Location vs Feature: Reaction Time Reveals Dissociation Between Two Visual Functions

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Reaction time in a detection or a location discrimination task was longer when a target appeared at the same location as in the previous trial (inhibition of return; IOR). However, it became shorter when the task was color or orientation discrimination (facilitation of return: FOR). This dichotomy was observed in the single target as well as in the popout displays. In additional experiments, vernier, size, and luminance discriminations all led to FOR, whereas eye-movement and arm-reaching tasks led to IOR. Moreover, identical stimuli could lead to the opposite patterns of result depending on the nature of the task: inhibition in global location tasks, and facilitation in feature analysis tasks. These may correspond to "where" vs "what" or "action" vs "recognition" pathways neurophysiologically. Copyright © 1996 Elsevier Science Ltd.

Reaction time   Inhibition of return   Facilitation   "Where" vs "what"

INTRODUCTION

Spatial attention is an indispensable aspect of visual information processing. This is because the brain has a limited capacity whereas infinite amount of information flows in the sensory channels. Without selection and filtering by attention, it would be impossible to perceive what is important and where to respond appropriately (James, 1890; Helmholtz, 1910; Broadbent, 1958).

Reaction time (RT) has been often employed as a sensitive measure to access the selection and filtering processes, and it has revealed various effects in a spatio-temporal context. For instance, consider a situation where a cue and a target are presented sequentially, either at the same or at different locations. When the target is presented at the same location as the cue, RT is longer than that at a different location. This is true particularly when the interval between the onset of the cue and the target (stimulus onset asynchrony; SOA) is relatively large (300–1500 msec) (Posner & Cohen, 1984). This has been called inhibition of return (IOR) and has been repeatedly duplicated by other researchers (Maylor, 1985; Kwak & Egeth, 1992; Tassinai et al., 1994).

However, the underlying mechanism is unknown. It is said that IOR occurs:

(i) in detection tasks (Posner & Cohen, 1984; Kwak & Egeth, 1992);
(ii) in location discrimination tasks (Maylor, 1985); and
(iii) in saccadic eye movements (Rafal et al., 1989).

It has been argued that IOR occurs somewhere in the visual motor link. On the other hand, facilitation, instead of inhibition, occurs in character discrimination tasks (Terry et al., 1994). It is not clear what critical factors elicit inhibition and facilitation.

There are several hypotheses. One is that it could occur only in the detection, not in the discrimination task. But this has already been rejected by the fact that the IOR effect has been demonstrated even in the location discrimination task (Maylor, 1985). Or it could be that the cue/target distinction is necessary for the IOR: that is, it is necessary that the subject should respond only to the target, but not to the cue. In order to test this hypothesis, we first tried to duplicate the inhibitory effect in a simple detection task, which was similar to one employed by Kwak and Egeth (1992).

A single target was presented at a top-left or a top-right position of the display, while the subject fixated at a point in the bottom center (fixation point). The location of the target was randomized between these two across trials. The interval between the button pushing response and the next target appearance (response stimulus interval: RSI)

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was also randomized across trials (200/400/1000/ 2000 msec). (Note: In this case, the real interval between the previous target and the next one was RSI + RT, thus, previous RT could also contribute to the inter-target interval. However, the difference of RT between the same location and the different location was relatively small as compared to RSI. Thus we could neglect the actual influence of the previous RT towards the next one.)

The distance between the target and fixation point was 12 deg. Note there was no cue in this experiment, and we were mostly interested in the positional effect of the previous target on RT to the present target. Four subjects [two naive and two non-naive (authors)] were asked to detect a target, and press a mouse button as quickly as possible. In results, strong IOR was obtained at all RSIs, except for the longest (2000 msec) in all the subjects. These results were consistent with Kwak and Egeth's. Thus, the cue/target distinction is not a necessary condition for IOR.

