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Visual perceptual memory – anno 2008

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Introduction

The concept of perceptual memory refers to the neural and cognitive processes underlying the storage of sensory information along such basic stimulus dimensions as spatial frequency, orientation, and motion (Magnussen, 2000; Magnussen & Greenlee, 1999). The concept is related to, but not identical with, the concept of visual working memory (Baddeley, 2003). In perceptual memory experiments, memory is assessed in terms of the precision by which stimulus information is retained in memory, rather than in terms of the number of visual items or categories that can be retained; with a research strategy, that is closer to the correspondence metaphor of memory than it is to the storehouse metaphor (Koriat, Goldsmith, & Pansky, 2000).

Research on visual perceptual memory has a long scientific history, beginning with a paper by Fredrich Hegelmaier in 1852 on the memory for line length, in which he, prior to Fechner (1860), introduced the psychophysical method of constant stimuli and published the first experimental data on perceptual memory (Laming & Laming, 1992). Hegelmaier's paper was quickly forgotten – if indeed ever noticed – and the study of memory took a different course, largely owing to the impact of another German scientist, Herman Ebbinghaus. However, the study of perceptual memory survived in psychophysics (Laming & Scheiwiller, 1985) and was revived two decades ago, when it grew out of research on the mechanisms of visual processing (Magnussen, Greenlee, Asplund, & Dyrnes, 1990; Regan, 1985), a context in which it has remained, separated from mainstream memory research. The programme of modern perceptual memory research as formulated by Magnussen et al. (1990) has aimed to bridge the gap between perception and memory, noting that even if the simplest perceptual process involves the linking of online sensory signals with stored representations, perception and memory research progressed along parallel, isolated paths. Traditional research on visual memory employed alphanumeric stimuli or pictures of meaningful scenes that invited higher level categorical coding; thus, little could be concluded from these experiments regarding the perceptual component of visual memory. The strategy chosen by perceptual memory researchers was to start by investigating the storage of those elemental attributes of the visual stimulus that electrophysiological experiments on animal models and psychophysical studies on humans strongly indicated were the building blocks of visual perception – spatial frequency, orientation, motion, and colour (DeValois & DeValois, 1990; Pasternak, Bisley, & Valkins, 2003) – and from there to move on to more complex visual patterns and realistic pictures. The idea that visual memory recruited processes involved in online perceptual processing was not new (e.g., see Damasio, 1989), and several more recent brain imaging studies confirm the recruitment of early areas of visual analysis in visual imagery (Ganis, Thompson, & Kosslyn,

2004; Kosslyn & Thompson, 2003; Slotnick, Thompson, & Kosslyn, 2005). The new aspect in the study of visual perceptual memory was the use of experimental methods borrowed from psychophysics and theoretical models taken from research on spatial vision.

The basic experiment

Figure 1 illustrates the basic design of a visual perceptual memory experiment using the classic tool of vision research – sinusoidal gratings – which are computer-generated patterns where the luminance is modulated in a sinusoidal fashion. The grating may vary in spatial frequency (defined as the number of light–dark cycles per unit visual angle) or in contrast and orientation, and it may be stationary, flickering, or moving, varying in direction and speed of movement. The space-average luminance of the grating equals the background luminance, and in most modern experiments the grating is modulated by a orientation, contrast, and motion, which are the main features to which neurons in the primary visual cortex, area V1, are tuned (DeValois & DeValois, 1990; Pasternak et al., 2003). This chapter will limit the discussion to the features of spatial frequency and motion.

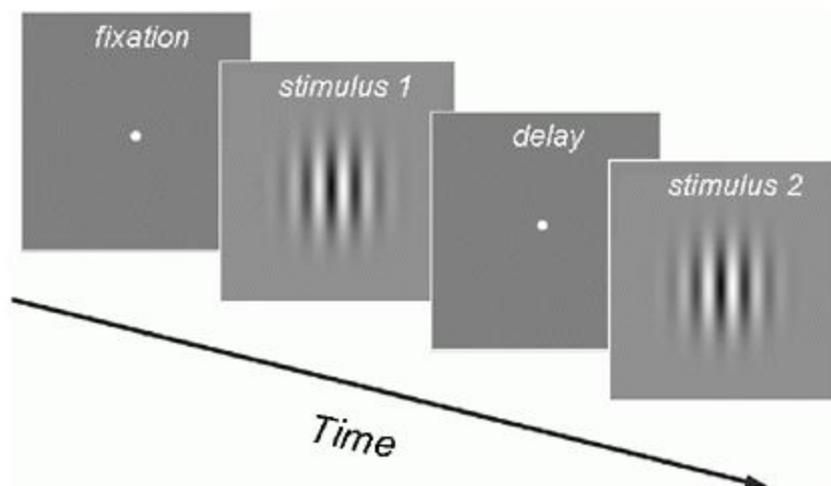


Figure 1 Illustrating the delayed discrimination experiment to explore visual perceptual memory with sinusoidal gratings modulated by a Gaussian envelope. In a two-alternative forced-choice task, the observer decides which of two gratings, Stimulus 1 or Stimulus 2, has the higher (or lower) spatial frequency. The gratings are separated by variable inter-stimulus intervals, and discrimination thresholds (or some equivalent measure) index the precision of perceptual storage of S1.

In a perceptual memory experiment, memory is measured in a delayed discrimination task with a variable interval between the two stimuli to be compared. The observer fixates a blank computer screen, a reference grating is briefly flashed, followed by an inter-stimulus interval of 1–60 s, and a brief presentation of a test grating of higher or lower value in, for example, spatial frequency, and the observer's task is to decide which of the two gratings had the higher value. With adaptive procedures, the computer algorithm selects two new stimuli whose spatial frequencies depend on whether the answer on the previous trial was correct or incorrect, whereas in other experimental designs a large range of stimulus pairs with preset values are presented in random order; in both cases, the reference spatial frequency is jittered so that the observer is never confronted with the exact same stimulus twice and, in order to solve the task, has to remember the spatial frequency of a novel reference grating on each trial. Such trial-by-trial jitter of the reference frequency is an important control in perceptual memory experiments to avoid forming permanent long-term representations of a

particular spatial frequency. Several authors have also pointed out the possible danger of testing regimes such as the method of constant stimuli, in which observers may form a representation of an imaginary “reference” by repeated exposure to a range of testing frequencies alone (Lages & Treisman, 1998) and no short-term memory of the individual reference grating is required to yield a psychometric function and discrimination threshold. In light of these precautions, memory for spatial frequency (or orientation, contrast, motion) is measured by the delayed discrimination threshold, $\Delta F/F$, or some equivalent measure, and the time course of memory decay can be tracked by varying the time interval between the two stimuli (ISI). Memory decay is indexed by changes in the discrimination threshold as the representation of the reference grating fades over time.

Somewhat surprisingly, the results of a number of experiments showed that at least for some basic attributes, such as spatial frequency and motion, discrimination thresholds did not change across intervals of 30–60 s, suggesting little or no decay in the precision of perceptual information in short-term memory (Bennett & Cortese, 1996; Blake, Cepeda, & Hiris, 1997; Lalonde & Chaudhuri, 2002; Magnussen & Greenlee, 1992; Magnussen et al., 1990). Furthermore, in many of the experiments, delayed spatial frequency discrimination thresholds were in the hyper-acuity range, with thresholds below the value expected based on cone spacing of the retina (Magnussen, 2000; Magnussen & Greenlee, 1999). Thus, sensory representations of the spatial frequency and the speed of a moving grating is maintained in short-term memory for periods exceeding 10 s with the same fidelity of simultaneous comparisons of test and reference stimulus pairs. Figure 2a illustrates this point, plotting some representative data for the memory of spatial frequency and motion. For other attributes, such as orientation, a slight decay is reported (Magnussen, Idås, & Holst Myhre, 1998), whereas memory for the contrast of gratings shows pronounced decay in short-term memory (Magnussen, Greenlee, & Thomas, 1996). The difference in decay across various attributes suggests different types of neural representations (Greenlee, Magnussen, & Thomas, 1991).

