Task-dependent transfer of perceptual to memory representations during delayed spatial frequency discrimination

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Abstract

Discrimination thresholds were obtained during a delayed spatial frequency discrimination task. In Experiment 1, we found that presentation of a mask 3 s before onset of a reference Gabor patch caused selective interference in a subsequent discrimination task. However, a 10 s interval abolished this masking effect. In Experiment 2, the mask was associated with a second spatial frequency discrimination task so that a representation of the mask had to be coded into short-term perceptual memory. The presence of this second discrimination task now caused similar interference effects on the primary discrimination task at both the 3 s and 10 s ISI conditions. The different results from these two experiments are best explained by a two-step perceptual memory mechanism. The results also provide further insight into the conditions under which stimulus representations are shared between the perceptual and memory domains.

Résumé

Dans cette étude, nous nous sommes attardés à mesurer le seuil limite de discrimination lors d'une tâche de discrimination de fréquences spatiales à laquelle, les deux stimuli étant jugés sont précédés par la présentation d'un stimulus masqueur à soit 3 ou 10 secondes avant le stimulus de référence de la tâche de discrimination. Lors de l'Expérience 1, nous avons mis en évidence que la présentation d'un stimulus masqueur engendre un effet d'interférence à l'endroit de la tâche de discrimination seulement lorsque le stimulus masqueur se situe à 3 secondes du stimulus de référence. Une période inter-stimuli de 10 secondes entre le masque et le stimulus de référence élimine l'effet d'interférence. Pour l'Expérience 2, le stimulus masqueur fut aussi impliqué dans une tâche de discrimination de fréquences spatiales puisqu'il fut possible, cette fois, de l'associer avec la présentation d'un quatrième stimulus qui se situe à la toute fin de la séquence de présentation des stimuli. Cette manipulation avait pour but de forcer les participants à encoder l'information rattachée à la fréquence spatiale du masque en mémoire perceptive à court-terme. Avec la présence de cette seconde tâche de discrimination perceptive, l'effet d'interférence fut similaire pour les deux conditions, c'est-à-dire que l'effet était présent indépendamment du temps (3 ou 10 s) qui sépare le masque et le stimulus de référence. Les résultats obtenus dans cette étude sont expliqués à l'aide d'un modèle de la mémoire perceptive à deux niveaux de représentation. Les résultats démontrent en fait qu'un niveaux de représentation perceptive et une mnémonique sont différemment activés lors de la résolution d'une tâche de discrimination perceptive.

General Introduction

Early models of delayed perceptual discrimination were based on neurophysiological organization of striate and extrastriate visual cortex (e.g., DeValois & DeValois, 1990; Wilson, Levi, Mafei, Rovamo, & DeValois, 1990). The results of masking and adaptation experiments raised the possibility that perceptual discrimination may be closely coupled to the computational output of multiple-tuned channels found in the early stages of visual processing. However, a number of findings that appeared to be inconsistent with this view raised the possibility that delayed perceptual discrimination involving basic attributes of visual function (e.g., spatial frequency, orientation, contrast, color, and motion) may not necessarily be the end result of low-level, multiple-tuned channels (Burbeck & Regan, 1983; Bradley & Skottun, 1984; Greenlee & Thomas, 1993; Heeley, Buchanan-Smith, & Heywood, 1993; Magnussen, Greenlee, Asplund, & Dyrnes, 1990; Magnussen, Greenlee, & Thomas, 1996; Regan, 1985). The results of dual-task studies, where observers were required to simultaneously judge two low-level visual attributes during a discrimination task, established the notion that perceptual discrimination may instead be the product of a higher-level cortical mechanism (Greenlee & Thomas, 1993; Magnussen, Greenlee, & Thomas, 1996). It was proposed that this mechanism is responsible for directing an ensemble of special-purpose, limited-capacity subsystems that independently process and store perceptual information associated with each visual attribute for brief durations. The concept of perceptual memory has been used to describe this assembly of independent higher order subsystems. In two recent literature reviews about perceptual memory, it as been argued that this memory system

could be best described as a non-declarative or implicit memory system which operates as a subsystem of the Tulving and Schacter (1990) perceptual representation system (Magnussen, 2000; Magnussen & Greenlee, 1999).