An alternative hypothesis is that inhibition occurs only in location-related tasks such as detection or location discrimination. That is, IOR is closely related to spatial location, rather than any other visual attributes such as color or orientation of the target. What could happen if the task itself was changed, that is, the task was a color or an orientation discrimination? Since these tasks could be classified as feature-related, rather than location-related, they might be expected to generate different results. Terry et al., for instance, have shown that there is an interaction between location change and task type (location vs letter discrimination) (Terry et al., 1994). Kwak and Egeth (1992) manipulated the color or orientation of the target but didn't change the task (the task was still simple detection). Consequently it is possible that feature discrimination tasks in general lead to the opposite result, facilitation. Thus, here we propose a hypothesis that the task difference itself determines the occurrence of inhibition and facilitation: that is, an inhibition should occur in location-related tasks and a facilitation occur in feature-related tasks.

To test this hypothesis, we performed experiment 1 where we manipulated the task with an identical set of stimuli. Results were consistent with the hypothesis, as we will describe in detail. In experiment 2, the size, the luminance, and the vernier discriminations were employed as further examples of a feature discrimination task. In experiment 3, the target was presented in various locations, and the detection and the color discrimination tasks were again employed. This was done to see if detection would still lead to IOR and feature discrimination would lead to facilitation under such a condition, and also to examine the spatio-temporal characteristics of inhibition and facilitation more closely. In experiment 4, we tested whether the dichotomy still holds in a popout display. Finally in experiment 5, a variety of motor tasks such as saccadic eye-movement and arm-reaching tasks were employed to see if IOR occurred.
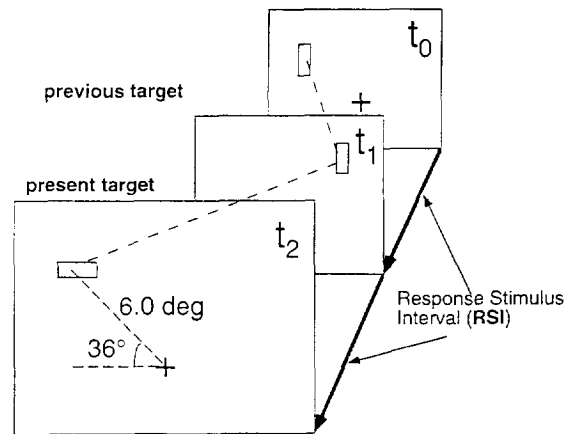

FIGURE 1. Stimulus sequence for the single target experiment. Target was randomized in terms of location (left/right), color (red/green), and orientation (vertical/horizontal) across trials. Response Stimulus Interval (RSI) was also randomized among 100/300/500/1200 msec.

EXPERIMENT 1: INHIBITION AND FACILITATION OF RETURN

This experiment included several subexperiments in which stimuli consisted of different visual attributes (location, color, and orientation) and different tasks were employed.

Subjects

Six subjects [four naive (MIT undergraduate and graduate students) and two non-naive (authors)] participated in the experiments. All subjects had normal visual acuity and normal color vision. Naive subjects did not know the purpose of the experiment.

Procedure

The target (rectangle) was randomized in terms of location (left/right), color (red/green), and orientation (vertical/horizontal) across trials. The response stimulus interval (RSI; the interval between onset of response in the previous trial to onset in the present trial) was also randomized among 100/300/500/1200 msec (see Fig. 1). The target size was 0.5 deg $\times$ 0.4 deg and its luminance was 6.4 cd/m^2 [hue:R(0.555, 0.344) G(0.320, 0.555)]. Fixation point's size was 0.1 deg $\times$ 0.1 deg. Luminance of the background was 0.01 cd/m^2. Viewing distance was 114 cm. The stimuli were presented on a CRT display (Commodore 1840S, non-interlaced frame frequency of 60 Hz) controlled by a microcomputer (Commodore Amiga 500) in a complete dark room. The temporal sequence in each trial was as follows. First a fixation point appeared for 150 msec. Then the target appeared at the upper left or upper right side of the fixation point until a response was made. RT was measured as the time between the onset of target and the onset of response. As soon as the subject responded to the target, it disappeared. The fixation point remained throughout the trial. After a randomized RSI, the next trial was started.

