedure

A delayed spatial frequency matching paradigm (Fig. 1) was used to measure performance and employed a two-alternative forced choice procedure in conjunction with a method of constant stimuli. Each trial began with the presentation of a reference stimulus of set spatial frequency (typically 1 c/deg, 3 c/deg or 5 c/deg, depending upon the experiment) which was presented for 380 ms (see Fig. 1). This was followed by an inter-stimulus interval (ISI) of 5 s during which masking stimuli of different spatial frequencies were presented for 2 s. At the end of the ISI a test stimulus was presented for 380 ms the spatial frequency of which was selected randomly from one of seven different levels which spanned a range above and below the reference spatial frequency. The offset of the test stimulus was marked by an auditory cue at which point the participants were required to indicate, using a response box (model CB3; Cambridge Research Systems), whether the test stimulus was perceived to be of higher or lower spatial frequency than the reference. In order to prevent the representation

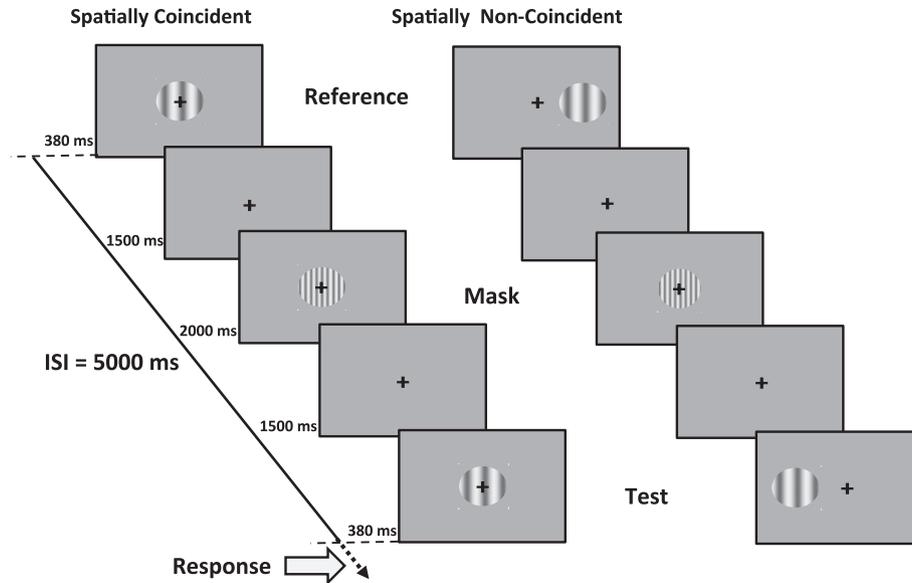


Fig. 1. A schematic representation of the delayed spatial frequency discrimination paradigm used in this study. Each cycle began with the presentation of a reference stimulus (1, 3 or 5 c/deg) for 380 ms. Following the presentation of a blank screen for 1500 ms a mask stimulus was displayed for 2000 ms. After another 1500 ms presentation of a blank screen a test stimulus was presented and at the offset of this stimulus the observer was instructed to respond by button press whether they judged the test to be of higher or lower spatial frequency than the reference stimulus. Following the response the next presentation cycle began. There were two forms of the experiment: (A) a spatially coincident version where the reference, test and mask stimuli were all presented at the same spatial location centred on the fixation point and (B) a spatially non-coincident version where the stimuli were horizontally displaced from one another by separations of up to 6 deg.

of stimulus features being built up in long-term memory over consecutive trials we introduced small random increases and decreases in the contrast (between $\pm 10\%$) and spatial phase (between ± 90 deg) of the test and reference stimuli. These variations were balanced over the trials to minimise any bias (Magnussen & Greenlee, 1992).

2.3. Curve fitting

The psychometric data were fitted by a logistic function of the form:

$$y = \frac{100}{1 + e^{\frac{\alpha - \mu}{\theta}}} \quad (1)$$

where y is the percentage of times the test was perceived as being of higher spatial frequency than the reference, x is the spatial frequency of the test stimulus, μ is the spatial frequency corresponding to the 50% level on the psychometric function (i.e. the point of subjective equality (PSE)) and θ is an estimate of the spatial frequency matching threshold. This final value (θ) was divided by the reference spatial frequency to give a Weber fraction for spatial frequency discrimination ($\Delta f_x/f_x$). Each psychometric function was based upon 70 trials (7 levels, 10 repetitions of each level) and the logistic curves were fitted to an average of at least three of these functions.

