

Visual Imagery Facilitates Visual Perception: Psychophysical Evidence

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Abstract

■ Visual imagery is the invention or recreation of a perceptual experience in the absence of retinal input. The degree to which the same neural representations are involved in both visual imagery and visual perception is unclear. Previous studies have shown that visual imagery interferes with perception (Perky effect). We report here psychophysical data showing a direct facilitatory effect of visual imagery on visual perception. Using a lateral masking detection paradigm of a Gabor target, flanked by peripheral Gabor masks, observers performed imagery tasks that were preceded by perceptual tasks. We found that both perceived and imaginary flanking masks can reduce contrast detection threshold. At short target-to-mask distances imagery

induced a threshold reduction of 50% as compared with perception, while at long target-to-mask distances imagery and perception had similar facilitatory effect. The imagery-induced facilitation was specific to the orientation of the stimulus, as well as to the eye used in the task. These data indicate the existence of a stimulus-specific short-term memory system that stores the sensory trace and enables reactivation of quasi-pictorial representations by top-down processes. We suggest that stimulus parameters dominate the imagery-induced facilitation at short target-to-mask distances, yet the top-down component contributes to the effect at long target-to-mask distances. ■

INTRODUCTION

Visual imagery is the mental invention or recreation of a visual-perceptual experience in the absence of retinal input. There have been two main approaches to the scientific study of visual imagery. In one, researchers have looked at the intrinsic properties of mental images. For example, Shepard and Metzler (1971) have demonstrated the three-dimensional nature of mental images by means of mental rotation tasks, and Pinker and Kosslyn (1978) have shown that observers were able to scan mental images of two- and three-dimensional objects. In the second approach, researchers have explored the effects of mental imagery on perceptual processes. For example, Segal and colleagues have shown that imagery interferes more with like-modality perception than with different-modality perception (Segal & Fusella, 1970).

What are the effects of mental imagery on perceptual processes—facilitation or interference? Neisser (1976) has proposed that images generally function as perceptual “anticipations”—imagining an object would speed up perception by initiating the appropriate perceptual processes in advance (Neisser, 1976). Farah (1985) has carried out experiments that support the anticipation hypothesis. By imagining letters of the alphabet (H and T) that match presented letters, the ability to detect the

letters increased. The subjects were more accurate in detecting the letters when the images matched the targets in both shape and location, relative to the control condition, in which detection was performed without imagery (Farah, 1985). However, the facilitation effect was probably due to a spatially localized shift of criterion rather than to a change in sensitivity (Farah, 1989a). Thus, facilitation may reflect processes other than changes in visual sensitivity.

McDermott and Roediger (1994) have reported that imagery can promote priming on implicit memory tests. When subjects were given words during a study phase and asked to form mental images of corresponding pictures, more priming was obtained on a picture fragment identification test, compared to a study phase in which subjects performed semantic analyses of the words. Imagery produced selective facilitation—imagining *pictures* primed picture fragment identification but not word fragment completion, whereas imagining *words* primed word fragment completion but not picture fragment identification. The authors concluded that imagery is perceptual in nature; that is, imagery engages some of the same mechanisms used in perception and thereby produces priming (McDermott & Roediger, 1994).

Other findings show that imagery interferes with performance in various visual tasks (Segal, 1971). An early

study by Perky (1910) reported a curious phenomenon. When subjects were told to imagine looking at an object (such as a banana) on a supposedly blank screen while actually being shown a faint picture of the object, the object was not seen (Perky, 1910). The so called "Perky effect" is defined as the reduction in performance from the no-imagery to the imagery condition. Evidence that visual, as opposed to nonvisual, imagery can impair visual perception was reported by Segal and Fusella (1970). Subjects were presented with faint geometric forms or auditory tones as target stimuli while imagining other objects or sounds. Using the method of signal detection, they found that perceptual sensitivity was maximally reduced when the modality of the image matched that of the target. For instance, it was harder to detect a faint geometric form when imagining a visual scene than when imagining a familiar sound (Segal & Fusella, 1970).

Finke (1986) has tried to sort out the conflicting findings on image facilitation and interference by employing two different types of tasks. In an experiment on visual *identification*, subjects had to indicate on each trial whether a horizontal or vertical bar had been presented. On most trials, the subjects were instructed, in advance of presentation, to visualize a bar that was horizontal, vertical, or at some intermediate orientation. In comparison with their performance on control trials, in which subjects were told not to form an image, they needed less time to identify bars when the imagined and presented bars were perfectly aligned and more time when the imagined bars were oriented in between the target bar orientations. In a corresponding experiment on visual *detection*, the subjects merely reported whether either of the two bars had been presented, without having to identify them. In this case, reaction time increased as the imagined and presented bars became more closely aligned, in contrast to the results for the identification task. Thus, concluded Finke, whether imagery facilitates or interferes with performance on a perceptual task depends not only on whether the image matches the target but also on the nature of the task (Finke, 1986).

Craver-Lemley and Reeves (1987) have explored the imagery-induced interference with a two-line vernier acuity task in which observers had to report whether the bottom line was offset to the left or the right of the top line. Imagery of vertical or horizontal lines, and even of a gray mist, affected performance but only when the image overlapped or was very close to the target (Craver-Lemley & Reeves, 1987). At which of several levels of processing might the Perky effect occur? Craver-Lemley and Reeves (1992) have reviewed different types of explanations of the Perky effect. Optical factors such as fixation, pupil size, and accommodation failed to explain the imagery-induced interference as did shifts in criteria for responding in imagery and demand characteristics. Perceptual and sensory explanations,

such as assimilation (that is, parts of the stimulus are assimilated into or fused with the mental image) and masking (images reduce acuity by mimicking the effects of real-lines masks), did not account for the Perky effect. Diversion of attention (the withdrawal of attention from the visual task to the image) also could not explain the Perky effect. Craver-Lemley and Reeves concluded that imagery reduces visual acuity by reducing sensitivity—that is, imagery reduces the target energy in the region of the visual field where the images are located (Craver-Lemley & Reeves, 1992). Interestingly, the interference was found to be specific to the depth plane—accuracy for the target decreased when an image was projected in front of, but not behind, the target (Craver-Lemley et al., 1997).

During the past decade the cognitive neuroscience approach to the study of mental imagery was developed in which researchers have studied the neural bases of mental imagery using brain imaging techniques and data from neuropsychological case studies. Brain imaging studies implicate activity in cortical visual areas during visual imagery. Recording of event-related potentials (ERPs) while observers hold mental images has shown an imagery effect having the same time course as that of the visual ERP waveform, which is localized to the occipital recording sites (Farah et al., 1988). Using positron-emission tomography (PET), visual-association areas were shown to participate in the generation of visual images of spatial scenes from the memory (Roland et al., 1987). Measuring regional cerebral blood flow patterns by means of single photon emission computerized tomography (SPECT) has indicated that visual imagery is related to activity of inferior-temporal and occipital regions (Goldenberg et al., 1989). Using a functional magnetic resonance imaging technique (fMRI), activation of the primary visual cortex was found by both visual stimulation and during visual recall of the same stimulus (LeBihan et al., 1993). Another PET study has shown that visual imagery activates topographically mapped cortex, that is, V1 and V2 (Kosslyn et al., 1993). Recently, Kato et al. (1996) have shown, using functional MRI, the involvement of both the lateral geniculate nucleus (LGN) and V1 in visual perception and visual imagery.

Despite the evidence for a common neuroanatomical substrate shared by visual perception and visual imagery, the mechanisms that subservise "seeing with the mind's eye" are controversial (Farah, 1989b). At issue is whether visual imagery activates early visual areas or higher association areas only (Roland & Gulyas, 1994; Kosslyn & Ochsner, 1994; Sakai & Miyashita, 1994). While Roland and colleagues have not found activation of primary visual cortex during visual imagery task (Roland & Gulyas 1994, 1995), Kosslyn and colleagues have reported topographical representations of mental images in primary visual cortex, suggesting pictorial representations (Kosslyn et al. 1993, 1995). The debate is whether the cortical areas subserving visual imagery are

anatomically *separate*, a *subset* of, or *identical* to the areas subserving visual perception. Sakai and Miyashita (1993, 1994) have proposed a model that represents visual imagery as an interaction between memory retrieval and focal attention mechanisms. According to their view, topographical representation might subserve visual imagery (that is, activation of V1 and V2) when the subject is attentively scrutinizing local features (Sakai & Miyashita 1993, 1994). It is worth noting that in all the above-mentioned studies, different tasks and experimental procedures were used; hence it is difficult to reconcile the inconsistency of the results obtained by the different groups.