A close association between mechanisms of perceptual discrimination and memory does not imply that they represent the same processes; most concepts of memory assume a process that is distinct from online perceptual analysis, in the sense that information is transformed into a memory code. In psychophysical and cognitive research, memory is defined operationally by the time factor – memory starts when the stimulus goes off – rather than in terms of separate brain processes. The measure of accuracy of memory performance indexes the final outcome of the memory process and cannot distinguish between intermediate processes. However, measurements of the time spent on the decision in delayed discrimination might indicate the time of transfer from a perceptual code to a memory code, on the logic that if information is transferred to a memory code and later retrieved, the process of retrieving information would be added to the discrimination task in the memory condition. Thus, the observer should spend more time on the decision in the delayed compared to the simultaneous discrimination task, and the retention interval at which response times starts to increase should be an indicator of the time of transfer from a perceptual mode to a memory mode (Magnussen, 2000; Magnussen & Greenlee, 1999).

The results of several experiments confirmed that choice reaction times were prolonged in delayed discrimination tasks (Baumann et al., 2008; Greenlee, Koessler, Cornelissen, & Mergner, 1997; Reinvang, Magnussen, & Greenlee, 2002; Reinvang, Magnussen, Greenlee, & Larsson, 1998; Rothmayr et al., 2007). A systematic study of the short-term memory for spatial frequency and orientation (Magnussen et al., 1998) showed, first, that this increase was not the result of increased uncertainty in predicting the arrival of the test grating at longer ISIs, and, second, that the transfer from a perceptual mode to a memory mode occurred after 3–4 s following termination of the reference grating. The shape of this function is illustrated in Figure 2b, which plots results from several

unpublished experiments from our laboratory, probing a series of spatial frequencies and ISIs. Choice RTs start to rise after about 4 s, then increase with retention time in the short-term interval of 10 s. These results suggest that during the first 3 to 4 s following termination of a visual stimulus, information of elemental attributes of the visual stimulus is maintained in a real-time-like form, as accessible as online representations, before the transformation from a perceptual-type representation to a memory-type representation takes place. Furthermore, the physiological representation of spatial frequency (and motion) is maintained in short-term memory with a fidelity that matches the real-time physiological image. Thus, the transfer from a sensory representation to a short-term memory representation does not imply a loss of resolution of the spatial frequency or motion signals.

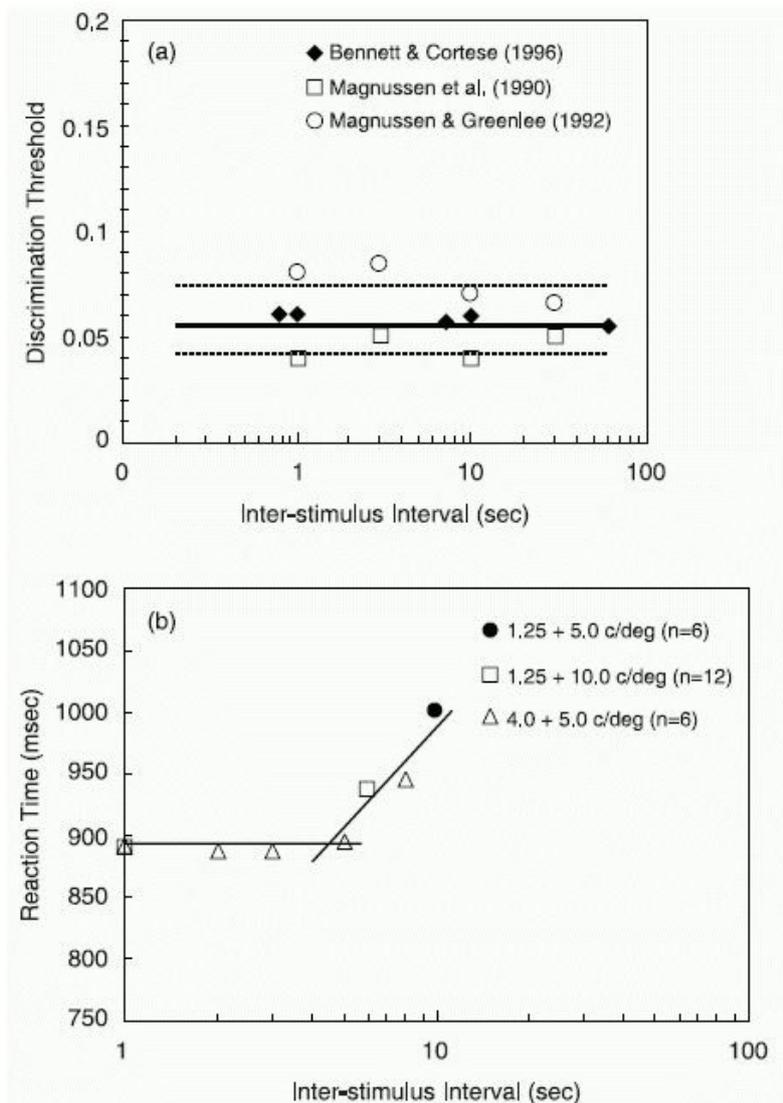


Figure 2a Delayed discriminations thresholds for spatial frequency and motion as a function of inter-stimulus interval. Results for spatial frequency are single-subject data re-plotted from Magnussen et al. (1990, Fig. 4) and Bennett and Cortese (1996, Fig. 1); results for motion are re-plotted from Magnussen and Greenlee (1992, Fig. 2), representing the average of two observers. **(b)** Choice reaction times in a delayed discrimination of spatial frequency as a function of inter-stimulus interval (ISI). Results are pooled from a number of experiments testing different spatial frequencies and ISIs, normalized to a common RT value for ISI = 1 s.

In describing this memory feat, we use the term “perceptual short-term memory” rather than the currently more popular “working memory concept” (Baddeley, 2003), chiefly because the memory performance in these experiments cannot be understood as an expression of episodic memory. Obviously, in most situations, including the experimental situations probing perceptual memory, several memory systems are activated in parallel, and the resulting performance may be supported by several systems (Tulving, 2002). In these experiments episodic memory is activated as the observer remembers seeing a grating and perhaps whether stripes were thick or thin, but the memory performance in delayed discriminations with a spatial resolution in the hyper-acuity range only turns up in forced choice experiments and does not have a conscious counterpart. On the contrary, the observer often has the feeling of just guessing, but also a feeling of guessing correctly. From these observations we conclude that the high-fidelity memory performance in delayed discrimination experiments is based on an implicit or non-declarative type of memory (Schacter, Wagner, & Buckner, 2000), rather than on explicit or declarative memory. Consistent with this interpretation, Tanaka and Sagi (1998a, 1998b) found evidence for sub-threshold priming of detection of Gabor patterns in the short-term memory range, and the priming effect was selective for features of the visual stimulus such as spatial frequency and orientation. Additional support for the hypothesis that visual perceptual memory performance is based on implicit memory is the finding that the performance on this memory task is similar for young and elderly subjects (Bennett, Sekuler, McIntosh, & Della-Maggiore, 2001; Della-Maggiore et al., 2000). Several studies of memory and aging have shown that indicators of implicit memory, such as priming, are not affected by age whereas tests of explicit memory performances exhibit age decline (Bäckman, Small, & Wahlin, 2001; Nilsson, 2003).