The resulting PSE data were plotted as a function of mask spatial frequency and fitted by a first derivative of a Gaussian function described by the equation:

$$y = y_{pos} + \left[\left(A * \log \left(\frac{x}{x_{pos}} \right) \right) * e^{-\left(\frac{\left(\log \left(\frac{x}{x_{pos}} \right) \right)^2}{2\sigma^2} \right)} \right] \quad (2)$$

where y is the point of subjective equality (PSE), x is the spatial frequency of the mask, σ is the standard deviation of the Gaussian, A is a constant related to the amplitude of the function and x_{pos} , y_{pos} is the origin of the function (when $x = x_{pos}$, PSE = y_{pos}). The maxima

and minima of this function occur at mask spatial frequencies $\pm \sigma$ units from the origin (i.e. $x/x_{pos} = \pm \sigma$). The half amplitude of this function represents the magnitude by which the PSE deviates from baseline.

2.4. Observers

A total of five observers took part in the experiments; two were authors (DM, VN) and the remaining three (FF, JH and PS) were naive to the aims of the study. The experiments were performed binocularly at a viewing distance of 114 cm. The observers had their viewing positions stabilised by a chin rest and their foreheads were supported by rest that restricted, but did not completely immobilise, head movement. Data were collected during four 2 h sessions in which the participants completed 610 trials in each session. Prior to the start of data collection the observers completed 140 practice trials in order to familiarise them with the experimental procedure.

3. Results

3.1. Spatial bandwidth of memory masking

Fig. 2 shows the group averaged results from an experiment where participants performed the delayed spatial frequency matching task for a reference stimulus of 5 c/deg in the presence of different mask stimuli ranging from 1 to 15 c/deg. Fig. 2A shows how discrimination threshold varies as a function of the mask spatial frequency. These data replicate the findings of Magnussen et al. (1991) and demonstrate the spatial frequency selectivity, in terms of the effects on discrimination thresholds, that occurs for the memory masking paradigm. When the mask spatial frequency is close to that of the reference stimulus, performance is minimally affected and thresholds are similar to those obtained when no mask is presented during the ISI (horizontal dashed line). However, as the mask spatial frequency starts to shift away from that of the reference, either in a lower or higher direction, then thresholds

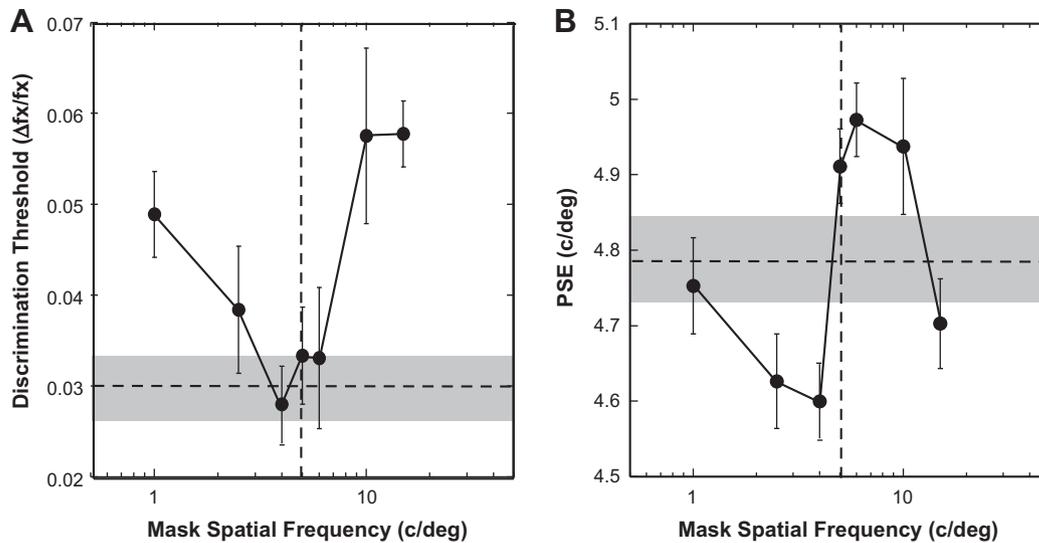


Fig. 2. Group averaged results ($n = 3$) for a delayed spatial frequency discrimination experiment (reference = 5 c/deg) where mask stimuli of variable spatial frequency were presented during the 5 s ISI. (A) Shows the variation in discrimination threshold as a function of mask spatial frequency. (B) Plots PSE as a function of mask spatial frequency. In these and subsequent plots the horizontal dashed lines refer to the level of (baseline) performance when no mask stimulus was introduced during the ISI. The grey area above and below this line represents ± 1 S.D. of the mean performance for this condition. The vertical dashed line represents the reference spatial frequency and error bars refer to ± 1 S.D. of the mean.

increase giving rise to a characteristic 'V-shaped' function that is approximately centred on the reference spatial frequency.