In order to test whether visual imagery can facilitate visual perception, we used a lateral masking detection paradigm developed by Polat and Sagi (1993). In this paradigm, the effect of two mask stimuli on the perception of a target stimulus is measured using a simultaneous masking. Since localization of stimuli is crucial for exploring spatial interactions, Gabor signals were chosen as target and masks. A Gabor signal is a sine or cosine periodic luminance modulation within a Gaussian envelope (Gabor, 1946), assumed to minimize joint localization in space and spatial frequency and to evoke optimal response from simple cells in the primary visual cortex (Pollen & Ronner, 1983). Polat and Sagi (1993) have measured the changes in detection threshold of a foveal target induced by the flanking Gabor masks as a function of their eccentricity. They obtained a biphasic response curve—both an increase and decrease of target thresholds were seen in the presence of the adjacent masks. Threshold elevation was observed for target-to-mask distances smaller than twice the target wavelength. A decrease in threshold was observed when the distance ranged between two wavelengths and twelve wavelengths (Polat & Sagi, 1993). This pattern of results was found to be specific for orientation and spatial frequency—no significant effects were found when target and mask orientations differed by more than 45° and when their spatial frequencies differed by more than two octaves (Polat & Sagi, 1994a).

Recently we have used the lateral masking paradigm to study the interactions between perception and imagery (Ishai & Sagi, 1995). Observers performed a detection task of a foveal Gabor target, either while perceiving flanking Gabor masks placed at different eccentricities or while imagining the masks. Using a novel experimental procedure of alternating tasks of perception followed by imagery, we obtained a threshold reduction in both perception and imagery tasks (Ishai & Sagi, 1995). An imagery-induced facilitation was seen when a delay period of up to 5 min was introduced between the perceptual and the imagery tasks, suggesting the involvement of short-term memory (Ishai & Sagi, 1995).

We extend our previous report, showing additional features of the imagery-driven facilitation that shares the same characteristics with the perceptual facilitation. The

imagery effect is subserved by a stimulus-specific memory trace for orientation and eye used. In our experiments, imaginary Gabor signals facilitated perception only under short-term memory conditions. When the imagery task was based on long-term memory, no facilitation was obtained (the comparison between short- and long-term memory is discussed in Ishai and Sagi, 1997). Orientation-specific memory masking, masks of opposite phase, and high-contrast stimuli interfere with the accumulation of the trace, hence reducing the imagery effect. While previously we have studied mainly the effect of short target-to-mask distances on visual imagery (Ishai & Sagi, 1995), here we extend our report and describe the imagery-induced facilitation at long target-to-mask distances. Previously we have found that at short target-to-mask distances imagery induced a threshold reduction of 50% relative to the perception (Ishai & Sagi, 1995). Here we show that at long target-to-mask distances perception and imagery have a similar effect on target threshold. Moreover, we report here that mental rotation and “visual noise” reduce the imagery effect only at short, but not at long, target-to-mask distances. We suggest that at short target-to-mask distance the imagery-induced facilitation is dominated by a stimulus-specific memory trace, while at long target-to-mask distance the imagery effect is dominated by the top-down manipulation. Our results indicate the existence of common representational structures that can be used by both perception and image generation and provide psychophysical evidence for the involvement of the primary visual cortex in visual imagery.

RESULTS

Imagery-Induced Facilitation: Experiments 1A and 1B

In order to test whether perception and imagery have the same facilitatory effect, contrast detection thresholds of a Gabor target were measured, as a function of target-to-mask distances, under the following three conditions: perception, imagery, and control. Each session included alternating tasks of either perception and control or perception and imagery (Ishai & Sagi, 1995). Results from two observers are depicted in Figure 1. In the perception condition two zones were seen—suppression (threshold elevation) and enhancement (threshold reduction), as was reported by Polat and Sagi (1993). In the control condition, where no masks were presented, both suppression and enhancement disappeared. However, probably because of the lack of a cue on the screen, detection of the isolated target was more difficult than detection of the target in the presence of the peripheral crosses; hence contrast thresholds were slightly higher than the baseline threshold. In the imagery condition, the positive, suppression region disappeared, while a negative, enhancement region was seen. This imagery-

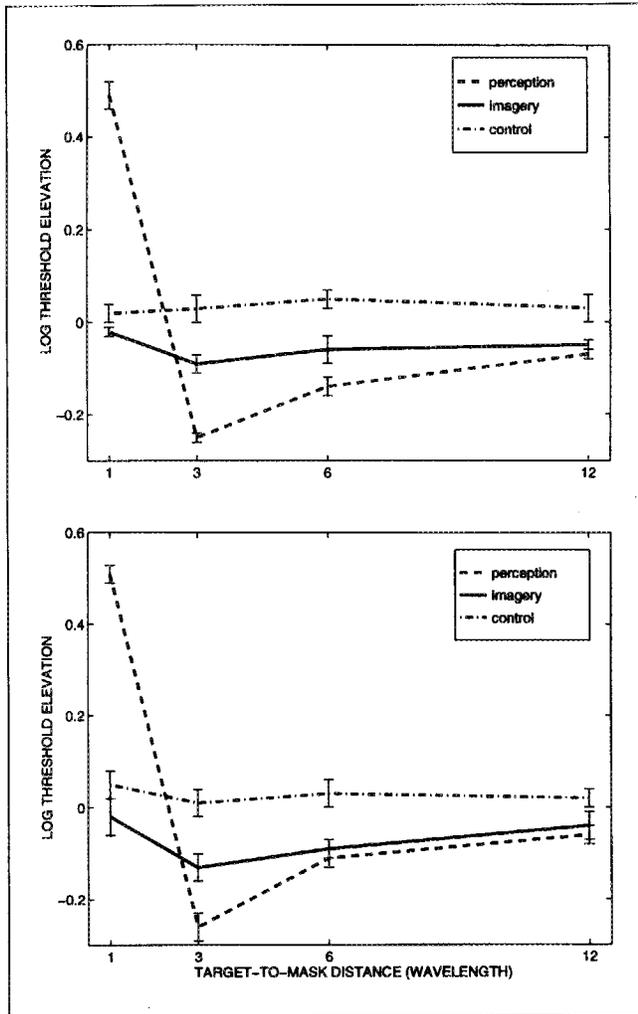


Figure 1. Target threshold as a function of target-to-mask distance, for observers ES (top) and OY (bottom). Data are presented for vertical target and masks, arranged along the vertical meridian. Each point, in this and subsequent graphs, represents 13 blocks for each observer. Error bars, in this and subsequent graphs, indicate standard error of the mean (SE). Note that in the control condition target-to-mask distances correspond to those in the preceding perception condition.

induced facilitation shared similar characteristics with the perceptual enhancement—maximal threshold reduction at 3λ and an asymptotic return to the baseline threshold as the target-to-mask distance increased. These results suggest that visual imagery can mimic the facilitatory effect of the perceived masks.

To evaluate the similarity between the facilitation obtained in both perception and imagery conditions, the areas in the negative zones, from 3 to 12λ , were compared (Figure 2). The differences between the enhancement area in the imagery and perception conditions were not statistically significant; however, the differences between the control and perception conditions were significant, as were the differences between the control and imagery conditions (repeated measures analysis of variance, followed by Scheffe multiple comparison, $F(2, 3) = 16.9, p < 0.001$).