Perceptual short-term memory is robust

Visual perceptual short-term memory is astonishingly robust, with memory decay being resistant to a number of factors that affect spatial frequency or motion discrimination performance. The absence of age effects has already been noted, and several studies of patients with focal brain damage show intact short-term memory performance, albeit overall impaired discrimination performances. Greenlee, Rischewski, Mergner, and Seeger (1993) tested patients with focal lesions in the infero-temporal (IT) and superior temporal (ST) cortex on delayed spatial frequency discrimination and found that both groups were impaired in spatial frequency discrimination compared to normal controls, but that there were no significant effects of memory delay (1–10 s) – that is, discrimination performance is impaired but the subsequent course of memory is not affected – and the short-term memory functions for the patient and control participants were comparable. A similar pattern of results was reported by Greenlee, Lang, Mergner, and Seeger (1995) in a study of delayed velocity discrimination, with impaired velocity discrimination, but the overall effect of memory delay in the patients with lesions in ST, IT, or lateral parietal cortex (LP) was only significant for the ST region. Greenlee et al. (1997) tested patients with lesions in the occipito-temporal (OT), ST, and frontal cortex for the short-term memory of block patterns, and again they observed no additional impairment of the discrimination performance (assessed by d') across memory delay.

Some factors that might be expected to affect spatial frequency or motion discrimination do not act either on thresholds in simultaneous discrimination or on the subsequent memory function as indexed by delayed discrimination. For example, delayed spatial frequency discriminations are not affected by the relative orientation of reference and test gratings (Magnussen et al., 1990, 1998) and, in a similar

fashion, delayed orientation discriminations are not affected by the relative spatial frequency of the gratings (Magnussen et al., 1998). Discrimination thresholds of single components of complex gratings are similar to those of simple gratings, and with no memory decay (Magnussen & Greenlee, 1999). The contrast of the gratings may be varied randomly across trials without affecting spatial frequency discrimination thresholds or the decay function, and in delayed discrimination of spatial frequency and contrast in a dual-task design, neither thresholds nor the subsequent course of memory are affected for either component, when the effect of stimulus uncertainty is factored out (Magnussen et al., 1996; Thomas, Magnussen, & Greenlee, 2000). Similar results were obtained for dual judgments of two contrast components (Magnussen et al., 1996); thus, even if contrast information declines, the slope of the decay function appears to be quite resistant to interference.

A number of experimental factors that degrade the perceptual discrimination process leave the memory function intact. Magnussen et al. (1990) found that thresholds increased as the contrast of the test and reference grating increased, but the decay functions were parallel for low- and high-contrast gratings. Similar results were reported for velocity discrimination of gratings with low and high velocities; thresholds were higher for high-velocity gratings, but the short-term memory functions were parallel (Magnussen & Greenlee, 1992). When observers are required to remember more than one spatial frequency or spatial frequency combinations, thresholds increase or accuracy scores decline, but the subsequent memory function is uncorrupted (Kahana & Sekuler, 2002; Magnussen & Greenlee, 1997, 1999). Similar results were reported by Blake et al. (1997) for motion. When the task load was increased by having the observer remember several directions of motion presented in sequence, the discrimination performance decreased in proportion to the number of motion components that had to be remembered, but this task load factor did not interact with retention time on memory performance. Taken together, these findings are consistent with the recent hypothesis that decay in perceptual memory is deterministic rather than the result of random perturbations of visual representations as time goes by (Gold, Murray, Sekuler, Bennett, & Sekuler, 2005). The course of memory decay is remarkably unaffected by subject factors and by experimental manipulations that impair the over-all level of discrimination performance. So far, two exceptions to this general rule have been reported. First, Ben-Yehudah and Ahissar (2004) have found that delayed as compared with simultaneous spatial frequency discrimination is consistently impaired among adult dys-lectics, suggesting that a deficit in perceptual short-term memory may be involved. Second, Magnussen et al. (1996) showed that when participants had to keep track of spatial frequency information in a design where the absolute spatial frequency of the reference grating varied across a wide spatial frequency range, the short-term memory for spatial frequency started to decay. Similarly, the decay of memory for grating contrast was more pronounced with large variations in reference contrast.

A model of perceptual memory

Based on the psychophysical results, we proposed a model of perceptual discrimination and memory that assumes that information about elementary stimulus attributes is processed in a network of independent special-purpose memory stores, each devoted to a particular attribute or dimension of the visual stimulus. Each attribute or dimension is represented by an array of memory elements that extract information about one dimension (e.g., spatial frequency) across other dimensions (e.g., orientation). It is further assumed that each individual element in an array represents a limited range along a given stimulus dimension and that elements are linked in a lateral inhibitory network. This

arrangement allows inhibition within but not between dimensions. It is further assumed that the special-purpose memory stores draw on independent attentional resources.

The model assumes that discrimination and memory are based on representations that are located at an early stage in the visual process, but beyond visual area V1; this higher order processing stage combines information from V1-type neural representations that are tuned to multiple dimensions of the visual stimulus (DeValois & DeValois, 1990; Pasternak et al., 2003). Results of Magnussen et al. (1998) suggest that this extraction process is performed in terms of a “cortical search” of low-level (V1) representations. They found that when, in delayed spatial frequency discrimination, the relative orientation difference of the reference and test gratings was altered, discrimination thresholds remained unaffected but choice reaction times increased linearly with the separation angle of the reference and test gratings. Likewise, changing the relative spatial frequencies of the gratings in an orientation discrimination task did not affect discrimination accuracy but increased choice RTs. For both conditions the increase in RT added linearly to the increase in choice RT produced by changing the memory delay. The effect is analogous to mental rotation and size transformation (Bundesen, Larsen, & Farrell, 1981), except that it is not accompanied by a conscious strategy of rotation. Rather, it appears as if the brain performs a search across multiple representations in an arrangement of multiple-tuned channels where the functional distance between units coding neighbouring spatial frequencies is greater for units that simultaneously code very different orientations than for units that code neighbouring spatial frequencies and similar or neighbouring orientations. The functional organization in orientation columns and spatial frequency rows of multiple-tuned neurons of V1 proposed by Maffei and Fiorentini (1977) and DeValois and DeValois (1990) would be ideally suited for such a systematic search, but more recent results indicate that this very orderly anatomical organization is probably too simple (Everson et al., 1998; Sirovich & Uglesich, 2004). However, the precise functional organization map of orientation and spatial frequency coding is not critical to the theory.

Thus, the important assumptions of the models are, first, that perceptual short-term memory is based on dimension-specific neural representations beyond V1 that extracts information from multiple-tuned early (V1) representations, and, second, that memory representations are separate from perceptual representations, with a transfer between representational modes after 3–4 s following termination of a stimulus.

Psychophysical evidence

This model fits most of the psychophysical data. First, discrimination and memory of one attribute are not affected by variations along an irrelevant dimension (Magnussen et al., 1998). Second, dual-judgment experiments comparing discrimination and short-term memory for two simultaneously processed stimulus components show that different dimensions (e.g., contrast and spatial frequency) are processed in parallel, but the task of keeping track of two components on the same dimension (e.g., two spatial frequencies or two contrasts) leads to strong interference and substantial increase in discrimination thresholds (Magnussen & Greenlee, 1997; Magnussen et al., 1996; Thomas et al., 2000); however, the memory functions remain unaffected. Third, manipulations of stimulus complexity by varying one dimension of the stimulus acts on the discrimination threshold of that dimension but leaves discrimination and memory for simultaneously processed other dimensions unaffected (Magnussen et al., 1996).

Fourth, the most powerful psychophysical evidence for the model comes from experiments on so-called memory masking. Memory masking, originally demonstrated by Magnussen, Greenlee, Asplund, and Dyrnes (1991) and confirmed in a number of studies of the memory for spatial frequency (Bennett & Cortese, 1996; Lalonde & Chaudhuri, 2002) and motion (Magnussen & Greenlee, 1992; McKeefry, Burton, & Vakrou, 2007), refers to the detrimental effect on delayed discrimination thresholds produced by a masker stimulus presented briefly during the interval between reference and test. The basic phenomenon is illustrated in Figure 3, re-plotting results from experiments on spatial frequency and motion.