Fig. 2B illustrates how PSE varies as a function of mask spatial frequency relative to the baseline condition (i.e. when no mask is present). For mask spatial frequencies below that of the reference, perceived equality between reference and test occurs at spatial frequencies that are lower than the baseline PSE. Conversely, when the mask frequency is greater than the reference PSE are greater than for the baseline condition. Either side of the reference spatial frequency the perceived shift in the PSE reaches a local maximum (for higher mask frequencies) and local minimum (for lower mask frequencies). When the mask spatial frequency moves even further away from the reference the perceived shifts in the PSE decrease in magnitude and return back towards baseline values. Thus the perceived shifts in the matched spatial frequency appear highly dependent upon the spatial frequency of the masking stimuli. If the mask spatial frequency differs by a small amount from the reference stimulus, the resultant PSE is 'pulled' towards the spatial frequency of the mask stimulus. If, however, the difference between the reference and mask spatial frequency becomes too great then the effect is reduced and the PSE starts to return to values closer to those obtained under no mask conditions – as if the mask stimulus can be ignored or discounted if the spatial frequency difference between it and the reference is too great.

The spatially tuned nature of these PSE changes prompted us to fit this data with functions that were first derivatives of Gaussian functions (see methods). These functions have the advantage of providing an estimate of the bandwidth of the effects in terms providing a value (σ). Fig. 3 shows results obtained from three individual observers whose data have been fitted with these curves giving values for $\sigma = 0.638$, 0.453 and 0.543 octaves for observers FF, VN and DM, respectively. Similarly tuned functions were also obtained when the memory masking experiments were repeated for different reference spatial frequencies (1 and 3 c/deg) and the group averaged data fitted with the same first derivative Gaussian functions, are shown in Fig. 4.

The induced shifts in the remembered spatial frequency of the reference stimulus demonstrated here using the 'memory masking' paradigm mirror the kind of effects that also occur with contrast or pattern adaptation experiments (Blakemore, Nachmias, & Sutton,

1970). In these experiments prolonged exposure to a particular spatial frequency alters the perceived frequency of subsequently viewed grating stimuli. Results from these adaptation experiments have been central to the formulation of models of spatial vision processing that rely upon the existence multiple filters or channels that are responsive to relatively narrow spatial frequency bandwidths. In Fig. 5 data from Blakemore, Nachmias, and Sutton (1970) have been re-plotted in order to show how the perceived spatial frequency of various test stimuli vary following prolonged exposure to either a 3 c/deg (Fig. 5A) or a 5 c/deg (Fig. 5B) grating. As in the case of the 'memory masking' data shown Fig. 3 these contrast adaptation data show a similar dependency as a function of test spatial frequency and have been fitted by first derivatives of Gaussian functions which generates values of $\sigma = 0.60$ octaves for the 3 c/deg data and 0.66 octaves for the 5 c/deg data.

3.2. Location specificity of memory masking

In order to rule out the possibility that this spatially tuned effect of the memory masking stimulus is not simply down to local adaptation we examined the extent to which memory masking was specific to retinal location. A number of studies have demonstrated that the effects of contrast adaptation on sensitivity for subsequently presented test stimuli are highly localised to the retinal areas that have experienced adaptation (Ejima & Takahashi, 1984, 1985; Williams, Wilson, & Cowan, 1982). Decreases in sensitivity for grating patterns are greatest when adapting and test stimuli are spatially coincident but as the spatial separation between them increases to greater than 1 cycle (0.33 deg for a 3 c/deg stimulus) the shifts in sensitivity are minimal. For separations greater than this magnitude there may even be facilitation, i.e. increases in sensitivity in retinal areas immediately surrounding the region of adaptation. Beyond 12 cycles (3.96 deg for a 3 c/deg stimulus) the after-effects induced by spatially localised adaptation disappear (Ejima & Takahashi, 1984). Fig. 6 shows the results from a delayed spatial frequency matching task where the reference, mask and test stimuli appeared at different non-overlapping locations (horizontal separation = 6 deg) across the visual field. As can be observed the effects of the different masking stimuli exhibit similar spatial frequency tuning to that found when the reference, mask and test