simple detection

location discrimination

color discrimination
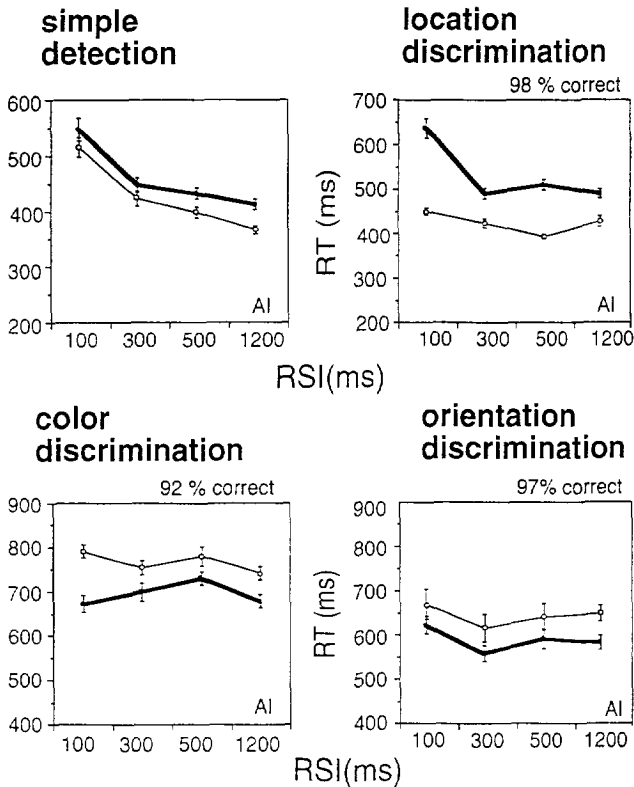

orientation discrimination

FIGURE 2. Results of the single target experiment. RT is plotted as a function of RSI. The results in four different tasks are shown separately in separate panels. Thick curve, same location; and thin curve, different location. Vertical bars indicate standard errors.

The subject engaged binocularly in four tasks in separate sessions:

1. simple detection;
2. location discrimination (left/right);
3. color discrimination (red/green); and
4. orientation discrimination (vertical/horizontal).

Note that the stimuli and their sequence were identical across all the tasks, the only difference being the nature of the task. The subject was asked to make a two alternative forced choice (2AFC) by button pushing for all the tasks, except for the simple detection task. The left mouse button was pressed in the simple detection task, and the left or the right button was pressed in response to the target on the left or right side of the fixation point in the location discrimination task. In the color discrimination task, the left or the right button was pressed in response to the red or green target. In the orientation discrimination task, the left or the right button was pressed in response to the vertically or horizontally elongated target.

The data were analyzed in terms of the positional relationship between the previous and the present trial (same/different). The total trial number was 300 in each session. RTs in error trials were eliminated from the data analysis. RTs which were below 100 msec and above 1300 msec were eliminated. Sessions where the error rate for discrimination exceeded 10% were also eliminated. The subject's head was stabilized by a chin rest. Eye fixation was monitored in selected sessions using the eye monitor, Ober 2 (Permobil Corp.). The subject performed

TABLE 1. Summary of results in the single target experiment (YT and SS were non-naive, others were naive)

	Orienting tasks		Feature tasks	
Subjects	Simple Detection	Location Discrim.	Color Discrim.	Orientation Discrim.
YT	$-$**	$-$**	$+$**	$+$**
SS	$-$**	$-$**	$+$**	$+$**
KS	$-$**	$-$**	$+$**	$+$**
AM	$-$**	$-$**	$+$**	ns
AI	$-$**	$-$**	$+$**	$+$**
SP	$-$**	$-$**	$+$**	$+$*

The polarity of difference in reaction time (RT) was reversed depending on the task. Orienting tasks (simple detection or location discrimination) lead to IOR (indicated by "$-$"), whereas feature tasks (color discrimination or orientation discrimination) lead to FOR (indicated by "$+$"). Data were analyzed by ANOVA for statistical significance, as indicated by * at 5% level and ** at 1% level.

a practice session (100 trials) before each session of the experiment.