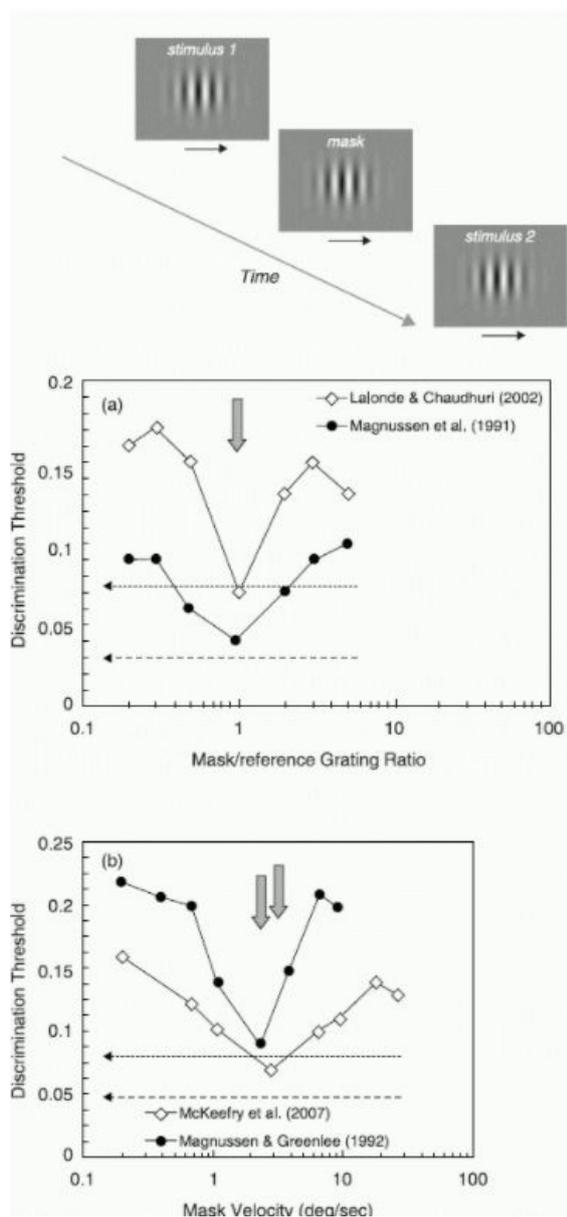


Figure 3 Memory masking. (a) Results for spatial frequency, re-plotted from Magnussen et al. (1991, Fig. 2, average of two observers) and Lalonde and Chaudhuri (2002, Fig. 2, average of three observers). Horizontal dashed lines indicate discrimination thresholds in the absence of a masker. (b) Memory masking of motion thresholds. Results are re-plotted from Magnussen and Greenlee (1992, Fig. 3c, average of two observers) and McKeefry et al. (2007, Fig. 2, average of three observers).

Basically, in a memory masking experiment, a masker stimulus is presented during a 10-s ISI, at a point in time during the ISI that is well out of reach of conventional sensory masking in both forward and backward directions (Ogmen, Breitmeyer, & Melvin, 2003). The masking effect is precisely the opposite of sensory masking, in which maximal masking effect is observed with identical test and masker stimuli and the masking effect decreases when the masker moves away from the test stimulus in spatial frequency or orientation. In memory masking of spatial frequency, no masking effect is observed when the spatial frequency of the test/reference and masker gratings are similar, and the masking effect increases as the masker frequency moves away from the reference/test frequency in both directions and reaches a maximum value of a difference of approximately ± 1 octave; beyond this value there is evidence for a gradual return to baseline. The size of the masking effect is about a doubling in delayed discrimination thresholds in the various experiments (Bennett & Cortese, 1996; Lalonde & Chaudhuri, 2002; Magnussen et al., 1991; McKeefry et al., 2007). The stimulus selectivity of the memory masking effect fits the hypothesis of inhibition between channels, as the selectivity of the masking effects agrees well with the results of classical psychophysical studies of channel width by masking and spatial adaptation, which is believed to reflect the selectivity of V1 neurons (Blakemore & Campbell, 1969; Greenlee & Magnussen, 1988; Greenlee, Magnussen, & Nordby, 1988). However, memory masking is selective to the perceived spatial frequency rather than to the retinal spatial frequency, suggesting that the mechanism of masking is located at a level in the processing stream at which size and shape constancies are computed (Bennett & Cortese, 1996).

Further evidence for a location of the perceptual memory mechanism beyond V1 is the observation that, in contrast to sensory masking, memory masking is selective to interference along the dimension on which perceptual discrimination is required but not along other dimensions. Thus, in delayed discrimination of spatial frequency, interference is observed when masker frequency is varied but the discrimination performance is insensitive to changes in the orientation of the masker (Magnussen et al., 1991), and, conversely, changing the spatial frequency of the masker does not affect orientation discrimination (Lalonde & Chaudhuri, 2002). Likewise, memory masking of motion is selective to the speed of the masker grating, but not to the direction of motion (Magnussen & Greenlee, 1992), nor to the spatial/ temporal frequency of the grating (McKeefry et al., 2007). Direct evidence for the involvement of cortical areas beyond V1 in the perceptual memory was provided by Campana, Cowey, and Walsh (2002), who showed that transcranial magnetic stimulation (TMS) applied to area V5/MT disrupted perceptual priming of speed discrimination, whereas stimulation to V1 or posterior parietal cortex (PPC) had no effect. Furthermore, TMS applied to V5/MT selectively affected priming of motion, leaving priming of colour discrimination intact. In a follow-up study, Campana, Cowey, and Walsh (2006) found that disruption of V5/MT activity is also inefficient in disturbing memory for spatial position.

Lalonde and Chaudhuri (2002) tested the hypothesis of a two-stage mechanism of perceptual memory, taking advantage of the memory masking effect. They reasoned that if perceptual representations and memory representations were different, the effect of a masker grating required that the masker and the stimulus on which it acted had to be in the same representational mode. They performed two experiments. In the first experiment the masker was presented 3 s or 10 s before the reference grating, which was followed by the test grating after 6 s. Thus, when representation of the masker stimulus was in a perceptual mode (3-s interval; see Figure 2), memory masking would be normal, but when the masker representation had transferred to a memory mode, it would not affect a subsequently presented reference grating and no masking would be observed. The results confirmed the prediction. However, the results of the second experiment modified this conclusion. In this experiment, information about the masker stimulus had to be kept alive, because the subject had to perform a second (and easier) discrimination task on the same trials, where the masker had to be

compared to a fourth grating presented after the principal discrimination task had been completed. The results now showed normal memory masker functions for both 3-s and 10-s masker-reference intervals. This suggests that some form of attentional control of information, perhaps through a refreshing mechanism similar to the visuospatial sketchpad (Baddeley, 2003), is necessary. These findings suggest either that information may be maintained in a perceptual mode by the refreshing mechanism or, if transferred to a short-term memory representation, that there is interference between spatial frequencies at the level of short-term memory representation. This question remains unsettled.

Brain imaging of perceptual memory

All experimental tasks requiring focal attention and conscious perception recruit a common set of overlapping brain regions (Naghavi & Nyberg, 2005). In visual perceptual memory experiments, conventional visual working memory mechanisms are obviously activated in parallel with the memory mechanisms responsible for the high-fidelity perceptual memory performance. This parallel activation of memory systems makes it difficult to isolate the perceptual memory component of the activation patterns.