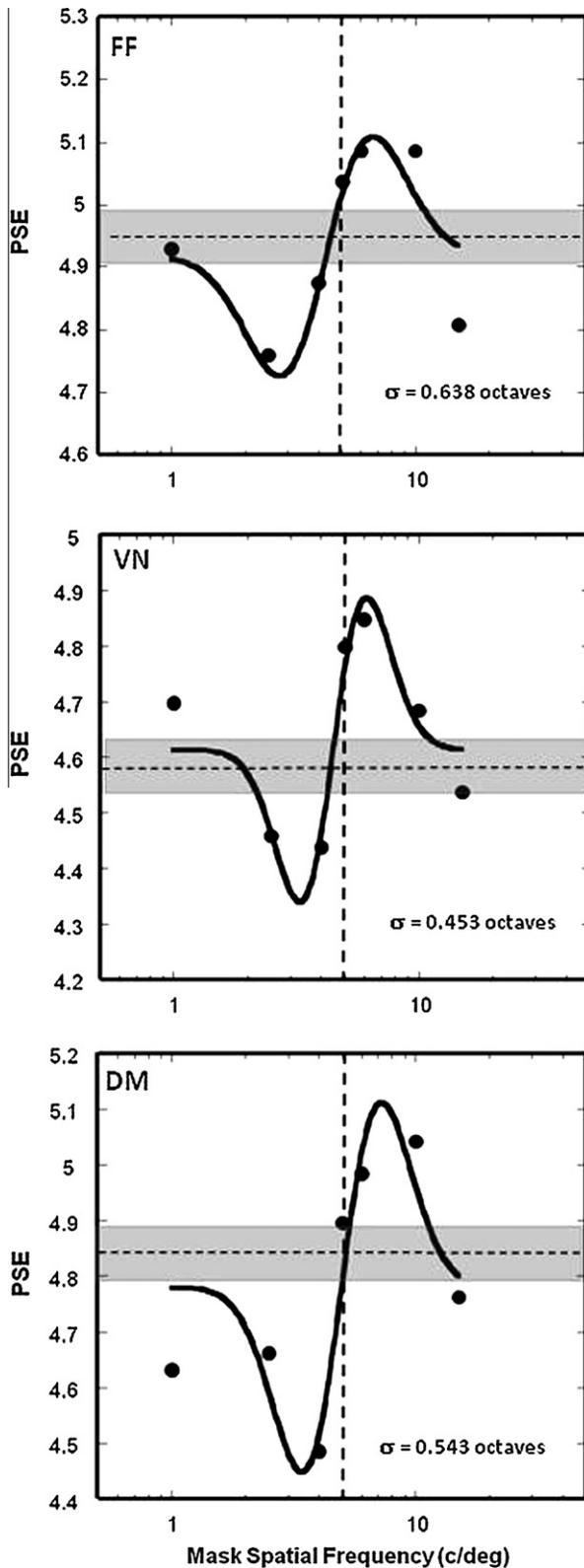


Fig. 3. PSE data plotted as a function of mask spatial frequency for three observers who performed a delayed spatial frequency matching paradigm (reference = 5 c/deg). The data have been fitted by a first derivative of a Gaussian function (see text) which provides an estimate of bandwidth (σ) for each function given in octaves.

stimuli were spatially co-incident and curve fits generated bandwidth estimates (σ) equal to 1.202, 1.196 and 0.664 octaves for the 1, 3 and 5 c/deg reference stimuli, respectively.

The data shown in Fig. 7 demonstrate that perceived shifts in matched spatial frequency for a reference stimulus of 3 c/deg that are induced by effective masks (1.5 and 6 c/deg) still occur for stimulus separations up to 6 deg without any diminution in magnitude. This non-spatially localised property of memory masking therefore differs markedly from that exhibited by contrast adaptation (Ejima & Takahashi, 1984).

3.3. Orientation specificity of memory masking

Another important property of perceived shifts in spatial frequency that occur following contrast adaptation is that the effects are orientation specific (Blakemore, Nachmias, & Sutton, 1970). Perceived shifts in spatial frequency only occur for test stimuli that are within a range of approximately ± 40 deg of the orientation of the adapting grating. We therefore wanted to examine whether induced shifts in remembered spatial frequency are also tuned for orientation. Earlier studies using the memory masking paradigm have demonstrated that changes in the orientation of the masking stimulus have no effect on spatial frequency discrimination thresholds (Magnussen et al., 1991) and indicate that memory masking occurs only for relevant stimulus attributes (Magnussen & Greenlee, 1999). In Fig. 8 results are shown for an experiment in which the orientation of masking stimuli were systematically varied and the effects on PSEs were measured for the non-coincident version of the delayed spatial frequency discrimination task. The spatial frequency of the reference stimulus was 3 c/deg and masks of 1.5, 3 and 6 c/deg were presented with orientation shifts relative to the reference stimuli that varied between 0 deg and 90 deg in a counter-clockwise direction. As can be observed mask orientation appears to have little or no effect on the induced shifts in matched spatial frequency. The effective masks (6 and 1.5 c/deg) induce respective shifts that are above and below baseline performance for all orientations. The ineffective mask (3 c/deg) continues to have little effect of PSE regardless of its orientation, consistent with previous findings (Magnussen et al., 1991).