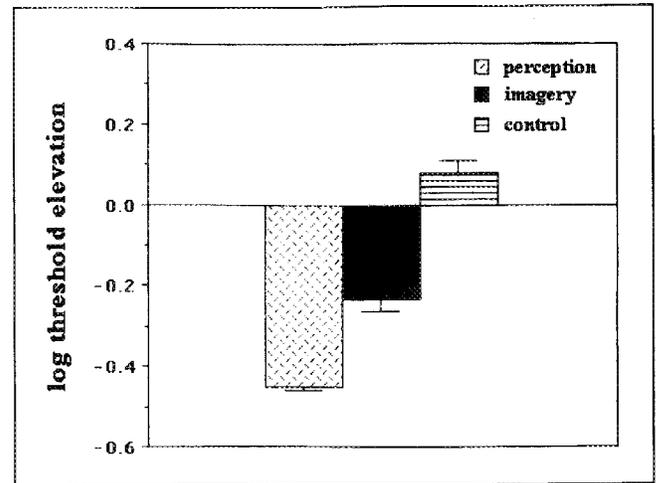


Figure 2. Enhancement area, averaged across two observers (ES and OY). The area from 2 to 12λ was computed for each session.

The magnitude of the imagery-induced facilitation was very similar in most of the experiments. If grouping was involved, maybe a chain of flanking masks would increase the imagery-driven facilitation. To test this hypothesis, observers perceived and imagined different numbers of flanking vertical masks. In the perceptual task the target was flanked by either one, two, four, six, or eight targets (see Figure 3, top). In the imagery task observers had to imagine the previously presented chain of masks. For example, if four masks were presented in the perception, observers were instructed to imagine a chain of four masks. The results were surprising (Figure 3, bottom). The perceptual enhancement was independent of the number of masks, indicating that the first pair was sufficient to maximally enhance detection of the target. Moreover, the imagery-induced facilitation was also independent of the number of previously presented masks.

Memory Trace: Experiments 2A and 2B

The imagery-induced facilitation described in Experiment 1 was found to depend on the preceding perceptual enhancement. Previously we have shown that introducing a delay period of up to 5 min between the perception and imagery tasks abolished the imagery-induced facilitation (Ishai & Sagi, 1995). To understand the role of the preceding perceptual task, contrast detection thresholds in imagery and control conditions were measured when the perceptual task was reduced to 10 trials only (a block usually consisted of 50 trials—see "Experimental Procedures"). The rationale was that these 10 trials will indicate the precise location of the Gabor masks to be imagined during the task immediately following. Reducing the length of the perceptual input completely abolished the imagery-induced facilitation at all target-to-mask distances (Figure 4). The differences

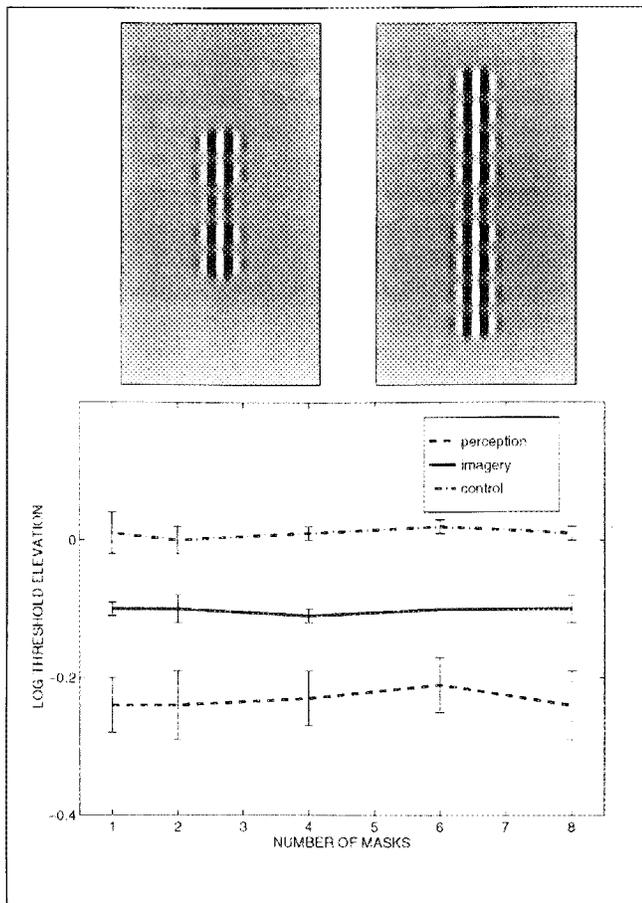


Figure 3. Chain of masks. Top: Two flanking Gabor masks (left), placed at a distance of 3λ , and four flanking Gabor masks (right). Bottom: Target threshold as a function of number of presented and imagined masks flanking the target. Data are presented for vertical target and masks, averaged across three observers (AI, NK, and SS).

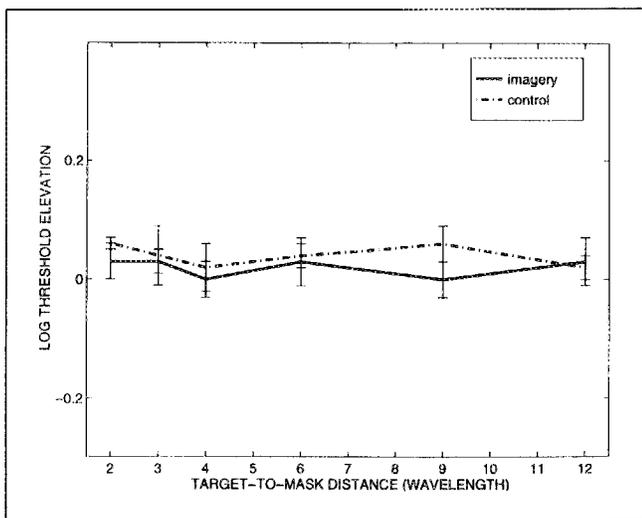


Figure 4. Target threshold as a function of target-to-mask distance, averaged across three observers (EM, OY, and YP). Data are presented for vertical target and masks, when the perceptual task was reduced to 10 trials. Note that perception thresholds are not presented since only 10 trials were measured.

between control and imagery conditions were not statistically significant (repeated measures analysis of variance, followed by Scheffe multiple comparison, $F(1, 4) = 0.1, p > 0.05$). We interpret these results as an indication for a memory trace that is being accumulated during the perceptual task.

Is the memory trace specific for orientation? To test the orientation specificity, we measured contrast detection thresholds of a *vertical* target flanked by *horizontal* masks (the global orientation of the configuration was vertical) in the perception condition. In the control condition, observers detected an isolated vertical Gabor target. In the imagery condition, observers had to imagine the horizontal masks while detecting a vertical target. Previously, Polat and Sagi (1993) showed that both suppression and enhancement disappeared when target-mask orientation differences were larger than 20° , indicating that masks of different orientation have no effect on target detection threshold. We found that the orthogonal masks had almost no effect on target detection either in perception or in imagery conditions (Figure 5). The differences between perception, control, and imagery conditions were not statistically significant (repeated measures analysis of variance, followed by Scheffe multiple comparison, $F(2, 6) = 0.4, p > 0.05$). These results suggest that the imagery-induced facilitation for colinear target and masks is not only similar to but is also dependent upon perception. Also, this shows that the imagery-driven facilitation is not merely an effect of attention or concentration of the observers.

Memory Masking: Experiments 3A and 3B

Recently we have shown that "visual noise" abolished the imagery-induced facilitation (Ishai & Sagi, 1995).

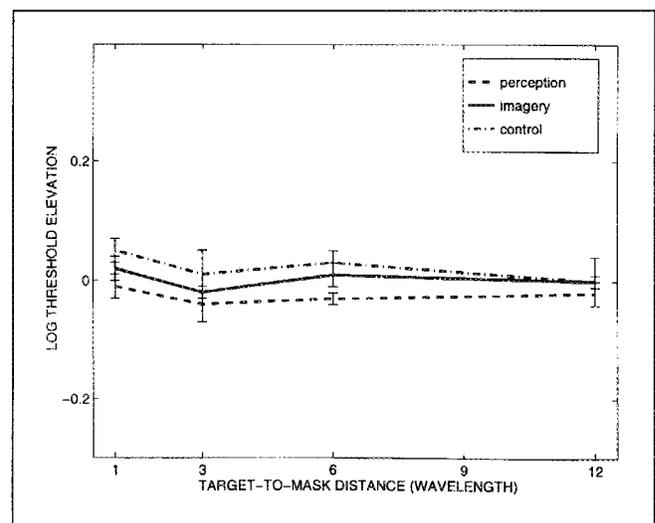


Figure 5. Target threshold as a function of target-to-mask distance, averaged across three observers (ES, OP, and OY). Data are presented for a vertical target flanked by horizontal masks.