The mechanisms that are operative during a delayed perceptual discrimination task are complicated by the results of a recent study using multivarying gratings (Magnussen, Idås & Myhre, 1998). Of particular interest is the data on choice reaction times (RTs) for both a spatial frequency and orientation discrimination task. In each of these perceptual tasks, the two stimuli being compared (sinusoidal gratings) were presented at different interstimulus intervals (ISI). The RT measures between the four different ISI conditions (0, 1, 3, and 10 seconds) revealed that distinctive levels of representations were operative, depending on the particular ISI value. For intervals of 3 s or less, the RTs for the Same-Different decisions were identical whereas for intervals beyond 3 s , the RTs increased significantly. The authors interpreted this result as evidence for a dichotomy between perceptual representation and memory representation of the information involved in the task (Magnussen et al., 1998). Thus, two different representations may be implicated in the perceptual discrimination process—one based on comparisons of perceptual representations over a short time-course and another based on memory representations that operates over longer time periods. The early mechanism may be based on a representation that maintains information accessible in a form similar to real-time information whereas prolonged perceptual discrimination exceeding 4-5 seconds ISI would require storage and subsequent retrieval from a short-term memory domain (Magnussen, 2000; Magnussen & Greenlee, 1999).

An important question concerns how visual information is transferred or shared from a perceptual representation mechanism to a memory-based one. Of particular interest is whether a discrimination task is necessary to have transfer to a memory representation or whether that transfer occurs automatically but that a discrimination task is required to retain the information for later use in perceptual discrimination. A related issue concerns the extent to which information is re-coded when transferred to a memory representation. It has been recently proposed that re-coding of visual information is a necessary condition for permanent storage (Magnussen, 2000; Magnussen & Greenlee, 1999), suggesting that a re-coded representation may be less susceptible to masking interference. These issues currently remain unresolved.

In the present study, we used a masking paradigm to explore the relationship between perceptual and memory representations. We found that the presence of visual information in a discrimination task is an essential requirement for transfer from a perceptual to a memory representation. Furthermore, the concurrent presence of a secondary source of information in short-term perceptual memory produces a selective interference effect similar to that observed in perceptual representations. These results suggest that re-coding of the perceptual representation is subject to higher order mechanisms that may involve a filtering mechanism that selectively maintains relevant information.

General Methods

Apparatus and stimuli.

Stimuli were 2D Gabor patches generated on a calibrated 17″ AppleVision monitor using a Power Macintosh 7200/120 and Matlab 5.1 software for Macintosh. Screen resolution was set at 1064 x 768 pixels with a frame rate of 75 Hz (interlaced). The mean luminance of the display was approximately 22 cd/m^2. The Gabor patterns were viewed binocularly from a distance of 57 cm and subtended approximately 5° of arc. An adjustable chin-forehead rest was used to stabilize head movements and maintain a stable fixation distance.

Observers.

Three naïve observers (CM, AC, and EB) and the first author (JL) were the participants in this study. JL and CM were tested on both experiments whereas AC participated only in Experiment 1 and EB only in Experiment 2. The three naïve observers were paid for their participation and none had training other than initial practice trials. All observers had normal or corrected-to-normal acuity and no history of ocular disease.

General procedures.

Discrimination thresholds were measured for three different base spatial frequencies (2, 3, and 6 c/deg). Base spatial frequency values were assigned to both the mask (S_1) and the reference patch (F_1). Preliminary testing was used to determine a set of five increments and decrements that spanned the discrimination threshold range. These values were exclusively associated to the

test patch (F_2) which always followed the presentation of the reference patch. Six different non-cardinal orientations were used. For all experiments, the Michelson contrast was maintained at 0.60.

The discrimination thresholds between F_1 and F_2 were measured using the Method of Constant Stimuli. Data from several testing blocks were collapsed and the thresholds determined for each mask/reference ratio point. We had a set of 7 mask/reference ratios because all possible base spatial frequencies pairings between the mask and reference patches were tested. A custom Matlab routine was employed to fit a psychometric function (Weibull function) through the data points of each mask/reference ratios. The discrimination thresholds were defined as the average between the 25% and 75% discrimination accuracy points on the psychometric function. Graphed points in the data figures typically reflect the average of four distinct measures.

Experiment 1

Introduction.

In Experiment 1, we examined masking effects on a spatial frequency discrimination task. Spatial frequency masking effects on a delayed spatial frequency discrimination task have been previously studied (Magnussen, Greenlee, Asplund, & Dyrnes, 1991; Bennett & Cortese, 1996). However, the mask in those studies was presented between the reference and test gratings. Because the longest interval between the mask and both of the gratings being discriminated was no more than 5 s, it was unlikely that the mask could fully probe the memory representation.

In our study, we adopted a similar task except that the mask was presented before the onset of the reference patch, as illustrated in Figure 1. The principal advantage to this stimulus sequence is that it allowed us to freely distance the mask presentation from the reference stimulus. For example, the mask could be presented under different temporal conditions that probe either perceptual or memory representations because of the greater flexibility in presenting the mask and discriminanda. Another advantage of our presentation sequence is that it limits masking interference to only the reference patch.