4. Discussion

The purpose of this paper was to investigate the proposed links between visual sensory processing and visual perceptual memory. Using a delayed spatial frequency discrimination task we assessed the extent to which information that is retained about the spatial frequency of a visual stimulus is vulnerable to disruption by the presentation of interfering stimuli during the inter-stimulus interval. Using this ‘memory masking’ paradigm we were able to measure the accuracy with which visual stimuli were retained by perceptual memory mechanisms and assess the effects that the interfering stimuli had on the fidelity of that memory store. Our central finding is that masking stimuli are able to shift PSE for matches made by observers between the remembered reference and test stimuli, as long as their spatial frequency is within a bandwidth of approximately 1.2 octaves of the reference spatial frequency. When mask spatial frequencies differ by more than this value, there is little or no change in PSE from baseline (no masking) levels. This selective pattern of masking is observed for reference stimuli of different spatial frequencies and points to the existence of multiple, spatially tuned mechanisms in visual perceptual memory similar to those which operate as part of the basic sensory analysis of spatial information.

4.1. Visual perceptual memory and low-level visual processing

The existence of multiple spatially tuned mechanisms in low-level perceptual memory is in accord with those models which

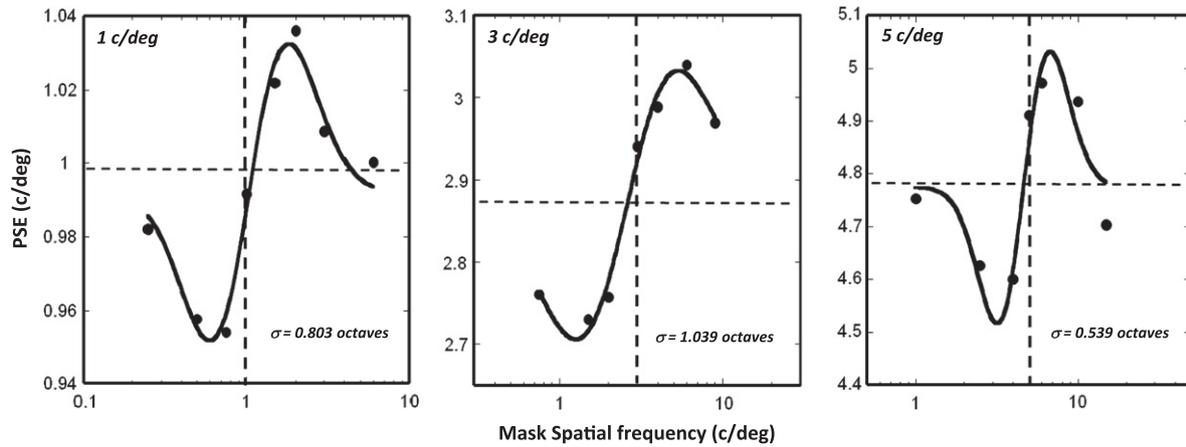


Fig. 4. Variation in PSE as a function of mask spatial frequency for three different reference spatial frequencies (1, 3 and 5 c/deg). The data in each case represent the average of three observers and have been fitted by a first derivative of a Gaussian function similar to the data in Fig. 3.