When visual noise composed of Gabor patches of random orientations and phases was presented after each trial in the perceptual task, the perceptual enhancement was seen, yet the imagery facilitation disappeared. We have proposed that the memory trace interfered with the accumulation of the memory trace (Ishai & Sagi, 1995). To further understand the effect of memory masking on the imagery-induced facilitation, a new experiment was designed in which arrays of vertical or horizontal Gabor patches were, respectively, presented 0.5 sec after each trial for a duration of 0.5 sec (see Figure 6, top). In these experiments observers perceived vertical flanking masks and in a subsequent task had to imagine the flankers. While the imagery-driven facilitation was obtained after horizontal visual noise, the vertical visual noise reduced the imagery effect (Figure 6, bottom). Both vertical and horizontal visual noise did not affect the perceptual enhancement (note that perception thresholds were combined in Figure 6). The differences between perception and imagery in horizontal and vertical visual noise experiments were not statistically significant. The differences between perception and control, as well as the differences between imagery and control, were statistically significant (repeated measures analysis of variance, followed by Scheffe multiple comparison, $F(3, 4) = 14.5$, $p < 0.05$). Note that at target-to-mask distance of 9λ the magnitude of the imagery-driven effect was independent of the visual noise orientation. Interestingly, the magnitude of the imagery effect at 9λ without visual noise was the same [a threshold reduction of 0.05 ± 0.02 logarithmic unit, as compared with 0.01 ± 0.02 in the perception condition and with a threshold elevation of 0.01 ± 0.02 in the control condition (mean \pm SE, $N = 2$ observers)], suggesting that the visual noise was not effective at large target-to-mask distances. When we compared the effect of horizontal and vertical visual noise at the optimal target-to-mask distance 3λ , the statistical differences between the two imagery conditions were significant (repeated measures analysis of variance, followed by Scheffe multiple comparison, $F(1, 2) = 11.3$, $p < 0.01$), indicating the contribution of the orientation-specific component to the imagery effect. The vertical Gabor masks are processed by the same filters needed for detection of the target, whereas the horizontal Gabor masks are processed by different filters, having no effect on the accumulation of the memory trace. These results indicate that the imagery-driven facilitation is a low-level process, where orientation is a crucial feature of the encoded stimulus.

Mental Rotation: Experiments 4A, 4B, and 4C

To test the effect of perceiving and imagining orthogonal masks, we designed mental rotation experiments. The experimental procedure was alternating blocks of perception followed by control, perception followed by imagery, or perception followed by rotation. In the per-

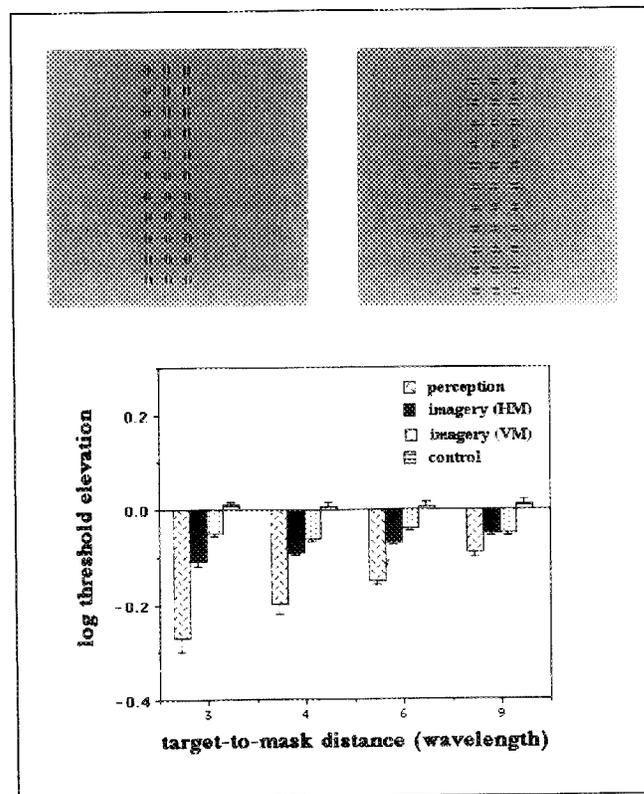


Figure 6. Memory masking. Top: Visual noise composed of arrays of vertical (left) or horizontal (right) Gabor stimuli, used for the memory masking experiments. The noise was presented 0.5 sec after each trial for a duration of 0.5 sec (see "Experimental Procedures"). Bottom: Target threshold as a function of target-to-mask distance, in the presence of vertical and horizontal visual noise, averaged across two observers (AI and NW). Data are presented for vertical target and masks. Each point represents 20 blocks for each observer.

ception condition observers were presented with vertical target and masks, and in the control condition an isolated vertical target was detected. In the imagery condition observers imagined the vertical masks, and in the rotation condition they were instructed to imagine horizontal masks. As shown in Figure 7, in the rotation experiments the facilitation was reduced. The areas in the enhancement zone of the perception, imagery, and rotation conditions were 0.44, 0.21, and 0.12 logarithmic units, respectively, as compared with a threshold elevation of 0.06 logarithmic units in the control condition. The differences between perception and imagery conditions were not statistically significant. The differences between imagery and control conditions, as well as the differences between perception and rotation conditions, were statistically significant (repeated measures analysis of variance, followed by Scheffe multiple comparison, $F(3, 8) = 19.4$, $p < 0.01$). The differences between imagery and rotation conditions were statistically significant (repeated measures analysis of variance, followed by Scheffe multiple comparison, $F(1, 4) = 7.2$, $p < 0.01$); however, the differences at the optimal target-to-mask distance, 3λ , were not significant (repeated

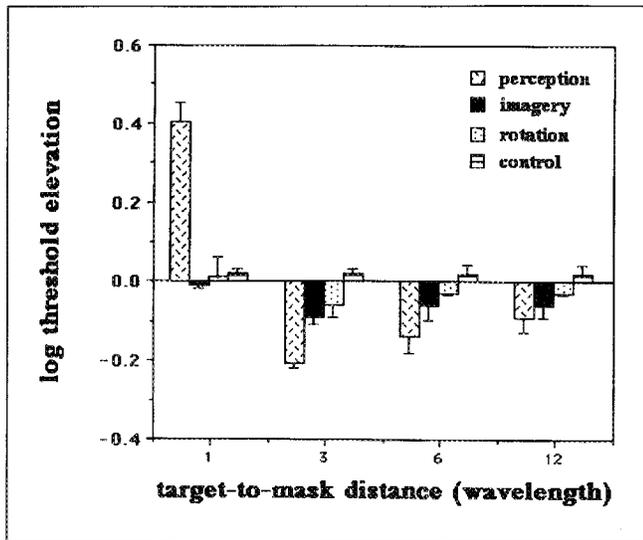


Figure 7. Target threshold as a function of target-to-mask distance, in *mental rotation* experiments, averaged across three observers (NW, OY, and YP). Data are presented for vertical target and masks in the perception condition. In the imagery condition observers imagined *vertical* masks, while in the rotation task observers were instructed to imagine *horizontal* masks.

measures analysis of variance, followed by Scheffe multiple comparison, $F(1, 4) = 0.8, p > 0.05$). It seems that at short target-to-mask distances the perceptual trace dominates the imagery performance, while at large target-to-mask distances the mental images dominate.