Insert Figure 1 here

Procedure.

Figure 1A presents a schematic diagram of the stimulus sequence used in Experiment 1. Each testing session was composed of 140 trials. After 12 consecutive sessions at a particular ISI condition (3 or 10 s), the alternate ISI condition was then tested. This sequence was counterbalanced among subjects. Thus, there were a total of 1680 trials for each ISI condition and a total of 3360 trials per subject. The sessions were carried out on average four times per week.

Trials began with presentation of a fixation point for 500 ms. This was followed by presentation of the mask for a duration of 210 ms during which participants were directed to scan the Gabor patch. However, they were not asked to retain or encode any specific information about this stimulus during its presentation or after its disappearance. After an ISI of either 3 or 10 s, the spatial

frequency discrimination task was initiated, involving F_1 and F_2. These two patches were presented for 210 ms at a constant ISI of 6 s. A two-interval forced-choice (2-IFC) procedure was used to probe which of the two Gabor patches had the highest spatial frequency. Subjects were required to provide their response through one of two keys on the keyboard. They were informed that the spatial frequency of the test patch had an equal probability of being higher or lower than the spatial frequency the reference patch in every session.

The base spatial frequency (i.e., 2, 3, or 6 c/deg) of the reference patch was randomly varied within a session to prevent long-term representation of the Gabor patches used in the discrimination task. Furthermore, although all three Gabor patches had the same orientation within a trial, we ensured that the actual orientation was randomly varied between the six different axes on each trial. Finally, the spatial frequency of the mask was constant within each testing block of 140 trials, but was randomly varied between sessions. Each of the three base spatial frequencies associated with the mask were presented four times per masking ISI condition.

A baseline performance measure was obtained for each subject on six different testing sessions involving the spatial frequency discrimination task between F_1 and F_2 but without the presence of a mask. The baseline values used in our analysis were derived from a composite of the six thresholds (2 for each base spatial frequency).

Results and discussion.

Figures 2A and 2B show the results of Experiment 1 for both the 3 and 10 s ISI conditions respectively. Discrimination thresholds are presented as Weber fractions (ΔF/F) and plotted as a function of the seven mask/reference ratios. The dashed line in each graph represents baseline discrimination threshold for each subject. The bar graphs on the right show the discrimination threshold averaged across three subjects after being normalized to the baseline for each mask/reference ratio.

Insert Figure 2 here

We observed a masking effect for the 3 s ISI condition that was similar in nature and of comparable intensity to that reported by Magnussen et al. (1991) and Bennett and Cortese (1996). The masking effect was present only when the mask and the reference patches were of a different spatial frequency. Elevation of the normalized discrimination thresholds ranged from 37% to 77%. The individual Weber fractions in the disparate spatial frequency conditions were nearly twice from those obtained when the mask and reference spatial frequencies were the same (ratio of 1.00). A comparison of the 3 s ISI condition with the 10 s condition shows that the latter produced a comparatively negligible effect on the spatial frequency discrimination task. This is reflected by the finding that virtually all thresholds, regardless of the mask/reference ratio, was barely distinguishable from the baseline measure. In all cases, the change in normalized discrimination threshold was less than 15 %.

Our results show that spatial frequency information contained in the mask had a measurable influence on the reference stimulus at 3 s but not at 10 s. This is consistent with the RT data reported by Magnussen et al. (1998) and provide further evidence for a two-step process in perceptual memory (Magnussen, 2000; Magnussen & Greenlee, 1999). It appears that for the 3 s ISI condition, the mask may have interfered with the perceptual representation of the reference stimulus and therefore reduced its coding efficacy. However, the negligible interference effect at 10 s may have occurred due to one of two reasons. The first possibility is that the longer ISI may have produced sufficient decay in masking the perceptual representation of the reference stimulus and that the masking stimulus did not transfer into short-term perceptual memory. If true, then it suggests that transfer of perceptual representations to memory representations is task dependent and requires an ongoing discrimination process. The alternative possibility, however, is that the masking representation does indeed transfer into perceptual memory but that it fails to interact with the reference stimulus at long ISI values. This would imply that transfer of the masking representation into short-term perceptual memory is an automatic process. The distinction between these two alternatives is that the first effect is presumed to occur in the perceptual representation whereas the second occurs in the memory representation.

The results of Experiment 1 do not allow us to drawn any conclusions as to which alternative is favored. To address this issue, we performed a second experiment in which we used a stimulus sequence where the conditions favored transfer of the mask into short-term perceptual memory. This sequence

therefore allowed us to probe the memory representations of both the mask and reference stimuli.