Blakemore et al (1970) Contrast adaptation data

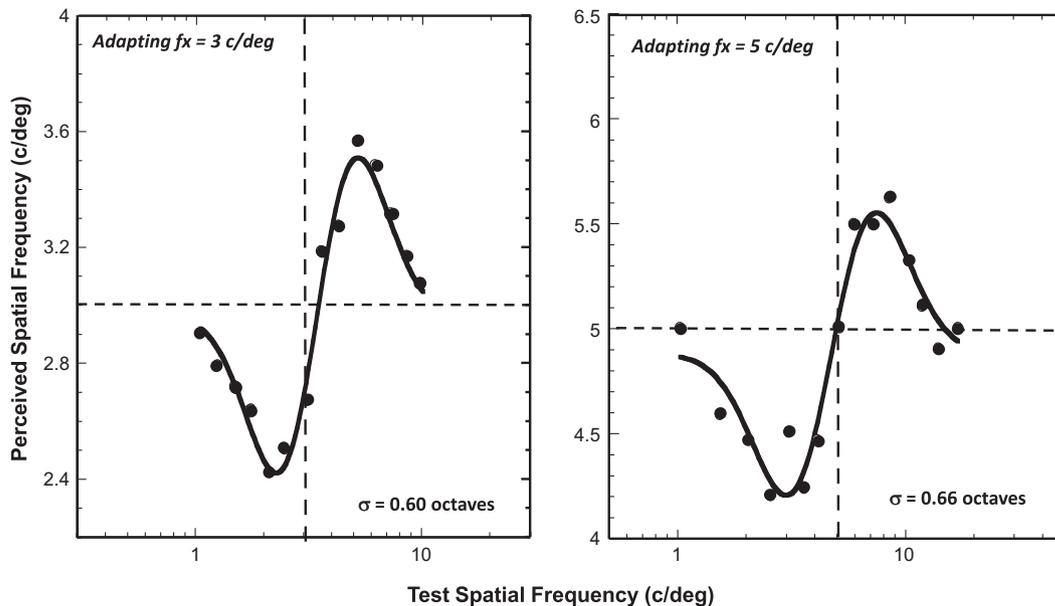


Fig. 5. Contrast adaptation data from Blakemore, Nachmias, and Sutton (1970) which plot the variation in perceived spatial frequency of test stimuli following prior adaptation to a 3 c/deg (A) and a 5 c/deg (B) grating stimulus. The data, similar to the memory masking data shown in Figs. 3 and 4, have been fitted by a first derivative of a Gaussian function.

describe perceptual memory as comprising an array of stores that are able to retain information about a particular stimulus dimension within only a limited range or bandwidth (Magnussen, 2000, 2009; Magnussen & Greenlee, 1999; Magnussen et al., 1991). The masking bandwidths we have measured for different reference spatial frequencies range between 0.54 and 1.04 octaves for the spatially co-incident versions of the task and between 0.86 and 1.15 octaves for the non-coincident versions. These bandwidth measures are in good agreement with those obtained from adaptation and traditional sensory masking paradigms (e.g. Georgeson, 1980; Greenlee & Magnussen, 1988; Wilson, McFarlane, & Philips, 1983) which in turn are similar to those that have been measured in primate V1 neurons. DeValois, Albrecht, and Thorell (1982) for example, have shown that the bandwidth range for macaque foveal V1 neurons is between 0.7 and 2.5 octaves. The consistency between the tuning bandwidths displayed by perceptual memory mechanisms and visual neurons in V1 implies that the former

are closely linked to sensory discrimination properties of the latter (Magnussen, 2009). Thus, it would appear that the neural mechanisms that serve to retain spatial frequency information in perceptual memory adhere to similar organisational principles to those exhibited by the sensory channels/filters that are involved in the earliest visual analysis of this information. In this respect, the data presented here further strengthen the links that are increasingly being drawn between mechanisms that underpin basic visual sensory processing and those which are involved in the short term retention of this information (Pasternak & Greenlee, 2005).

Results from contrast adaptation experiments have made fundamental contributions to the elucidation of the organisation of low-level sensory processing of spatial frequency information in the primate visual system (Björklund & Magnussen, 1981; Blakemore & Campbell, 1969; Georgeson & Harris, 1984). Whilst perceptual memory mechanisms appear to share common properties with basic sensory processing, it is important to note that there

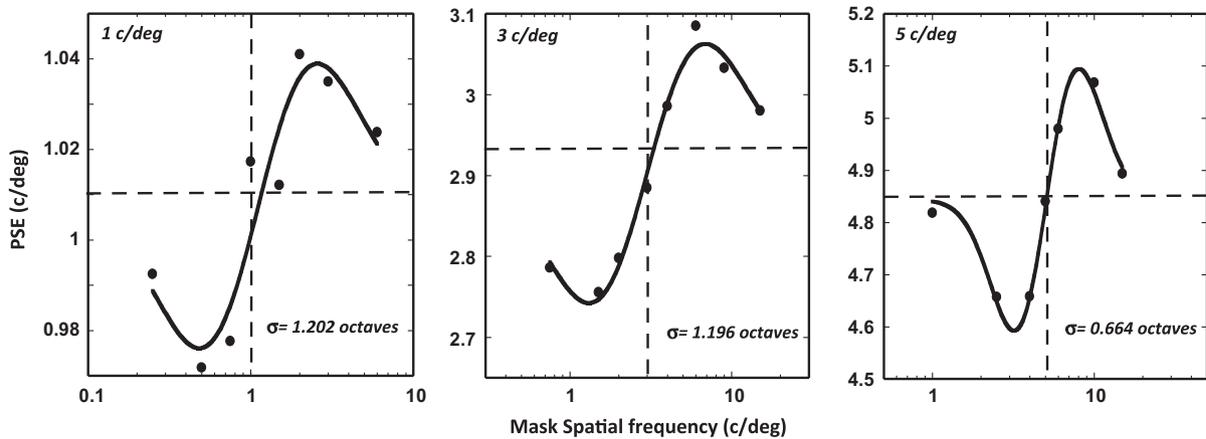


Fig. 6. The variation in PSE as a function of mask spatial frequency for the spatially non-coincident version of the task. In this version of the experiment the centres of the reference, mask and test stimulus were horizontally separated from each other by 3 deg. The data in each case represent the average of 3 observers and have been fitted by functions similar to those in previous figures.