Next, we tested the effect of perceiving and imagining orthogonal configuration. In the perception condition, target and masks were *vertical* (the global orientation was vertical). In the following control condition, observers detected an isolated *horizontal* Gabor target. In the imagery condition, observers had to detect a *horizontal* target while imagining coaxial *horizontal* masks, that is, a configuration rotation of 90°. In each session the baseline thresholds were measured for both the vertical and horizontal targets. As Figure 8 shows, no threshold reduction was seen in the imagery condition. This result, along with the previous findings, suggests that "rotation with the mind's eye" is insufficient for inducing facilitation and indicates a stimulus-specific memory trace that subserves the imagery-induced facilitation. It is worth mentioning that when we used horizontal target and masks, arranged along the horizontal meridian, for the perception condition, and the imagery task was to imagine the horizontal masks, an imagery-induced facilitation was obtained [a threshold reduction of 0.19 ± 0.03 logarithmic unit in the perception condition, as compared with 0.08 ± 0.03 in the imagery condition, and a threshold elevation of 0.05 ± 0.03 in the control condition (mean \pm SE, $N = 10$ blocks, for observer AI)]. These results indicate that the lack of imagery effect in the orthogonal configuration experiments was not due to the global orientation (vertical versus hori-

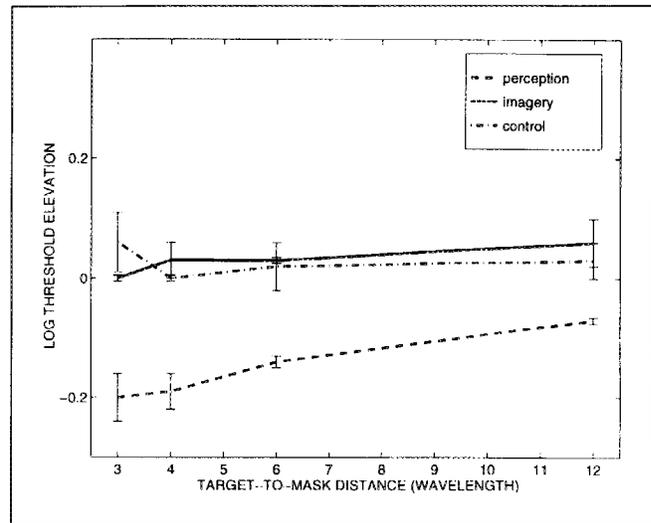


Figure 8. Target threshold as a function of target-to-mask distance, in *configuration rotation* experiments, averaged across two observers (NW and YP). In the perception condition target and masks were *vertical*, while in the imagery task target and imaginary masks were *horizontal*.

zontal) of target and masks, since imagery-induced facilitation is seen for both orientations, as long as the presented and imagined stimuli are of the same orientation.

To understand what component of the sensory input (that is, target or mask) is being stored and reactivated during the imagery task, an experiment with orthogonal targets was designed. In the perception condition observers detected *horizontal* target flanked by *vertical* masks (the global orientation was vertical). In the following control condition the observers detected an isolated *vertical* target. In the imagery condition observers detected a *vertical* target while imagining *vertical* masks. In each session the baseline thresholds were measured for both vertical and horizontal targets. As Figure 9 shows, no facilitation was seen in either perception or imagery conditions. It is reasonable to infer that both target and masks units need to be activated to create the memory trace that subserves the image generation and enables facilitatory effect of visual imagery on perception.

Monocularity: Experiments 5A and 5B

If indeed a low-level memory trace subserves the imagery-induced facilitation, it would be interesting to test the effect of the eye used in the task. In this experiment, observers performed the perceptual task with one eye covered with a blurring lens and the subsequent imagery task with target presented to the other eye (see "Experimental Procedures"). In our earlier study, using a target-to-mask distance of 3λ , we showed absence of imagery facilitation when the targets in the perception and imagery tasks were presented to different eyes (Ishai &

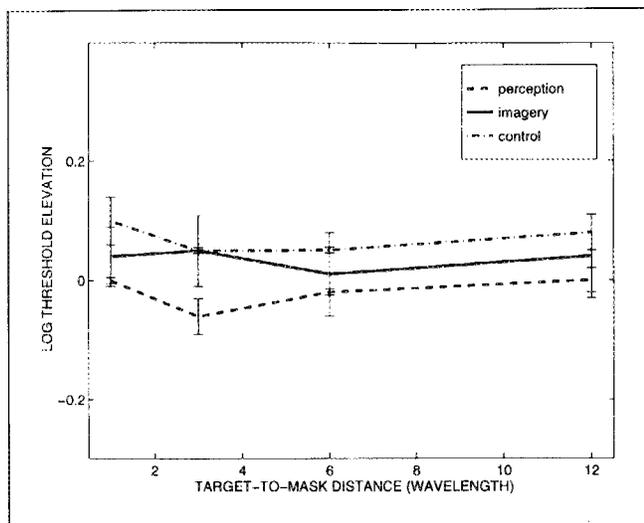


Figure 9. Target threshold as a function of target-to-mask distance, in *orthogonal target* experiments, averaged across two observers (AI and NW). In the perception condition *horizontal* target was flanked by *vertical* masks, while in the imagery task target and imaginary masks were *vertical*.

Sagi, 1995). As depicted in Figure 10, no imagery-induced facilitation was obtained across all target-to-mask distances. The differences between the perception and control conditions, and the differences between the perception and imagery conditions were statistically significant (repeated measures analysis of variance, followed by Scheffe multiple comparison, $F(2, 6) = 18.6$, $p < 0.001$), but the differences between control and imagery conditions were not significant (repeated meas-

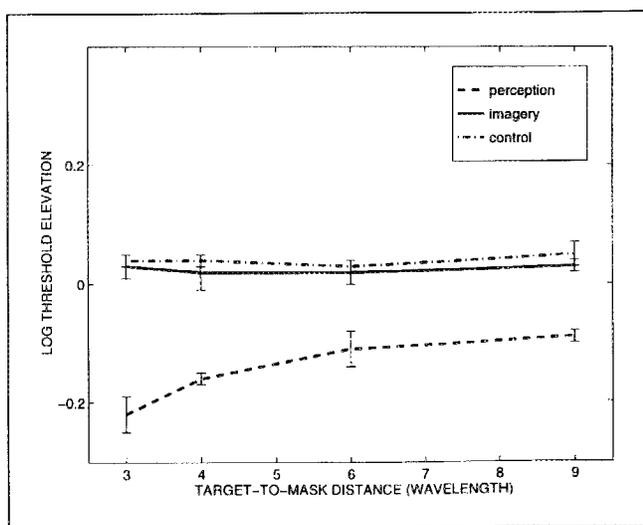


Figure 10. Target threshold as a function of target-to-mask distance, in *monocular* experiments, averaged across three observers (DG, EVS, and YP). Data are presented for vertical target and masks. Perceptual task was performed with one eye, while the following control or imagery tasks with the other eye (see "Experimental Procedures").

ures analysis of variance, followed by Scheffe multiple comparison, $F(1, 4) = 0.3$, $p > 0.05$). These results indicate the necessity of matching between the sensory and the imagined Gabor stimuli, not only in orientation but also in eye used during the task.

To verify that it is possible to perform the imagery task with one eye only, observers had to perform the perception, control, and imagery tasks with the same eye. The results for one observer are depicted in Figure 11. When the same eye was used for both perceiving the stimulus and performing the imagery task, an imagery-induced facilitation was obtained. The differences between the perception and control conditions were statistically significant (repeated measures analysis of variance, followed by Scheffe multiple comparison, $p < 0.001$), but the differences between imagery and control conditions were not significant (repeated measures analysis of variance, followed by Scheffe multiple comparison, $p > 0.05$). The imagery-induced facilitation is, therefore, monocular in the sense that the same eye needs to be stimulated by the perceptual input and to be activated during the imagery task.