Experiment 2

Introduction.

The aim of Experiment 2 was to probe short-term perceptual memory with two different stimuli. We hope to clarify which of the two proposed explanations best accounts for the results of the 10 s ISI condition in Experiment 1. If transfer of a perceptual representation to memory is task dependant, and if memory representations are subject to a similar masking effect as are perceptual representations, then we would expect a selective masking effect for both the 3 and 10 s ISI conditions in this second experiment.

Procedure.

Figure 1B shows a schematic diagram of the stimulus sequence used in Experiment 2. The main difference with the previous experiment is the presentation of a fourth Gabor patch (S_2) at the end of the stimulus sequence. Subjects were required to couple S_2 to the masking patch (S_1) in order to perform a second 2-IFC task. Thus, subjects were now forced to encode and retain the spatial frequency information of the mask as well as the reference. We used a Same-Different discrimination task between the S_1 and S_2, where S_2 could either be similar to the mask or have a spatial frequency content that differs by ±30%. Within a testing block of 140 trials, the subjects were presented an equal number of each possibility, with the exception that S_2 could not be similar or different to

the mask on no more than three consecutive trials. The discrimination thresholds between F_1 and F_2 were measured the same way as in Experiment 1. All possible pairings between the base spatial frequency of the mask and reference patches were maintained. Consequently, in Experiment 2 we find the same seven mask/reference ratios that were used in the first experiment.

The subjects were required to provide two responses in order to correctly perform a trial. The first was the discrimination judgment (J_1) between F_1 and F_2. This response was made immediately after the presentation of F_2 so that it was not influenced by the presentation of S_2. S_2 was presented for 210 ms after a short interval (500 ms) following J_1. The trial was concluded after the subject made a second discrimination judgment (J_2), this time between S_1 and S_2. Performance on this second discrimination task was used to judge whether or not the subjects encoded the spatial frequency information of S_1 as a memory representation.

Finally, two additional precautions were added to prevent long-term representation of the mask and stimulus sequence. First, we shuffled all of the trials (1680 per ISI condition) so that the base spatial frequency of the mask (i.e., 2, 3, and 6 c/deg) was randomly changed from one trial to the other. The same number of trials per ISI condition and mask/reference ratio were maintained as in Experiment 1. The second precaution was applied to two of the three subjects in this experiment (JL and EB). The two ISI conditions were collapsed into one large block, shuffled, and then regrouped into 24 testing blocks of 140 trials. As before, the same number of trials per ISI condition and ratio were maintained. As a result, it was not possible for the two subjects performing this version of

Experiment 2 to know the ISI value between mask and reference patches from one trial to another. The third subject in this experiment, CM, was asked to complete 12 testing blocks for the 3 s ISI condition followed by a further 12 testing blocks at the 10 s ISI condition. Both of these manipulations were performed to test the robustness of the masking effect and to further diminish the possibility that subjects developed a long-term representation of the stimulus quality and sequence.

Results and discussion.

Figures 3A and 3B show the Weber fractions ($\Delta F/F$) as a function of the mask/reference ratio at both the 3 s and 10 s ISI conditions respectively for the first discrimination judgment (J_1). This is the parameter that is of most interest to us. Dashed lines again represent the individual baseline values. The bar graphs on the right show the discrimination threshold averaged across three subjects after being normalized to the baseline for each mask/reference ratio.

Insert Figure 3 here

As Figure 3 clearly shows, the selective masking effect is now similar between the two ISI conditions and comparable to that previously obtained in Experiment 1 for the 3 s ISI condition. Whereas the 10 s ISI condition in Experiment 1 produced discrimination performance that did not significantly deviate from baseline, the corresponding measure in Experiment 2 shows that discrimination thresholds at non-uniform mask/reference ratios were

considerably higher from the baseline threshold and when the mask/reference ratio was 1.0 (i.e., Figure 2B vs. 3B). Both masking effects are similar to those reported by Magnussen et al. (1991) and Bennett and Cortese (1996). The masking effect occurred at all ratios except when the Gabor patches had the same base spatial frequency. Elevation of the normalized discrimination thresholds ranged from 21% to 80.93%. The individual Weber fractions in the disparate spatial frequency conditions were nearly twice the value of those obtained when the mask and reference spatial frequencies were the same (ratio of 1.00). This was true for both the 3 s and 10 s ISI conditions.