Results

The results were straightforward. The IOR was obvious, that is, RT at the same location was longer than that at a different location, in the simple detection and the location discrimination tasks [Fig. 2(A)]. The opposite pattern of results, however, was found in the color and the orientation discrimination tasks; RT at the same location as the previous trial was shorter than that at a different location [Fig. 2(B)]. We call this "facilitation of return (FOR)" which is contrary to IOR. The consistency of results across six subjects is shown in Table 1. To the author's knowledge, this is the first report of a clear dissociation between IOR and FOR only by task manipulation, while maintaining the stimulus parameters identical. The data obtained from the six subjects were

TABLE 2. ANOVA results of experiments 1.1–1.4

	F Value	$Pr > F$
ANOVA results of experiment 1.1		
Location	20.19	0.0001**
Orient.	9.89	0.0017**
RSI	67.26	0.0001**
Location × RSI	8.23	0.0042*
ANOVA results of experiment 1.2		
Location	15.87	0.0001**
Color × Orient.	8.39	0.0039**
ANOVA results of experiment 1.3		
Location	50.1	0.0001**
Color	8.50	0.0036**
Location × Color	10.14	0.0015**
Color × Orient.	10.54	0.0012**
ANOVA results of experiment 1.4		
Location	6.38	0.0117*
Location × Orient.	16.60	0.0001**
Color × RSI	5.22	0.0225*

Only the main effects and interaction which have turned out to be significant are listed here. Statistical significance at 5% level is indicated by *, and that at 1% level is indicated by **.
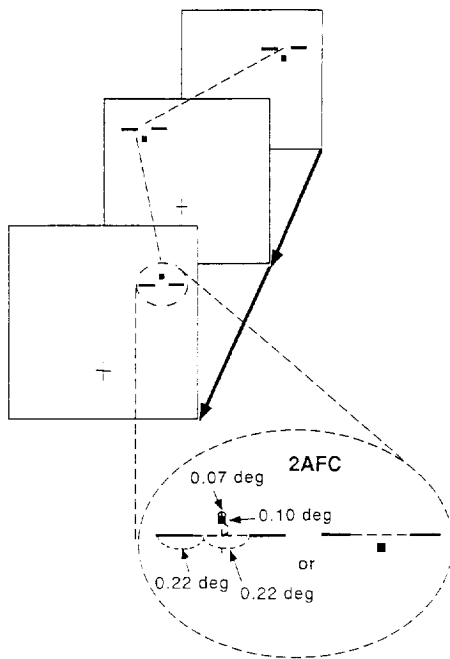
FIGURE 3. Stimulus configuration for vernier discrimination experiment. The subject was asked to do a 2AFC judgment as to whether the target dot was above or below the reference lines. Location and RSI were randomized across trials.

combined for the statistical analysis. They were analyzed with a four-way repeated measures ANOVA (RSI × location × color × orientation) in each subexperiment. The results are summarized in Table 2. As indicated in Table 2, the main effects of location, orientation and RSI, the interaction between location × RSI were significant in experiment 1.1. In experiment 1.2, the main effects of location and the interaction between color × orientation were significant (Table 2). In experiment 1.3, the main effects of location and color, the interactions between location × color and color × orientation were significant (Table 2). In experiment 1.4, the main effects of location, the interactions between location × orientation, and color × RSI were significant (Table 2).

Discussion

In this experiment, we obtained IOR in the simple detection and the location discrimination tasks, but FOR in the color and the orientation (shape) discrimination task. It was not the distinction between detection and discrimination tasks, but rather the nature of the task, that led to the distinction of IOR and FOR. IOR occurred in location-related tasks and FOR occurred in feature-related tasks.

In the simple detection and the location discrimination task, information about global location seems to be crucial to orient and to respond to the target (Posner, 1980; Maylor, 1985; Kwak & Egeth, 1992). This is why these tasks are classified as location-related tasks. On the other hand, in the color and the orientation discrimination tasks, it is necessary to attend to one specific object and to analyze its features (Kahneman & Treisman, 1984). We therefore call them feature-related tasks.