Masks of Opposite Phase: Experiment 6

The flanking masks enhance detection of the target, probably via excitatory connections, but within receptive field integration may also play an important role. Previous studies have shown that masks of opposite phase ($A_{m1} = -A_{m2}$) decreased the perceptual enhancement (Zenger & Sagi, 1996), reflecting the reduction of within receptive field activity. What would be the effect of masks of opposite phase on the memory trace and the imagery-induced facilitation? In the memory trace condition contrast thresholds of a vertical target were meas-

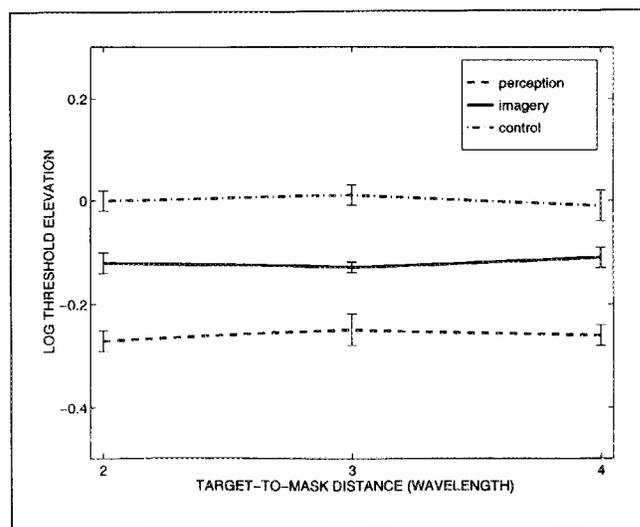


Figure 11. Target threshold as a function of target-to-mask distance for observer AI. Perceptual, imagery, and control tasks were performed with the *left* eye. Data are presented for vertical target and masks (note that only 2, 3, and 4λ were tested).

ured in the presence of opposite phase masks. In the control condition an isolated target was detected, and the imagery task was to imagine the previously presented masks. As Figure 12 shows, the perceptual enhancement at 3λ was reduced, and the imagery effect disappeared. The enhancement area in the perception condition was 0.25 logarithmic unit, as compared with threshold elevation of 0.2 and 0.07 in the control and imagery conditions, respectively. The differences between perception and control, and the differences between perception and imagery, were statistically significant (repeated measures analysis of variance, followed by Scheffe multiple comparison, $F(2, 6) = 16.1$, $p < 0.01$). The differences between control and imagery were not significant (repeated measures analysis of variance, followed by Scheffe multiple comparison, $F(1, 4) = 0.13$, $p > 0.05$). These results indicate that the imagery-driven effect depends on both components of the memory trace that was established previously—that is, the target (within receptive field integration) and masks (outside receptive field integration).

Mixed Trials: Experiments 7A and 7B

The memory trace that subserves the imagery-induced facilitation is stimulus-specific. As was shown before, masks placed at 3λ had an excitatory trace, yet masks placed at 0 or 1λ had no effect on target threshold in the imagery task (Ishai & Sagi 1995; see also Figure 1). What memory trace will be created when masks placed at 3λ are mixed with masks at different eccentricities? In this experiment, the perceptual task was a mixture of two blocks with masks presented at 3λ and one of the other target-to-mask distances (from 0 to 12λ). Observers were instructed to detect a vertical target in the pres-

ence of the masks. In the control condition they had to detect an isolated target. In the imagery condition observers were instructed to imagine the masks at a distance of 3λ . As Figure 13 shows, while the mixing procedure had no effect on the perceptual enhancement, imagery of the masks at 3λ after mixing with 0 and 1λ had no facilitatory effect. Perceiving a high-contrast stimulus at the perceptual task seems to interfere with the image generation, probably due to inhibition of the memory trace. Interestingly, after presenting five trials of the masks at 3λ and one trial at 0λ , the facilitation was obtained in both perception and imagery conditions (Figure 14), indicating that the high-contrast stimulus had no inhibitory effect on the memory trace when it was "diluted" at a ratio of 1:5.

DISCUSSION

The main effect uncovered by using the lateral masking paradigm is the imagery-induced facilitation that shared the same characteristics with the perceptual enhancement (Figures 1 and 2; see also Ishai & Sagi, 1995). This paradigm revealed the existence of facilitatory interactions between spatial channels (Polat & Sagi, 1993; Polat & Norcia, 1996) that were found to be orientation and spatial-frequency specific (Polat & Sagi, 1994a, 1994b). The average imagery-induced facilitation at short target-to-mask distances was 50% relative to the perceptual enhancement in most experiments (Figures 1, 2, 3, 6, 7, 11, 13, and 14). The attempt to increase the magnitude of the imagery-induced facilitation by increasing the number of the flanking masks (Figure 3) was not successful. Surprisingly, at large target-to-mask distances, the

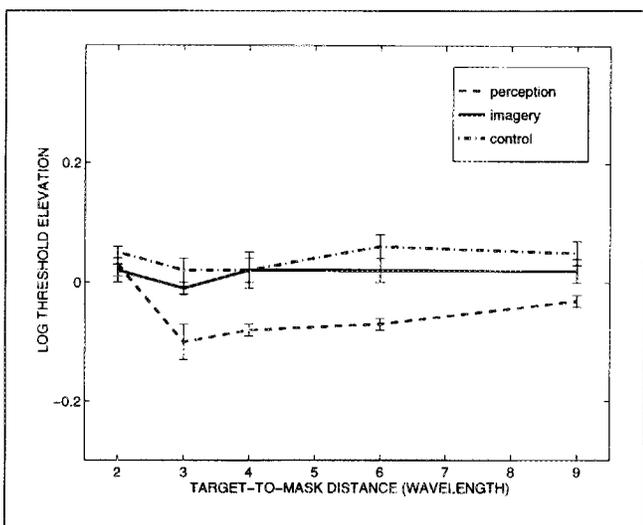


Figure 12. Target threshold as a function of target-to-mask distance, averaged across three observers (AI, DG, and EVS). Data are presented for vertical target and masks of opposite phases.

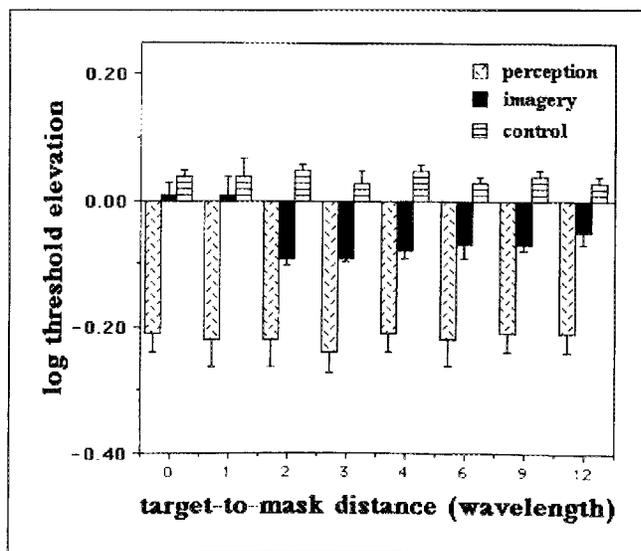


Figure 13. Target threshold at 3λ as a function of mixing with each of all other target-to-mask distances. Data are presented for vertical target and masks, averaged across three observers (AI, IE, and NK). In the imagery task observers had to imagine vertical masks at a distance of 3λ .

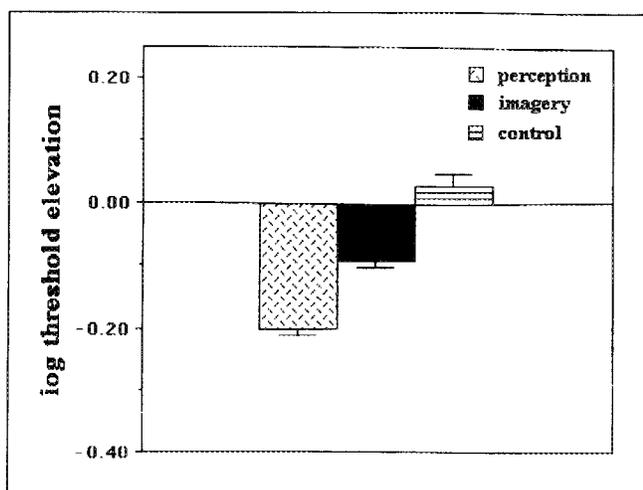


Figure 14. Target threshold at 3λ as a function of mixing five blocks with one block at a distance of 0λ . Data are presented for vertical target and masks, for observer NK. In the imagery task the observer imagined vertical masks at a distance of 3λ .

effect of perceiving and imagining the masks was almost identical (Figures 1, 6, and 7), indicating that the top-down component that contributes to the bottom-up analysis is very similar in both perception and imagery. McDermott and Roediger (1994) have found a facilitatory effect of visual imagery in an implicit memory test. When observers imagined pictures prior to a picture fragment identification test, interestingly, the priming effect was found to be half as much as that obtained from real pictures. The authors wrote: "Thus, it seems as though imagery, although perceptual in nature, produces less powerful effects than actual visual presentation. Imagery apparently involves a weak arousal of relevant perceptual processes" (McDermott & Roediger, 1994, p. 1388). Visual perception and visual imagery share common mechanisms (Ishai & Sagi, 1995), yet the absence of the retinal input is the ultimate explanation for the smaller effects induced by imagery, as compared with perception.