The evidence for encoding the mask as a memory representation is given by the performance of the subjects on the Same-Different task between the mask and S_2. Figure 4 shows accuracy data for the two ISI conditions. This data reveals nearly identical accuracy values—71.1% and 71.3%correct responses in the 3 s and 10 s ISI conditions respectively. We found that individual performance through several testing sessions was stable and showed no significant improvement. This indicates that floor or ceiling effects were not present during this task and that long-term representations of the S_1 and S_2 were unlikely to have occurred. If this had been the case, we should have observed a considerable increase in performance between the first testing session and the last one. We take this as evidence that spatial frequency information of the mask was accurately preserved as a memory representation during a trial.

Insert Figure 4 here

Our results also suggest that selective masking invoked separate representation substrates despite the similarity of the data from the two ISI conditions. The selective masking effect observed in the 3 s ISI condition likely involves perceptual representation of the mask where it interferes with coding of the reference stimulus. The selective masking effect in the 10 s ISI condition, however, may involve a different mechanism. The prolonged time course is likely responsible for re-coding the perceptual representation of the mask as a memory representation because the mask would not remain active in the perceptual domain for much greater than 3 s. Indeed, prior studies have shown that this temporal limit is likely reached at between 4 - 5 s (Magnussen et al., 1998; Magnussen & Greenlee, 1999). The same restriction would of course apply to the reference stimulus as well. Consequently, both representations were likely transferred to short-term perceptual memory where interference could have produced the selective masking effect observed in this experiment. Our results point to the contention that the 10 s ISI condition produced masking effects that had a mnemonic origin whereas the 3 s ISI condition produced masking effects within the perceptual domain.

General Discussion

There are now multiple lines of evidence to suggest that perceptual discrimination processes involve stimulus representations in the perceptual domain and, if adequate temporal conditions are present, representations in the memory domain. The clinical literature has shown that focal lesions in inferior temporal and superior temporal visual cortex can impair discrimination

processing, while leaving intact the storage and retrieval processes (Greenlee et al., 1993, 1995, 1997). These results have been used to suggest that perceptual discrimination relies on processing across multiple representation substrates.

Further evidence for this notion arises from functional studies involving delayed perceptual discrimination tasks. The study of event-related potentials recorded during a spatial frequency discrimination task suggest that a diversity of cortical regions are involved (Reinvang, Magnussen, Greenlee, & Larsson, 1998). The data raise the possibility that temporal sources are involved in encoding and storage of visual information while parietal sources are involved in memory retrieval. Several imaging studies of delayed discrimination of orientation (Orban et al., 1997; Dupont et al., 1998), motion (Orban et al., 1998; Cornette et al., 1998), and spatial frequency (Greenlee, Magnussen, & Reinvang, 2000) also showed that multiple brain areas are activated, such as striate, extrastriate, parietal, and prefrontal areas, during the actual discrimination component of a perceptual discrimination task. These functional studies raise the possibility that perceptual representations, memory representations, and discrimination mechanisms are all exerted by distinct neural substrates.

Psychophysical studies have made use of masking paradigms to study functional features underlying perceptual discrimination. These studies have shown that similar visual attributes can cause interference in perceptual memory (Magnussen & Greenlee, 1992; Magnussen et al., 1991; Cortese & Bennett, 1996). Furthermore, the masking effect remains robust even if the masker is changed along an "irrelevant" dimension. This dissociation between different visual dimensions suggests that the stimulus representations involved in a

discrimination task must occur beyond area V1 since at that level neurons are known to be sensitive to multiple stimulus attributes (DeValois & DeValois, 1990; Wilson, Levi, Mafei, Rovamo, & DeValois, 1990). This notion has been used to argue that masking effects upon perceptual discrimination is associated with mnemonic substrates.

The earlier masking studies, however, did not take into account the fact that perceptual memory itself involves two distinct levels of processing. The evidence for separable representation substrates within perceptual memory was first obtained with reaction time measures involving short and prolonged spatial frequency and orientation discrimination tasks (Magnussen et al., 1998). These results indicated that a temporal boundary exists for discrimination processes involving perceptual and memory representations. However, there was little known about how representations are exchanged between perceptual and memory domains because earlier masking studies did not probe the discrimination task with temporal intervals that would theoretically fall into the memory domain.

The results of our study provide further insight into the temporal conditions under which visual representations are shared between perceptual and memory domains. Our data support the notion of a two-step process in perceptual memory. Furthermore, we showed that transfer of a perceptual representation to a memory representation in the short-term domain of perceptual memory is task dependent. Memory representations of visual information are therefore "selectively" transferred to this processing level of perceptual memory under the right temporal conditions and in the presence of

an ongoing discrimination task. This contention is based on a comparison of the results from Experiment 1 and 2 where we found significant masking effects at the 10 s ISI condition only if subjects were engaged in discrimination task involving the masking stimulus.