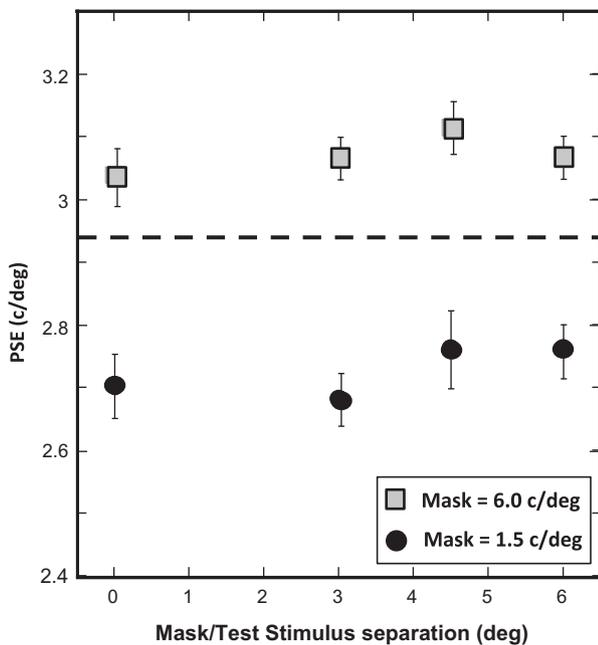


Fig. 7. Shifts in PSE for spatial frequency matches made for a 3 c/deg reference stimulus with masking stimuli (6 and 1.5 c/deg) placed at increasing larger horizontal separations. The results represent the average data from three observers.

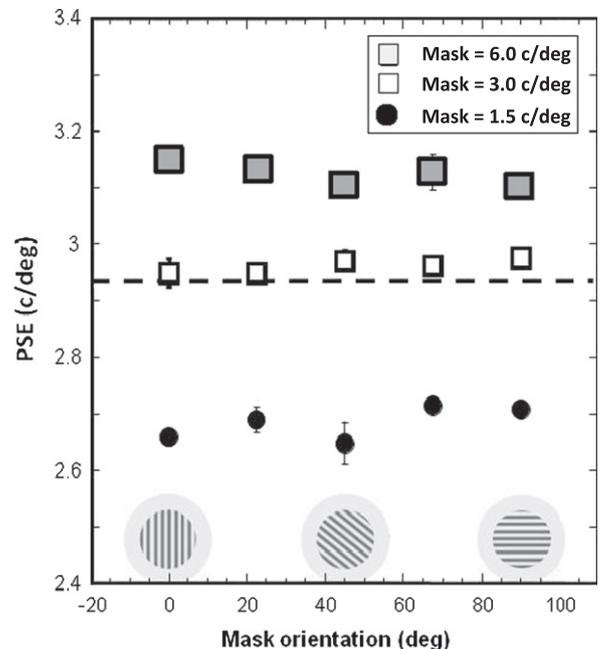


Fig. 8. Shifts in PSE for spatial frequency matches made for a 3 c/deg reference stimulus with masking stimuli (6 and 1.5 c/deg) at different orientations relative to the reference.

are differences between results that have emerged from contrast adaptation and memory masking experiments. These may serve to highlight the fact that the neural processes that underpin sensory and perceptual memory mechanisms are not completely overlapping. One such difference lies in the fact that the retention of spatial frequency information in perceptual memory lacks orientation selectivity (Regan, 1985). For perceptual memory mechanisms an effective masking stimulus remains effective regardless of its orientation (Magnussen, Greenlee, & Thomas, 1996). This is in stark comparison to contrast adaptation experiments (e.g. Blake-more & Nachmias, 1971; Blakemore, Nachmias, & Sutton, 1970) which have clearly shown that the effects of adapting to a luminance contrast grating are highly orientation dependent and are abolished if the adapt and test grating differ by more than 40 deg (Movshon & Blakemore, 1973). This study also demonstrates that the interference effects induced by memory masking stimuli have a much broader spatial extent across the retina compared to those