A limited set of brain areas have been identified as the neural correlates of visual short-term memory by means of PET (Bennett et al., 2001; Corrette, Dupont, & Orban, 2002; Della-Maggiore et al., 2000), ERP (Reinvang et al., 1998), and fMRI (Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Rothmayr et al., 2007). Among these is posterior parietal cortex, which may reflect the neural capacity limit of visual working memory (Todd & Marois, 2004). Using a multiple-stimulus display to test the capacity of visual working memory, Xu and Chun (2006) have proposed that the inferior intraparietal sulcus (IPS), the superior IPS, and the lateral occipital cortex (LOC) work in parallel to support visual memory encoding and maintenance. They suggest that representations in inferior IPS may be limited to a fixed number of objects, whereas capacity in LOC and superior IPS is limited by object complexity. LOC and superior IPS may thus participate in storing detailed representations of stimuli in visual working memory. In addition, various striate and extra-striate areas of the occipital cortex have been identified as visual perceptual memory correlates (Greenlee, Magnussen, & Reinvang, 2000). Interestingly, relatively early visual areas beyond V1, which have previously only been associated with visual perception, are also active during visual memory delays (for a review, see Pasternak & Greenlee, 2005). Most studies that investigated visual memory found activity in the prefrontal cortex (PFC). The dorsolateral prefrontal cortex (DLPFC; BA 46/9) seems to play a crucial role in working memory-related processes (e.g., Fuster, 2001; Goldman-Rakic, 1995; Zhang, Leung, & Johnson, 2003). DLPFC activity has foremost been found in studies that required the manipulation of relevant items in working memory (e.g., Baumann, Frank, Rutschmann, & Greenlee, 2007b; Corrette, Dupont, Bormans, Mortelmans, & Orban, 2001). Many of these studies have used n-back tasks in which the subject has to remember an item presented n trials ago and match it to the present item. Delayed discrimination tasks, on the other hand, show less DLPFC activity (e.g., Faillenot, Sunaert, Van Hecke, & Orban, 2001). Contrary to working memory tasks, delayed discrimination tasks only require the maintenance of an item and not its manipulation. A role for DLPFC in the active manipulation of material in visual working memory has been shown (Cabeza & Nyberg, 2000), and DLPFC appears to be involved also in the storage of visual information for several objects (Leung, Gore, & Goldman-Rakic, 2002). Dorsolateral pre-frontal cortex, posterior parietal cortex, and regions in the occipital cortex thus appear to work together, and their exact interactions will depend on task demands. In an attempt to highlight the perceptual memory process, we recently used fMRI to explore the neural correlates of the delayed

discrimination of Gabor stimuli differing in spatial frequency (Baumann, Endestad, Magnussen, & Greenlee, 2007a). Fifteen subjects were instructed to code the spatial frequency with retention periods of 6-s duration. Participants had to decide whether two Gabor stimuli, which were presented sequentially and separated by a delay period, had the same or a different spatial frequency. There were two different difficulty levels of the task: one involving Gabor stimuli with very low spatial frequency that were easily coded by counting the dark bars of the Gabor grating, the second involving Gabor stimuli with a high spatial frequency where the first strategy could not be employed. To prepare the subjects for an upcoming trial, a central prompt was presented 2 s before the appearance of the reference stimuli, indicating also whether it would be an easy or a difficult trial. Since the activation pattern for both conditions were highly similar, we report the average of both conditions (see Figure 4).

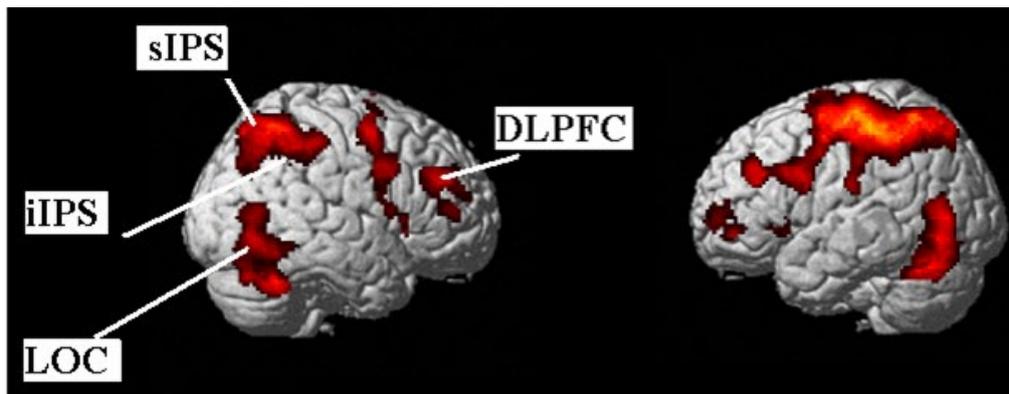


Figure 4 Group activation map illustrating significant activity associated with the 6-s retention period. The fMRI data was processed and analysed using Statistical Parametric Mapping SPM 2 (SPM2, Wellcome Department of Cognitive Neurology, London, UK; <http://www.fil.ion.ucl.ac.uk/spm/>) implemented in MATLAB (The MathWorks, Inc.). In a random-effects group analysis using the general linear model we found the expected activation pattern: DLPFC, superior and inferior parietal cortex, and lateral occipital cortex were clearly activated during the retention period of 6 s.

A region of interest (ROI) analysis was conducted using “Marsbar” (Brett, Anton, Valabregue, & Poline, 2002). We defined the DLPFC, the superior intraparietal sulcus (sIPS), the inferior intraparietal sulcus (iIPS), and the LOC as regions of interest (see Figures 4 and 5). The regions were activated in our group random-effects analysis, and the coordinates were congruent with the literature (Volle et al., 2005; Xu & Chun, 2006). The blood oxygen level dependent (BOLD) signal of the voxels for each of these regions was averaged, and the relative change of the BOLD signal during the retention period was computed in comparison to the average activity in these ROIs for the entire fMRI measurement. The BOLD signal in the LOC and sIPS showed separate peaks for the presentation of the prompt and the reference stimulus, whereby the amplitude related to the reference stimulus was much higher. In contrast, the BOLD response of the iIPS to the prompt was sustained until the presentation of the reference stimulus. Compared to the LOC and sIPS, the response in the iIPS to the test stimulus also exhibited a somewhat delayed and more enduring response. These findings suggest that the activation patterns of sIPS and LOC indicate their involvement in the encoding and retrieval processes for the Gabor stimuli, while the activity in the inferior IPS seems to be related to a more general attentional component. The DLPFC shows a left/right dissociation, with the left DLPFC activated during the encoding period and the right DLPFC during the retrieval period. This pattern is in concordance with the hemispheric encoding/retrieval asymmetry (HERA) model (Habib, Nyberg, & Tulving 2003). Virtually all studies that investigated visual working memory found activity in the prefrontal cortex. DLPFC activity has foremost been reported in studies that required the manipulation of relevant items

in memory (e.g., Baumann et al., 2007b; Cornette et al., 2001). Delayed discrimination tasks, on the other hand, show less DLPFC activity (Faillenot et al., 2001), and the present results are consistent with this finding.