In addition to color and orientation, there are other visual attributes of the object such as size or luminance. For example, size discrimination could be another case that requires feature analysis. In order to build up object representation, the evaluation of size is necessary. Thus, it is plausible to expect facilitation at the same place as for the previous trial in size discrimination. The same thing could be said about luminance discrimination. Thus, we conducted the next experiments, size discrimination (experiment 2.1) and luminance discrimination (experiment 2.2).

Discrimination of fine shape or vernier offset is of particular interest. This is because on the one hand it requires spatial information just as in the location discrimination, but on the other hand it also requires a typical local feature analysis. Thus, if IOR occurred in this task, pure spatial information even at a finer scale would be crucial for the IOR. If FOR occurred, on the other hand, it would indicate that global spatial information is critical for the IOR. This motivated us to conduct a vernier discrimination experiment (experiment 2.3) as well.

EXPERIMENT 2: FEATURE DISCRIMINATION TASK

Subjects

Five subjects [three naive (MIT undergraduate students) and two non-naive (YT and SS)] participated in experiment 2.1. Five subjects [three naive (MIT undergraduate students) and two non-naive (YT and SS)] participated in experiment 2.2. Four subjects [two naive (MIT undergraduate students) and two non-naive (YT and SS)] participated in experiment 2.3. Naive subjects
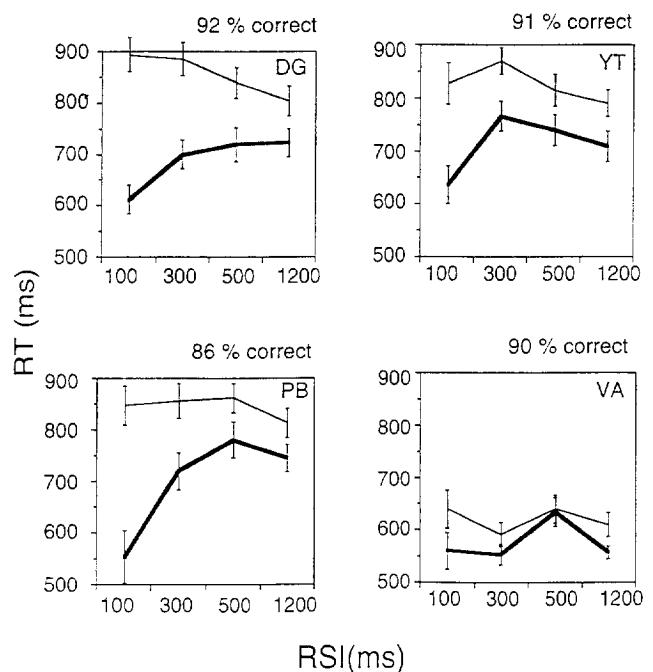

FIGURE 4. Results of the size discrimination experiment. RT is plotted as a function of RSI. The data obtained from four subjects are plotted separately in separate panels. Thick curve, same location; thin curve, different location. Vertical bars indicate standard errors.
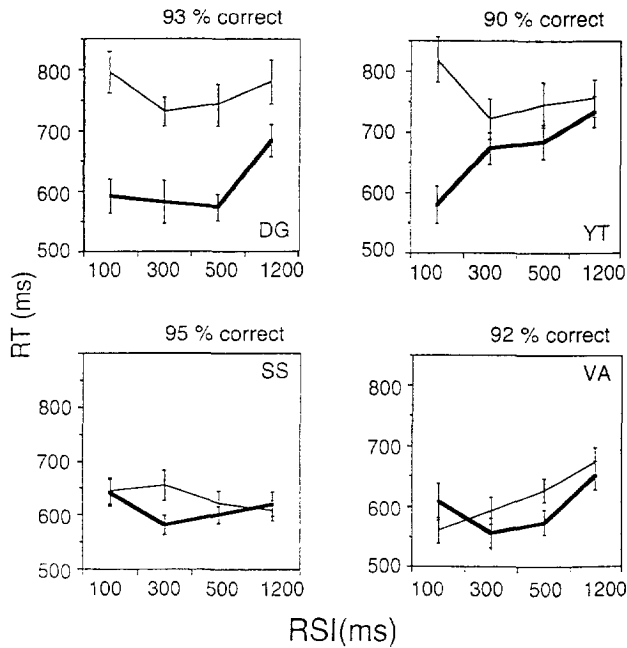
FIGURE 5. Results of the luminance discrimination experiment. RT is plotted as a function of RSI. The data obtained from four subjects are plotted separately in separate panels. Thick curve, same location; thin curve, different location. Vertical bars indicate standard errors.