Finally, our results show that re-coding of a perceptual representation to a memory representation does not render that information less subject to sources of interference. Although we cannot be certain that visual information represented into the short-term domain of perceptual memory may be similar to its perceptual representation, our results show that memory representations are nevertheless subject to similar interference effects and cross-stimulus interactions as are perceptual representations when both the temporal and task conditions are adequately met.

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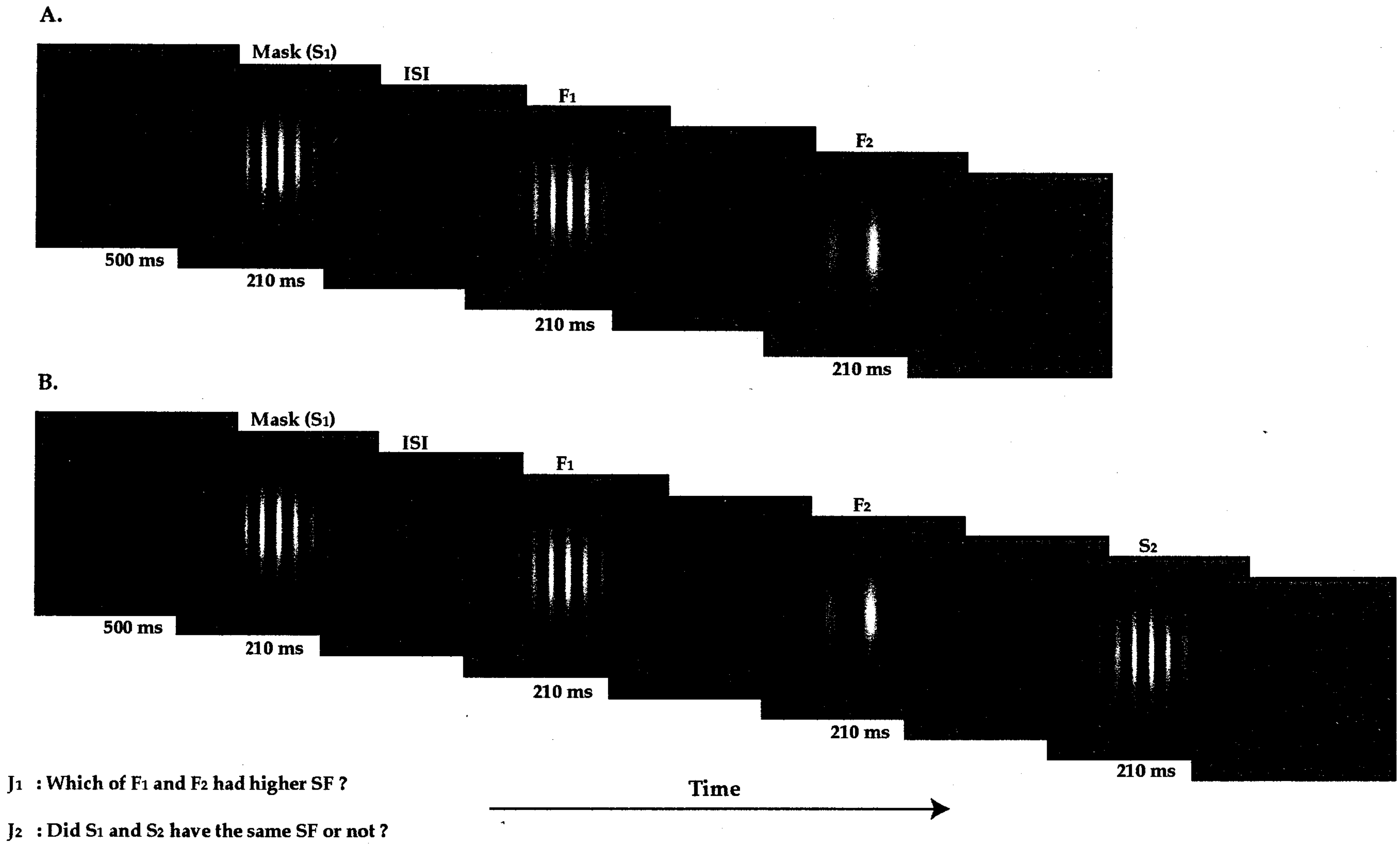

Figure 1. Schematic representation of the two experiments in this study. A mask (S1) precedes the two Gabor patches to be discriminated (F1 and F2) by an interstimulus interval (ISI) of either 3 or 10 s. In Experiment 1 (A), the mask is passively presented and no discrimination task is associated with its presentation. In Experiment 2 (B), the mask is coded into short-term perceptual memory by engaging the subjects to discriminate the spatial frequency content of the mask with the presentation of another Gabor patch (S2).