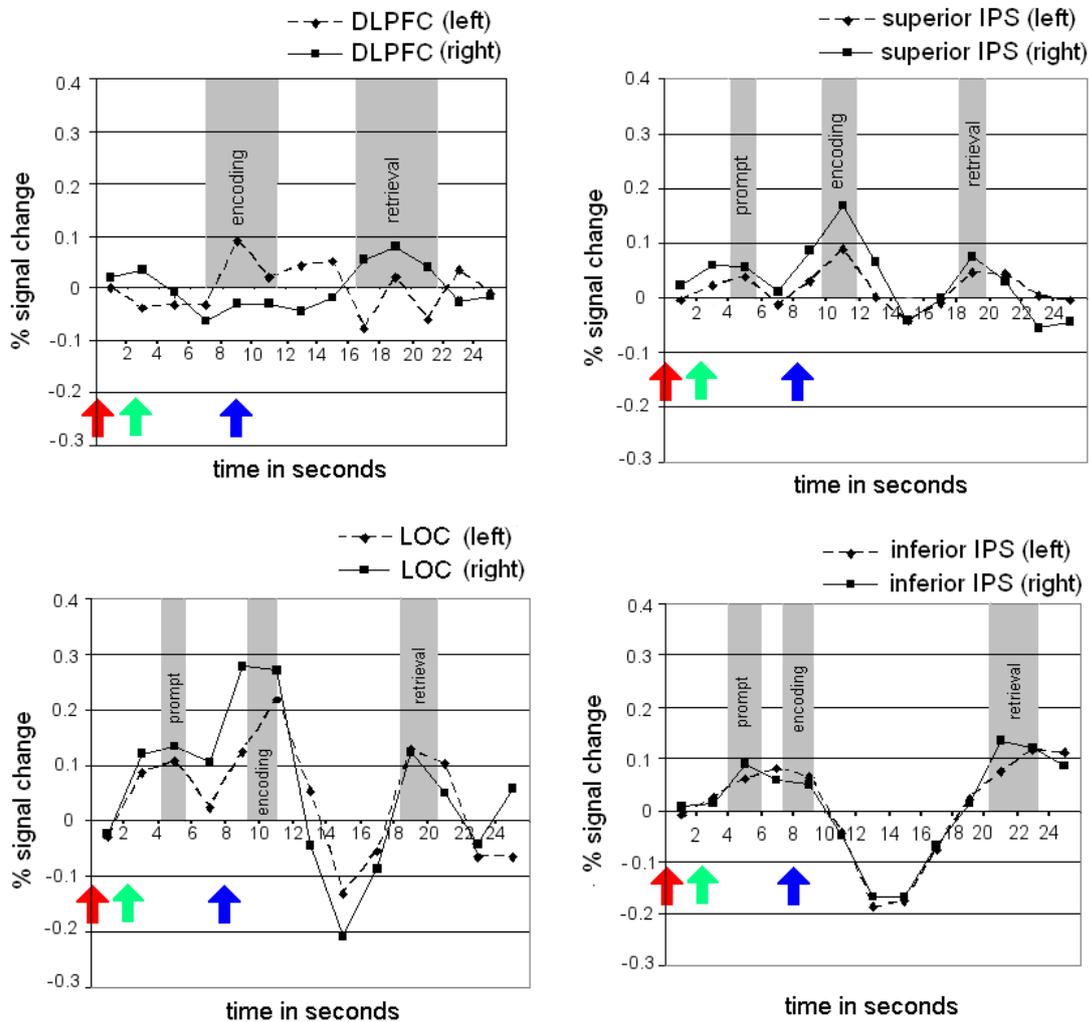


Figure 5 Time course of percent BOLD signal change for the four regions of interest. The dark-grey arrow indicates the appearance of the prompt at 0 s, the light-grey arrow the appearance of the reference stimuli at 2 s (subject had to encode the spatial frequency of a Gabor stimulus), and the black arrow with the test stimuli at 8 s (subject had to judge whether the test and the reference grating had the same spatial frequency). The grey-shaded areas indicate onset and duration of hypothetical cognitive processes associated with changes in the BOLD signal.

The results of this experiment shows that the activity pattern evoked in a perceptual memory experiment is basically similar to the activity pattern evoked by conventional visual working memory experiments (Naghavi & Nyberg, 2005), except for a generally lower DLPFC activity, which is to be expected as the experimental task itself must activate working memory mechanisms. In a further attempt to isolate a perceptual memory component, we recently conducted an fMRI experiment (Baumann et al., 2008) designed to test the concept of cortical serial search within a network of multiple-tuned channels, which was so far only based on behavioural findings (Magnussen, 2000; Magnussen & Greenlee, 1999). We used fMRI in a 3-T head scanner and a delayed discrimination task to investigate whether early visual cortex, or higher cognitive areas, are involved in the additional

processing of task-irrelevant stimulus properties indicated, for example, by prolonged reaction times for the discrimination of spatial frequencies with large orientation differences. Subjects were asked to remember for 8 s the spatial frequency of centrally presented Gabor stimuli that had either the same or a different orientation. The BOLD fMRI revealed significantly elevated bilateral activity in visual areas V1 and V2 (BA 17 and BA 18) when the gratings to be compared had an orthogonal orientation, compared to when they had the same orientation. The activation of low-level visual areas and the additional finding that no prefrontal and parietal activation was observed supports a model of perceptual memory in which task-relevant information from low-level resources for dimensions like spatial frequency and orientation is extracted by high-level components. It further suggests that the retrieval of high-fidelity visual information requires activation of different stores, which requires more time and higher metabolic costs even if an irrelevant stimulus dimension has been changed. The differential contrast between the activations evoked by the conditions in which stimuli had the same or the orthogonal orientation eliminates any non-specific activations related to the general nature of the memory task.

Therefore, these results point to an automatic “cortical search” process that compares information for one stimulus dimension (e.g., spatial frequency) over all other possible stimulus dimensions (e.g., orientation). The results of this study imply that the perceptual memory representations studied in delayed discrimination of orientation and spatial frequency are located quite early in the cortical processing streams.

What are the functions of perceptual memory?

Two decades of research on visual perceptual memory have provided solid evidence for a separate perceptual memory mechanism, closely associated with mechanisms of visual discrimination and located early in the processing stream and organized in terms of a set of parallel, independent domain-specific storage mechanisms. The model outlined above is consistent with most of the available experimental evidence. What is the function of this memory mechanism? One possibility is that it is a memory mechanism with a limited temporal operating range that assists the formation of high-precision long-term memories of structurally coherent images and meaningful patterns (Magnussen, 2000). According to this hypothesis, it is a supporting component of the perceptual representation system (PRS), located before the level of object descriptions (Tulving & Schacter, 1990). The supporting role of low-level storage of visual attributes may not be limited to a short-term memory range, as the consolidation process in long-term memory may proceed for weeks, even months.

A second possibility is that the perceptual memory represents a separate, parallel, implicit long-term memory mechanism storing high-precision information about the elemental visual dimensions and supporting pictorial memory and memory for visual scenes. Tulving (2002) reminds us that memory performances may be supported by several memory systems. The accuracy of episodic memory may be enhanced by the operation of implicit memory systems. According to this view one might expect high-fidelity long-term memory not only for pictures (Standing, 1973) but for specific values along V1 dimensions. However, the existence of long-term memory for elemental dimensions such as spatial frequency is debated. Lages and Treisman (1998) have pointed out methodological weaknesses in the early demonstrations of high-fidelity long-term memory of spatial frequency (Magnussen & Dyrnes, 1994) and have shown that the method of constant stimuli used in that study might produce an artificial short-term reference against which the test gratings might be compared. In a more recent study (Magnussen, Greenlee, Aslaksen, & Kildebo, 2003), this problem was solved by having a large number of observers view a single test grating and decide whether the spatial frequency of the test

grating was higher or lower than the spatial frequency of the reference grating presented on a previous occasion, with different groups of participants tested with different spatial frequencies. The resulting group psychometric functions were identical for immediate testing and a 24-hour test interval, suggesting high-precision storage of spatial frequency. However, a recent report failed to replicate the results, showing shallower psychometric functions for long intervals (Lages & Paul, 2006). Thus, the question of a high-fidelity long-term store for spatial frequency is not settled.