were not necessarily the same across these subexperiments. Naive subjects did not know the purpose of the experiments.

Stimuli and procedures

The target always appeared on either the upper-left or the upper-right side of the fixation point in all the three subexperiments. The subject observed the target binocularly, and performed one of the three kinds of feature discrimination task (length, luminance, and vernier offset). In experiment 2.1, the target was a vertically elongated bar, whose length was either 0.2 deg (short) or 0.4 deg (long). The luminance was 7.89 cd/m^2. The distance between the fixation point and the target was 6 deg. The length of the target was randomized across trials. The task was to discriminate the length of the target (2AFC judgment).

In experiment 2.2, the target was a vertically elongated bar, whose luminance was bright (7.80 cd/m^2, hue: 0.34, 0.48) or dark (0.35 cd/m^2, hue: 0.31, 0.42). The luminance of the target was randomized across trials. The task was to discriminate the luminance of the target (2AFC judgment). The length of the bar was stabilized at 0.4 deg. The distance between the fixation point and the target was 6 deg.

In experiment 2.3, the target consisted of two horizontal line-segments and one dot either above or below these reference lines (Fig. 3). The location of the dot relative to the reference lines (above or below) was randomized across trials. The subjects were asked to make a 2AFC judgment as to whether the target dot was above or below the reference line. The size of each line was 0.22 deg × 0.10 deg, and the dot size was 0.07 deg × 0.10 deg. The distance of the two lines was

0.22 deg, and the distance between the dot and the reference line was 0.10 deg. The distance between the two possible target locations was 20.2 deg, and the distance between the fixation and the target was 12.5 deg.

In all the subexperiments, the location of the target (left/right) and RSI (100/300/500/1200 msec in experiments 2.1 and 2.2, 200/400/100/2000 msec in experiment 2.3) were randomized across trials. The viewing distance was 114 cm, except for experiment 2.3 where it was 57 cm. The subject's head was stabilized by a chin rest. Eye fixation was monitored in selected sessions using Ober 2 (Permobil Corp.). The experiment was conducted in a dark room (with a 30 sec period for dark adaptation). There were 380 trials in each sub-experiment.

The data were analyzed based on the position relationship between the previous and the present trial. RTs in error trials were eliminated from the data analysis. In experiments 2.1 and 2.2, RTs which were below 100 msec and above 1300 msec were eliminated. In experiment 2.3, RTs which were below 100 msec and above 2500 msec were eliminated. Only sessions where the error rate for discrimination did not exceed 10% were included in analysis.

Results

The results of experiment 2.1 for each subject are shown in Fig. 4.

All five subjects showed clear evidence of FOR. RTs at the same location were in general shorter than at a different location across almost all RSIs.

The results of experiment 2.2 for each subject are shown in Fig. 5. All the subjects showed clear evidence for FOR (possibly with one exception, VA).