Interestingly, in our experiments no imagery-induced interference (Perky effect) was obtained (Figure 1; see also Ishai & Sagi, 1995). These results contradict previous findings, showing an interference when the image was projected on the target in vernier acuity task (Craver-Lemley & Reeves, 1987) or in a detection task of bars (Finke, 1986). Zenger and Sagi (1996) suggested that the threshold elevation seen when masks covered the target was due to within receptive field integration and lateral inhibition. Since we did not obtain suppression when observers had to imagine the masks on the target (i.e., at 0 and 1λ ; see Figure 1), it is reasonable to infer that visual imagery cannot mimic this effect in the absence of the retinal input. The lack of Perky effect in our experimental procedures of alternating perceptual and imagery tasks was probably due to the image generation

of Gabor stimuli from short-term memory. We obtained an imagery-induced interference only when observers imagined lines from long-term memory. The comparison between facilitation and interference, Gabor stimuli and lines, and image generation from short- and long-term memory are discussed elsewhere (Ishai & Sagi, 1997).

While most visual imagery tasks are based on long-term memory, the imagery-induced facilitation was based on recent memory that was established a few minutes prior to the imagery task (in our experiments the perception always preceded the imagery). We previously showed that introducing a delay period, longer than 5 min, between the perceptual and imagery tasks reduced the imagery-induced facilitation (Ishai & Sagi, 1995). The necessity of performing the perceptual task (more than 10 trials) before the imagery task (Figure 4), together with the stimulus-specificity of the effect, also suggest the involvement of short-term memory. We believe that the mechanism underlying the imagery-induced facilitation is a stimulus-specific short-term memory. Indeed, the perceptual task "primed" the imagery task. Priming is an experimental procedure by which effect of facilitation of performance by prior exposure is obtained, yet memory is the underlying mechanism. Similarly, if the mechanism was attention, we would have expected a global imagery effect in all experimental manipulations we have used; yet we found dependency on stimulus parameters.

The memory masking experiments exposed a limited-capacity memory system that is capable of storing the sensory trace. The interference obtained by co-oriented (vertical) visual noise was larger than the effect of orthogonal (horizontal) visual noise (Figure 6), indicating independent storage for different orientations. Interestingly, the main effect of masking the memory trace with visual noise was at eccentricity of 3λ , the optimal target-to-mask distance, where the perceptual enhancement was maximal. It seems that the imagery-driven effect at 3λ (the short-range facilitation) depends mainly on the memory trace being less sensitive to imagery manipulations, while the long-range effect, though dependent on the sensory trace, is also affected by mental manipulations (see Figure 7).

The stored information is accessible to higher-level processes. Reactivation by visual imagery can induce facilitation when the imagined Gabor stimuli match the stored stimuli in orientation and in eye used (Figures 1, 5, 7, 10, and 11). Moreover, mental rotation failed to induce facilitation when no enhancement was seen in the preceding perceptual task (Figure 9). The mixed blocks procedure revealed a suppressive effect of high-contrast stimuli on the memory trace (Figures 13 and 14). This stimulus-specific memory suggests that cortical cells which process the stimulus can also serve as memory cells or, alternatively, indicates synaptic memory. Previous studies have shown the involvement of monocular and orientation-specific cells in perceptual learning

(Karni & Sagi, 1991). It is possible that the memory system involved in imagery subserves learning by enabling spatio-temporal associations across a time window of few minutes (Polat & Sagi, 1994b).

In an attempt to isolate the within receptive field component of the imagery effect from the outside receptive field components, we performed the opposite phase experiments (Figure 12). Previous studies have shown that the long-range perceptual facilitation was due to outside receptive field integration (Zenger & Sagi, 1996). Since imagery could not mimic the suppressive effect at short target-to-mask distances (Figure 1), which was due to within receptive field integration and lateral inhibition (Zenger & Sagi, 1996), it is possible that the "constant" facilitation obtained by imagery is due to reactivation of the excitatory connections outside the receptive fields. The opposite phase experiments may indicate the necessity of the within receptive field integration of the masks. Interestingly, in the opposite phase experiments (Figure 12) where the within receptive field integration was eliminated, the reduced facilitation in perception was similar to the imagery-induced facilitation obtained with masks of equal phase (Figure 1).

Sakai and Miyashita (1993, 1994) have proposed a model that represents visual imagery as an interaction between memory retrieval and focal attention mechanisms. Based on studies in primates, the researchers drew the anatomical border between memory acquisition and memory consolidation in the temporal association area (the so-called memory storehouse). Our results show that both encoding (bottom-up) and decoding can occur at the level of the "feature analyzers" mentioned in the model, that is, in early visual areas.

Neuropsychological case studies have shown dissociation of visual imagery and visual perception. An agnostic patient (MS), who has shown severe difficulty in recognizing living things (faces, animals), has also shown selective loss of forming mental images of living, as opposed to nonliving, objects (Mehta et al., 1992). On the other hand, evidence for dissociation between mental imagery and object recognition in brain-damaged patients was reported. Patients (CK and MD) suffered from visual agnosia, yet their ability to generate mental images was normal. They could draw objects in considerable detail from memory but could not subsequently identify their own sketches (Behrmann et al., 1992; Jankowiak et al., 1992). These case studies suggest impairment in activation of internal representations. In this view, the results shown here indicate the existence of common representational structures that can subservise both perception (e.g., matching visual input to stored information for recognition) and image generation. As the Gabor stimuli used in our experiments had no semantic significance, it is reasonable to infer that the facilitatory effect of visual imagery on perception was due to activation of quasi-pictorial representations. Mental images can be interfaced with perceptual representations not

only at higher stages, but also at early stages of visual information processing. It is worth mentioning that previous studies with color aftereffects, a low-level phenomena explained in terms of fatigue of photoreceptors, failed to demonstrate equivalence between perception and imagery (Finke & Schmidt, 1977; Broerse & Crassini, 1984). The imagery-induced facilitation provides, therefore, psychophysical evidence for the involvement of the primary visual cortex in visual imagery.

Methods

Apparatus

Stimuli were displayed as gray-level modulation on an Hitachi HM-3619A color monitor, using an Adage 3000 raster display system. The video format was 56 Hz noninterlaced, with 512×512 pixels occupying a $9.6 \times 9.6^\circ$ area, each at 8 bits. The mean display luminance was 40 cd/m^2 . Stimulus generation was controlled by a Sun-3/140 workstation and the stimulus display by the Adage local processor. Gamma correction was applied using 10-bit lookup tables and DACs (enabling $1/1024$ gray-level resolution at selected screen regions).

In memory masking, chain of masks, and mixed trials experiments, stimuli were displayed as gray-level modulation on a Mitsubishi color monitor, using a Silicon Graphics Reality Engine system. The video format was 60 Hz noninterlaced, with 1280×1024 pixels occupying a $13 \times 10.4^\circ$ area. A 12-bit RGB mode was used, in which 12-bit pixels were converted by dithering into 10-bit values (using a 2×2 hardware implemented decorrelation matrix) and then by a 10-bit Gamma correction into 8-bit RGB DACs (this bit reduction scheme compensates effectively for the lost gray-levels at low luminance levels). Note that thresholds for small Gabor signals, as used here, are high enough (5 to 15%) to be effectively measured with 8 bits gray-level resolution. The mean display luminance was 40 cd/m^2 . Stimulus generation and display was controlled by a SGI Crimson/Reality Engine workstation.

Stimuli

Stimuli consisted of three Gabor signals arranged vertically or horizontally. A Gabor function is defined by:

$$G(x, y | x_0, y_0) = \cos \left\{ \frac{2\pi}{\lambda} [(x - x_0)\cos\theta + (y - y_0)\sin\theta] \right\} \exp \left\{ - \left[\frac{(x - x_0)^2 + (y - y_0)^2}{\sigma^2} \right] \right\}$$

and the stimulus is defined by:

$$I(x, y) = I_0 + A_{m1}G(x, y | x_0, y_0 + D) + A_tG(x, y | x_0, y_0) + A_{m2}G(x, y | x_0, y_0 - D)$$

where x_0 and y_0 represent the center of the Gabor signal with x and y being the coordinates over the Gabor's domain, θ is the orientation (in radians), λ is the wavelength, and σ is the standard deviation of the Gaussian envelope. A_t and A_{m1} , A_{m2} are the target and masks amplitudes, respectively. In all experiments mask amplitude was 40% of mean luminance, with $\lambda = \sigma = 0.15^\circ$, and $I_0 = 40 \text{ cd/m}^2$ being the mean screen luminance.