Indirect evidence for long-term storage of visual details was reported in a recent study by Vogt and Magnussen (2007), who showed that the long-term memory of naturalistic pictures – in casu pictures of doors – was substantially impaired by removing minor pictorial details that remained largely undetected by the participants (examples of the stimuli are shown in Figure 6). In that experiment, participants were presented with a study set of 400 pictures, each presented for 5 s, and were subsequently tested for recognition memory with samples consisting of 50 old and 50 new pictures, across an interval of 9 days. The results of the experiment showed that when pictorial details were removed, memory performance dropped by about 20% and the decay function followed a parallel, shallow slope. These results are in line with several other recent studies (e.g., Castelhana & Henderson, 2005; Hollingworth, 2005) and suggest that implicit memory may support explicit memory performance and also that the memory for perceptual details may be more important in memory for naturalistic scenes than was previously realized.



Figure 6 Examples of the stimuli used by Vogt and Magnussen (2007) in a study of long-term memory for a single category of objects: doors. The upper row shows the original photographs; the lower row shows the same photographs edited by removing minor details. This manipulation of the pictures caused the memory performance to drop by 20%.

References

- Bäckman, L., Small, B. J., & Wahlin, Å. (2001). Ageing and memory: Cognitive and biological processes. In J. E. Birren & K. W. Schaie (Eds.), *Handbook of the psychology of ageing* (5th ed., pp. 349–377). New York: Academic Press.
- Baddeley, A. D. (2003). Working memory: Looking back and looking forward. *Nature Neuroscience Reviews*, 4, 829–839.
- Baumann, O., Endestad, T., Magnussen, S., & Greenlee, M. W. (2007a). [Cortical activation during delayed discrimination of Gabor stimuli differing in spatial frequency]. Unpublished raw data.
- Baumann, O., Endestad, T., Magnussen, S., & Greenlee, M. W. (2008). Delayed discrimination of spatial frequency for gratings of different orientation: Behavioral and fMRI evidence for low-level perceptual memory stores in early visual cortex. *Experimental Brain Research*, 188, 363–369.
- Baumann, O., Frank, G., Rutschmann R. M., & Greenlee, M. W. (2007b). Cortical activation during sequences of memory-guided saccades: A functional MRI study. *NeuroReport*, 18, 451–455.
- Bennett, P. J., & Cortese, F. (1996). Masking of spatial frequency in visual memory depends on distal, not retinal frequency. *Vision Research*, 36, 233–238.
- Bennett, P. J., Sekuler, A. B., McIntosh, A. R., & Della-Maggiore, V. (2001). The effects of ageing on visual memory: Evidence for functional reorganization of cortical networks. *Acta Psychologica*, 197, 249–273.
- Ben-Yehudah, G., & Ahissar, M. (2004). Sequential spatial frequency discrimination is consistently impaired among adult dyslectics. *Vision Research*, 44, 1047–1063.
- Blake, R., Cepeda, N., & Hiris, E. (1997). Memory for visual motion. *Journal of Experimental Psychology: Human Perception and Performance*, 22, 353–369.
- Blakemore, C., & Campbell, F. W. (1969). On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology*, 203, 237–260.
- Brett, M., Anton, J. L., Valabregue, R., & Poline J. P. (2002). Region of interest analysis using an SPM toolbox. *NeuroImage*, 16, 497. B
- Bundesen, C., Larsen, A., & Farrell, J. E. (1981). Mental transformation of size and orientation. In J. Long & A. Baddeley (Eds.), *Attention and Performance IX* (pp. 279–294). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
- Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, 12, 1–47.
- Campana, G., Cowey, A., & Walsh, V. (2002). Priming of motion direction and area V5/MT: A test of perceptual memory. *Cerebral Cortex*, 12, 663–669.
- Campana, G., Cowey, A., & Walsh, V. (2006). Visual area V5/MT remembers “what” but not “where”. *Cerebral Cortex*, 16, 1766–1770.
- Castelhano, M. S., & Henderson, J. M. (2005). Incidental visual memory for objects in scenes. *Visual Cognition*, 12, 1017–1040.

- Cornette, L., Dupont, P., Bormans, G., Mortelmans, L., & Orban, G. A. (2001). Separate neural correlates for the mnemonic components of successive discrimination and working memory tasks. *Cerebral Cortex*, 1, 59–72.
- Cornette, L., Dupont, P., & Orban, G. A. (2002). The neural substrate of orientation short-term memory and resistance to distractor items. *European Journal of Neuroscience*, 15, 165–175.
- Damasio, A. R. (1989). Time-locked multiregional activation: A systems-level approach. *Cognition*, 33, 25–62.
- Della-Maggiore, V., Sekuler, A. B., Grady, C. L., Bennett, P. J., Sekuler, R., & McIntosh, A. R. (2000). Corticolimbic interactions associated with performance on a short-term memory task are modified by age. *Journal of Neuroscience*, 20, 8410–8416.
- DeValois, R. L., & DeValois, K. K. (1990). *Spatial vision*. Oxford, UK: Oxford University Press.
- Everson, R. M., Prashanth, A. K., Gabbay, M., Knight, B. W., Sirovich, L., & Kaplan, E. (1998). Representation of spatial frequency and orientation in the visual cortex. *Proceedings of the National Academy of Science USA*, 95, 8334–8338.
- Faillenot, I., Sunaert, S., Van Hecke, P., & Orban, G. A. (2001). Orientation discrimination of objects and gratings compared: An fMRI study. *European Journal of Neuroscience*, 13, 585–596.
- Fechner, G. T. (1860). *Elemente der Psychophysik*. Leipzig: Breitkopf & Härtel. Fuster, J. M. (2001). The prefrontal cortex – an update: Time is of the essence. *Neuron*, 30, 319–333.
- Ganis, G., Thompson, W. L., & Kosslyn, S. M. (2004). Brain areas underlying visual mental imagery and visual perception: An fMRI study. *Cognitive Brain Research*, 20, 226–241.
- Gold, J. M., Murray, R. F., Sekuler, A. B., Bennett, P. J., & Sekuler, R. (2005). Visual memory decay is deterministic. *Psychological Science*, 16, 769–774.
- Goldman-Rakic, P. S. (1995). Architecture of the prefrontal cortex and the central executive. *Annals of the New York Academy of Science*, 769, 71–83.
- Greenlee, M. W., Koessler, M., Cornelissen, F., & Mergner, T. (1997). Visual discrimination and short-term memory for random dot patterns in patients with a focal cortical lesion. *Cerebral Cortex*, 7, 253–267.
- Greenlee, M. W., Lang, H.-J., Mergner, T., & Seeger, W. (1995). Visual short-term memory of stimulus velocity in patients with unilateral posterior brain damage. *Journal of Neuroscience*, 15, 2287–2300.
- Greenlee, M. W., & Magnussen, S. (1988). Interactions among orientation and spatial frequency channels adapted concurrently. *Vision Research*, 28, 1303–1309.
- Greenlee, M. W., Magnussen, S., & Nordby, K. (1988). Spatial vision of the achromat: Spatial frequency and orientation-specific adaptation. *Journal of Physiology*, 395, 661–678.
- Greenlee, M. W., Magnussen, S., & Reinvang, I. (2000). Brain regions involved in spatial frequency discrimination: Evidence from fMRI. *Experimental Brain Research*, 132, 399–403.
- Greenlee, M. W., Magnussen, S., & Thomas, J. P. (1991). Different neural codes for spatial frequency and contrast. In A. Valberg & B. B. Lee (Eds.), *From pigments to perception: Advances in understanding visual processes* (pp. 451–454). New York: Plenum Press.