induced by contrast adaptation. Previous psychophysical studies have shown that the effects of contrast adaptation are greatest when the adapting and test stimuli are spatially coincident, but rapidly decrease when their separation increases (Ejima & Takahashi, 1984, 1985; Williams, Wilson, & Cowan, 1982). Memory masking for spatial frequency, on the other hand, still occurs for effective mask stimuli, with little decrease in magnitude, at horizontal separations of up to 6 deg – a distance well outside that measured for contrast adaptation effects (Ejima & Takahashi, 1984). These spatially long range effects are at odds with single-unit, behavioural and neuroimaging experiments which have shown that the short term retention of visual information is highly spatially localised (Hollingworth, 2006, 2007; Sneve et al., 2011; Zaksas, Bisley, & Pasternak, 2001). However, they are consistent with other studies which suggest the existence of a more spatially global mechanism that retains sensory information from across the visual field (Ester, Serences, & Awh, 2009). In addition,

psychophysical results obtained by Tanaka and Sagi (1998b), also indicate the presence of spatially long-range and long-lasting facilitation effects in the detection of Gabor contrast patterns. Tanaka and Sagi's work highlights the fact that low-level spatial filters do have the capability to retain information about visually presented patterns far beyond their normal limits of spatial and temporal integration. These properties may form the basis for the storage of spatial information in memory (Tanaka & Sagi, 1998a, 1998b). Nonetheless, the fact that the effects mediated by perceptual memory mechanisms appear to have a much broader range of transfer across space and orientation compared to those mediated directly by low-level sensory mechanisms, suggests they are likely to be supported by neural processing at a level beyond V1 where neurons have the ability to integrate across different stimulus attributes (DeValois & DeValois, 1990). In this respect the effects of memory masking have similar properties to more complex after-effects, such as the gender specific face after-effect, which are considered to be mediated by high level visual areas (Afraz & Cavanagh, 2009). Furthermore, the fact that memory masking has been shown to be dependent upon distal as opposed to retinal spatial frequency (Bennett & Cortese, 1996) also points to the fact that perceptual memory operates at a level beyond V1 where size and shape constancies are computed.

4.2. Visual perceptual memory and visual short term memory

A characteristic property of visual information that is retained within low-level perceptual memory is that it is malleable and vulnerable to interference. This suggests that there may be some overlap with a weak or fragile form of visual short term memory (VSTM), the existence of which has been mooted by certain studies (e.g. Sligte, Scholte, & Lamme, 2008, 2009). These studies form part of a wider body of work which describes the transfer of low-level sensory information into memory as a multi-stage process (Lalonde & Chaudhuri, 2002; Magnussen, Idas, & Holst-Myhre, 1998; Sligte, Scholte, & Lamme, 2008, 2009; Tanaka & Sagi, 2000). Within this process the weak form of VSTM operates for temporal durations of the order of around 4 s or less (Lalonde & Chaudhuri, 2002; Magnussen, Idas, & Holst-Myhre, 1998), is closely allied to low-level sensory processing and is vulnerable to interference. Currently, it is an open question as to whether this more volatile or fragile form of VSTM actually constitutes part of a continuum with iconic visual memory, or is in fact a distinct and separate process in itself (Sligte, Scholte, & Lamme, 2009). Regardless of this issue, the properties of volatile VSTM have much in common with the characteristics of low-level perceptual memory revealed in this study and in all likelihood constitute similar mechanisms. For longer durations a stronger and more robust form of VSTM is proposed to exist which is characterised as having a limited storage capacity but is less vulnerable to interference (Luck & Vogel, 1997; Sligte, Scholte, & Lamme, 2008, 2009). A key feature of this robust form of VSTM, which further differentiates it from the more volatile form of VSTM, is that it appears to be under the control of attention which gates low-level visual signals as part of the generation of more long term memory representations (Lalonde & Chaudhuri, 2002; Tanaka & Sagi, 2000). Recent brain imaging studies have shown that the neural activity that accompanies VSTM is distinct from that which accompanies attention and lies outside the early visual areas (Offen, Schluppeck, & Heeger, 2009). The extent of activation of area V4, in particular, may provide an index as to the degree to which the representation in VSTM is vulnerable to interference (Sligte, Scholte, & Lamme, 2009).

In conclusion, this study demonstrates that the mechanisms that underpin the short term retention of information about spatial frequency in perceptual memory are tuned in a similar manner to the channels or filters that operate right from the earliest levels of

low-level spatial processing. This further emphasises the link between memory mechanisms and basic sensory processing mechanisms that are being used as a basis for the retention of information. However, whilst certain characteristics of perceptual memory are highly consistent with the kind of analysis that occurs in the earliest stages of visual processing, the broad transfer properties of memory masking across location and orientation for example, suggest more complex interactions. Such interactions are likely to involve visual areas beyond the primary visual cortex. In this and other respects, low-level perceptual memory shares common properties with the more volatile forms of VSTM that have been described previously.

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