A. 3 seconds ISI

B. 10 seconds ISI

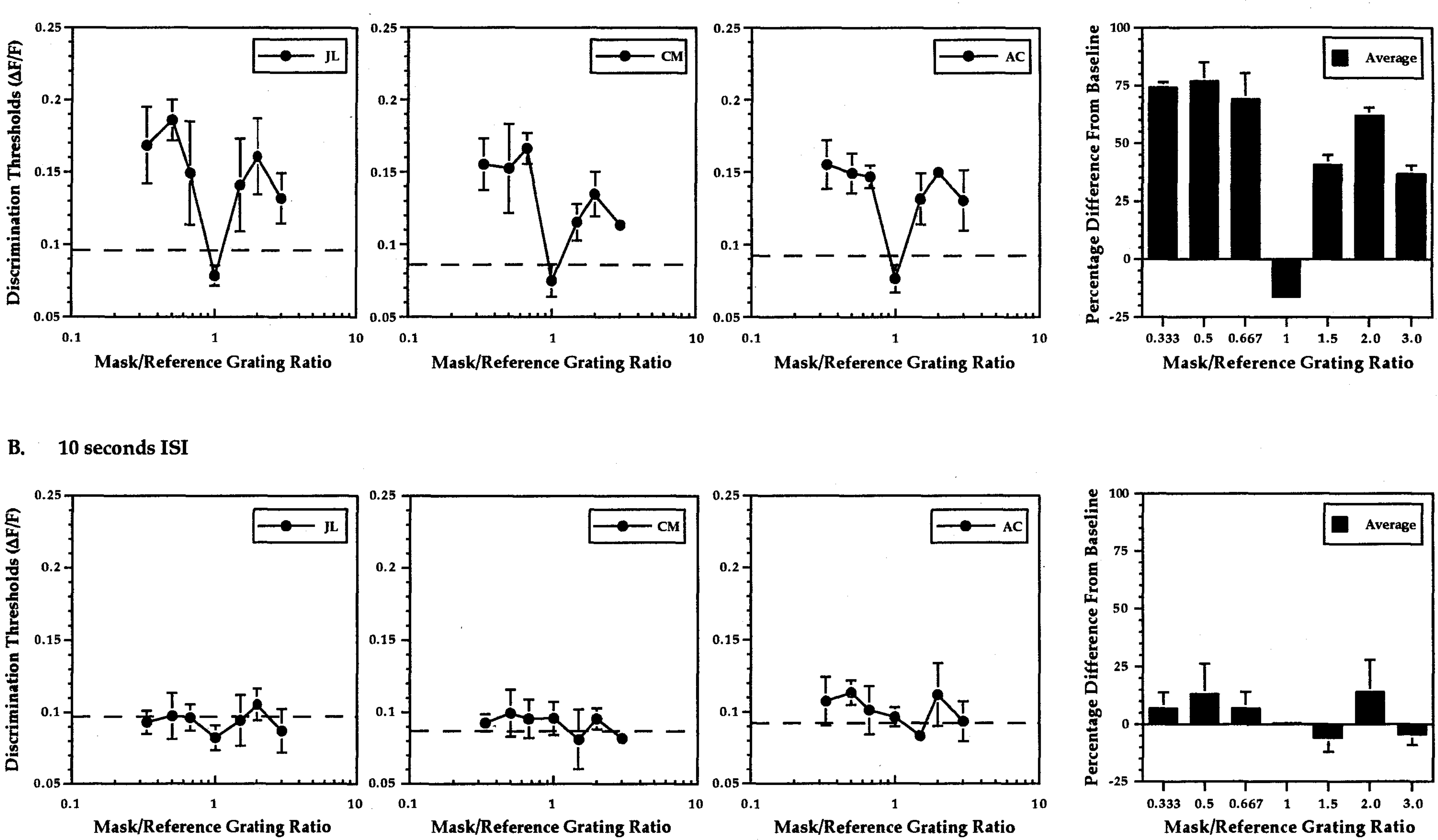

Figure 2. Spatial frequency discrimination thresholds from three observers in Experiment 1. The discrimination thresholds are represented as Weber fractions (ΔF/F) and plotted as a function of the seven mask/reference ratios for both the 3 s ISI condition (A) and the 10 s ISI condition (B). The dashed lines represent individual baseline discrimination thresholds. Baseline discrimination thresholds between F1 and F2 were measured with no mask preceding the presentation of F1. The bar graphs on the right are normalized thresholds for the three subjects with respect to their individual baseline measure. Error bars represent ±1 SE.