- Greenlee, M. W., Rischewski, J., Mergner, T., & Seeger, W. (1993). Delayed pattern discrimination in patients with unilateral temporal lobe damage. *Journal of Neuroscience*, 13, 2565–2574.
- Habib, R., Nyberg L., & Tulving E. (2003). Hemispheric asymmetries of memory: The HERA model revisited. *Trends in Cognitive Sciences*, 7, 241–245.
- Hollingworth, A. (2005). The relation between on-line visual representation of a scene and long-term scene memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 31, 396–411.
- Kahana, M. J., & Sekuler, R. (2002). Recognizing spatial patterns: A noisy exemplar approach. *Vision Research*, 42, 2177–2192.
- Koriat, A., Goldsmith, M., & Pansky, A. (2000). Toward a psychology of memory accuracy. *Annual Review of Psychology*, 51, 481–537.
- Kosslyn, S. M., & Thompson, W. L. (2003). When is early visual cortex activated during visual mental imagery? *Psychological Bulletin*, 129, 723–746.
- Lages, M., & Paul, A. (2006). Visual long-term memory for spatial frequency? *Psychonomic Bulletin & Review*, 13, 486–492.
- Lages, M., & Treisman, M. (1998). Spatial frequency discrimination: Visual long-term memory or criterion setting? *Vision Research*, 38, 557–572.
- Lalonde, J., & Chaudhuri, A. (2002). Task-dependent transfer of perceptual to memory representations during delayed spatial frequency discrimination. *Vision Research*, 42, 1759–1769.
- Laming, D., & Laming, J. (1992). F. Hegelmaier: On memory for the length of a line. *Psychological Research*, 54, 233–239.
- Laming, D., & Scheiwiler, P. (1985). Retention in perceptual memory: A review of models and data. *Perception & Psychophysics*, 37, 189–197.
- Leung, H. C., Gore, J. C., & Goldman-Rakic, P. S. (2002). Sustained mnemonic response in the human middle frontal gyrus during the on-line storage of spatial memoranda. *Journal of Cognitive Neuroscience*, 14, 659–671.
- Maffei, L., & Fiorentini, A. (1977). Spatial frequency rows in the striate visual cortex. *Vision Research*, 17, 257–264.
- Magnussen, S. (2000). Low-level memory processes in vision. *Trends in Neurosciences*, 23, 247–251.
- Magnussen, S., & Dyrnes, S. (1994). High-fidelity perceptual long-term memory. *Psychological Science*, 5, 99–102.
- Magnussen, S., & Greenlee, M. W. (1992). Retention and disruption of motion information in visual short-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 18, 151–156.
- Magnussen, S., & Greenlee, M. W. (1997). Competition and sharing of processing resources in visual discrimination. *Journal of Experimental Psychology: Human Perception and Performance*, 22, 1603–1616.
- Magnussen, S., & Greenlee, M. W. (1999). The psychophysics of perceptual memory. *Psychological Research*, 62, 81–92.

- Magnussen, S., Greenlee, M. W., Aslaksen, P. M., & Kildebo, O. Ø. (2003). High-fidelity long-term memory for spatial frequency revisited – and confirmed. *Psychological Science*, 14, 74–76.
- Magnussen, S., Greenlee, M. W., Asplund, R., & Dyrnes, S. (1990). Perfect visual short-term memory for periodic patterns. *European Journal of Cognitive Psychology*, 4, 345–362.
- Magnussen, S., Greenlee, M. W., Asplund, R., & Dyrnes, S. (1991). Stimulus-specific mechanisms of visual short-term memory. *Vision Research*, 31, 1213–1219.
- Magnussen, S., Greenlee, M. W., & Thomas, J. P. (1996). Parallel processing in visual short-term memory. *Journal of Experimental Psychology: Human Perception and Performance*, 22, 202–212.
- Magnussen, S., Idås, E., & Holst Myhre, S. (1998). Representation of orientation and spatial frequency in perception and memory: A choice reaction-time analysis. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 707–718.
- McKeefry, D. J., Burton, M. P., & Vakrou, C. (2007). Speed selectivity in visual short-term memory for motion. *Vision Research*, 47, 2418–2425.
- Naghavi, H. R., & Nyberg, L. (2005). Common fronto-parietal activity in attention, memory, and consciousness: Shared demands on integration? *Consciousness and Cognition*, 14, 390–425.
- Nilsson, L.-G. (2003). Memory function in normal ageing. *Acta Neurologica Scandinavica*, 107 (suppl. 179), 7–13.
- Ogmen, H., Breitmeyer, B. G., & Melvin, R. (2003). The what and where in visual masking. *Vision Research*, 43, 1337–1350.
- Pasternak, T., Bisley, J. W., & Valkins, D. (2003). Visual information processing in the primate brain. In M. Gallagher & R. J. Nelson (Eds.), *Biological psychology* (pp. 130–185). New York: Wiley.
- Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews Neuroscience*, 6, 97–107.
- Pessoa, L., Gutierrez, E., Bandettini, P. A., & Ungerleider, L. (2002). Neural correlates of visual working memory: fMRI amplitude predicts task performance. *Neuron*, 35, 975–987.
- Regan, D. (1985). Storage of spatial frequency information and spatial-frequency discrimination. *Journal of the Optical Society of America*, A2, 619–621.
- Reinvang, I., Magnussen, S., & Greenlee, M. W. (2002). Hemispheric asymmetry in visual discrimination and memory: ERP-evidence for the spatial frequency hypothesis. *Experimental Brain Research*, 144, 483–495.
- Reinvang, I., Magnussen, S., Greenlee, M. W., & Larsson, P. G. (1998). Electro-physiological localization of cortical regions involved in perceptual memory. *Experimental Brain Research*, 123, 481–484.
- Rothmayr, C., Baumann, O., Endestad, T., Rutschmann, R. M., Magnussen, S., & Greenlee M. W. (2007). Dissociation of neural correlates of verbal and non-verbal visual working memory with different delays. *Behavioral Brain Functions*, 3, 56, doi: 10.1186/1744-9081-3-56.
- Schacter, D. L., Wagner, A. D., & Buckner, R. L. (2000). Memory systems of 1999. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 627–643). Oxford, UK: Oxford University Press.

- Sirovich, L., & Uglesich, R. (2004). The organization of orientation and spatial frequency in primary visual cortex. *Proceedings of the National Academy of Sciences USA*, 101, 16941–16946.
- Slotnick, S. D., Thompson, W. L., & Kosslyn, S. M. (2005). Visual mental imagery induces retinotopically organized activation of early visual areas. *Cerebral Cortex*, 15, 1570–1583.
- Standing, L. (1973). Remembering 10,000 pictures. *Quarterly Journal of Experimental Psychology*, 25, 207–222.
- Tanaka, Y., & Sagi, D. (1998a). A perceptual memory for low-contrast signals. *Proceedings of the National Academy of Sciences USA*, 95, 12729–12733.
- Tanaka, Y., & Sagi, D. (1998b). Long-lasting, long-range detection facilitation. *Vision Research*, 38, 2591–2599.
- Thomas, J. P., Magnussen, S., & Greenlee, M. W. (2000). What limits simultaneous discrimination accuracy? *Vision Research*, 40, 3169–3172.
- Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, 428, 751–754.
- Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology*, 53, 1–25.
- Tulving, E. & Schacter, D. L. (1990). Priming and human memory systems. *Science*, 247, 301–306.
- Vogt, S. E., & Magnussen, S. (2007). Long-term memory for 400 pictures on a common theme. *Experimental Psychology*, 54, 298–303.
- Volle, E., Pochon, J. B., Lehericy, S., Pillon, B., Dubois, B., & Levy, R. (2005). Specific cerebral networks for maintenance and response organization within working memory as evidenced by the “double delay/double response” paradigm. *Cerebral Cortex*, 15, 1064–1074.
- Xu, Y., & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature*, 440, 91–95.
- Zhang, J. X., Leung, H. C., & Johnson, M. K. (2003). Frontal activations associated with accessing and evaluating information in working memory: An fMRI study. *NeuroImage*, 20, 1531–1539.