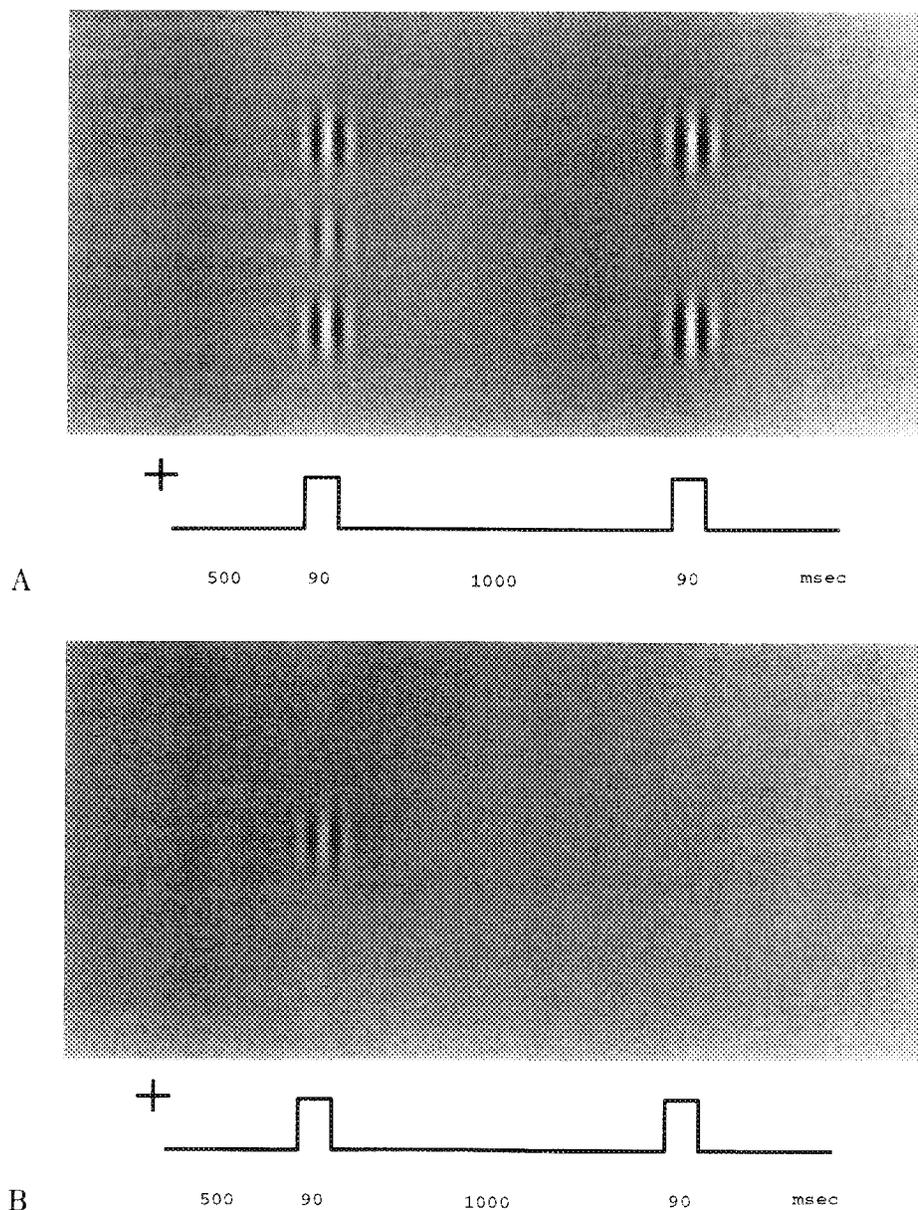
Experimental Procedures

A two-alternative forced-choice paradigm was used. Each trial consisted of two stimuli presented sequentially, only one of which had a target. Before each trial, a small

fixation cross was presented at the center of the screen. When ready, the observer pressed a key activating the trial sequence: a no-stimulus interval (0.5 sec), a first stimulus presentation (90 msec), a no-stimulus interval (1 sec), and a second stimulus presentation (90 msec) (see Figure 15). In the experiments that were done on the SGI, the stimulus presentation was 80 msec. In memory masking experiments, visual noise, composed of arrays of vertical or horizontal Gabor stimuli (see Figure 6), was presented 0.5 sec after the second stimulus presentation, for a duration of 0.5 sec. The observer was asked to perform a detection task, that is, to determine which of the stimuli contained the target.

Each block consisted of 50 trials on average, across

Figure 15. Temporal sequence of a trial. (A) A foveal Gabor target flanked by two high-contrast Gabor masks, at a distance of 3λ , used for the perception condition. (B) An isolated Gabor target used for the control and imagery conditions. In both examples target appeared on the first presentation of stimuli.



which the distance between the Gabor signals was kept constant. Screen luminance (I) was kept constant during the trials. The stimuli were viewed binocularly from a distance of 150 cm in a dark environment. Auditory feedback, by means of a keyboard bell, was given immediately after an erroneous response.

Three experimental conditions were used: (1) a *perception* condition, in which the observer detected the target in the presence of the flanking masks, (2) a *control* condition, in which the observer detected the target in the absence of the masks, and (3) an *imagery* condition, in which the observer was instructed to imagine the previously presented Gabor masks while detecting the isolated target. In each session the perception condition was immediately followed by either control or imagery conditions, that is, alternating tasks of perception and control, or perception and imagery. In the mental rotation experiments, a fourth condition was added—*rotation*—in which the observer had to imagine orthogonal masks while detecting the target (after perceiving vertical masks, the observer had to imagine horizontal masks, that is, a rotation of 90°). Each session included either perception and control, perception and imagery, or perception and rotation conditions.

The instructions in all experiments were to detect the foveal target. In the control experiments the observer was told to detect the target in the presence and in the absence of the flanking masks. In the imagery experiments the observer was told to detect the target in the presence of the flanking masks and to imagine the masks in the same location as previously presented. The observers were informed about the sequence of tasks in the session (i.e., alternating detection tasks with and without the flanking masks).

In the monocular experiments, eyeglasses with a blurring lens, for either the right or the left eye, were used. The blurring lens decreased the stimulus contrast and luminance and prevented the other eye from seeing the stimulus. Each session included eight alternating blocks of either perception followed by control or perception followed by imagery. Each control block was preceded by a perceptual block and was tagged by the target-to-mask distance of the perception. Each imagery block was preceded by a perceptual block, and the observer had to imagine the masks at the distance shown in the perception. One of two sets of target-to-mask distances was used: either 0, 2, 4, and 9 λ , or 1, 3, 6, and 12 λ . In some of the experiments only part of the enhancement region was tested (2, 3, and 4 λ).

Target threshold contrast (which ranged from 5 to 15%) was determined by a staircase method, which was shown to converge to 79% correct (Levitt, 1971). In this method, the number of threshold contrast reversals within each block was counted, and the block was terminated after eight such reversals; hence the number of trials in a single block was not constant. Threshold contrast of a block was the averaged value of the last six

reversals (the first two were ignored). A reversal was either an erroneous response, which led to an increase of 0.1 logarithmic unit (~26%) in target threshold or three consecutive correct responses, which led to a decrease of 0.1 logarithmic unit in target threshold. Baseline threshold was measured for detecting an isolated target in the presence of two peripheral high-contrast crosses, occupying 1° of the visual field, placed at the top and bottom of the display (eccentricity of 4° from the foveal target). The baseline threshold was measured twice in each session (the first and last blocks).

Observers

Eleven observers (DG, EM, ES, EVS, IE, NK, NW, OP, OY, SS, and YP) and one of the authors (AJ) participated in the experiments. The observers, high school and undergraduate students (between the ages of 16 and 25), were naive as to the purpose of the experiments and were paid in return. All observers had normal or corrected-to-normal vision.

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