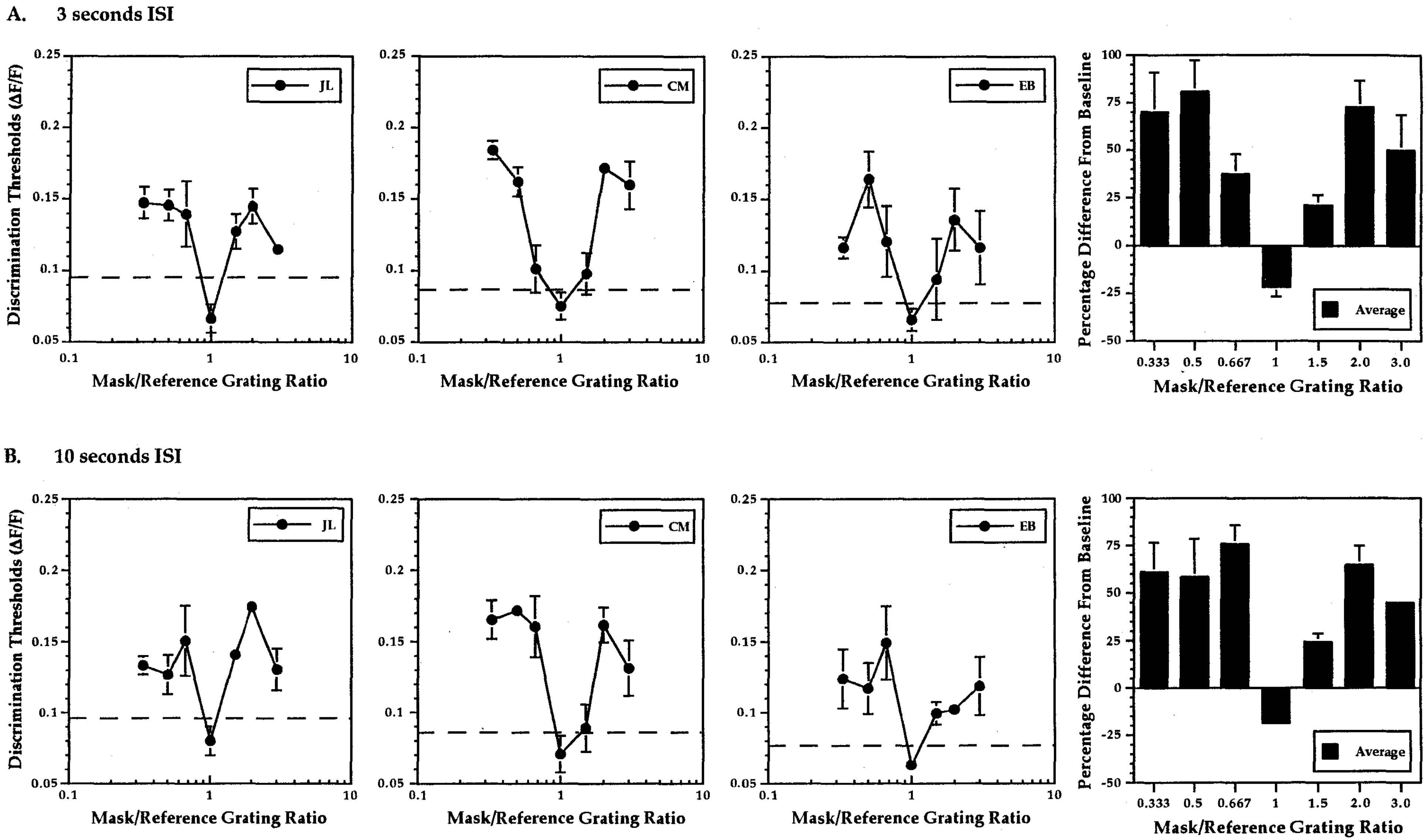

Figure 3. Spatial frequency discrimination thresholds from three observers in Experiment 2. The discrimination thresholds are represented as Weber fractions (ΔF/F) and plotted as a function of the seven mask/reference ratios for both the 3 s ISI condition (A) and the 10 s ISI condition (B). The experimental conditions were the same as in Experiment 1 except that the mask (S1) was used for a second spatial frequency discrimination task with the Gabor patch S2. The dashed lines again represent individual baseline discrimination thresholds. The bar graphs on the right are normalized thresholds for the three subjects with respect to their individual baseline measure. Error bars represent ±1 SE.