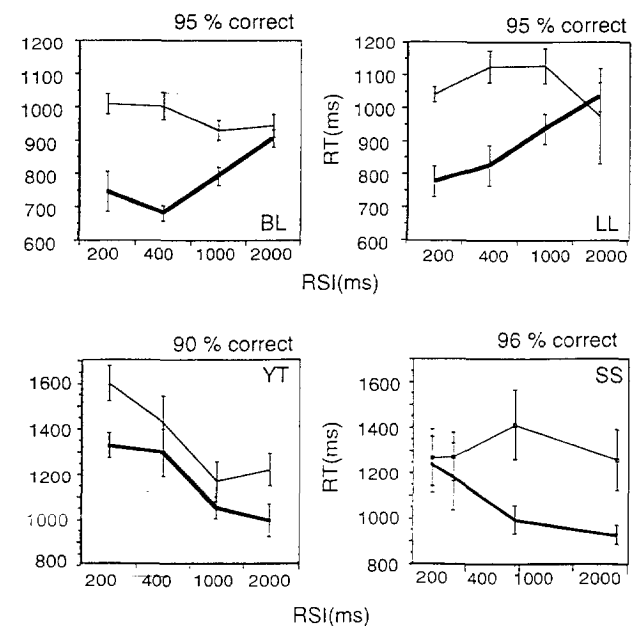The results of experiment 2.3 for each subject are

FIGURE 6. Results of the vernier discrimination experiment. RT is plotted as a function of RSI. The data obtained from four subjects are plotted separately in separate panels. Thick curve, same location; thin curve, different location. Vertical bars indicate standard errors.

TABLE 3. ANOVA results of experiments 2.1–2.3

	F Value	Pr > F
ANOVA results of experiment 2.1		
Location	93.73	0.0001**
Length	8.17	0.0043**
Location × Length	22.65	0.0001**
Location × RSI	21.03	0.0001**
ANOVA results of experiment 2.3		
Location	70.14	0.0001**
Luminance	5.28	0.0219*
Location × Luminance	24.79	0.0001**
Location × RSI	6.95	0.0085**
ANOVA results of experiment 2.3		
Location	7.93	0.0051**

Only the main effects and interactions which have turned out to be significant are listed here. Statistical significance at 5% level is indicated by *, and that at 1% level is indicated by **.

shown in Fig. 6. All subjects showed clear evidence for FOR. Facilitation tended to disappear at a longer RSI (2000 msec) in two subjects (BL, LL).

The data were combined among the subjects for statistical analysis. They were analyzed with a three-way repeated measures ANOVA (RSI × location × color × feature) in each subexperiment. The results are summarized in Table 3. As indicated in Table 3, the main effects of location, length, the interactions between location × length, location × RSI were significant in experiment 2.1. The main effects of location and luminance, the interactions between location × luminance and location × RSI were significant in experiment 2.2. The main effect of location was only significant in experiment 2.3.

Discussion

All these results are consistent with the hypothesis that the task difference itself could lead to IOR and FOR. The FOR was found in the size discrimination task (experiment 2.1), the luminance discrimination task (experiment 2.2) and even the vernier discrimination task (experiment 2.3). The results suggest that facilitation could occur in the constructing process of object representation, which requires feature analyses. The same location is more appropriate for comparing and evaluating (discriminating) object attributes such as size, luminance, or fine shapes. This is presumably the reason why it leads to FOR. The vernier result was especially informative as to the type of condition which elicits FOR. It supports the hypothesis that fine shape discrimination leads to FOR, whereas global spatial orienting is necessary for IOR.

(Note: We also conducted location discrimination experiments with the same stimuli as those in experiment 2.1 (different size), experiment 2.2 (different luminance), and that of experiment 2.3 (fine shape) to see if the same dichotomy in experiment 1 held. [Two subjects, YT (author) and GI (naive) participated.] As results, IORs occurred in all location discrimination tasks, which is consistent with the results of experiment 1 (single target).

Our knowledge about IOR and FOR was still very limited. Part of the reason was that there were only two

possible locations. What would happen if the target could appear in more than two locations? Could we still get the same dissociation between IOR and FOR across the tasks? Also, could we find some facilitatory or inhibitory effects at intermediate positions with various RSIs? If so, would we see a spatial shift or a spreading of these effects, as RSI increases? Some researchers claimed that spatial attention had a "spotlight" like character (Posner, 1980; Remington & Pierce, 1984). Others claimed that the focus of attention can shift rather quickly (Fischer & Breitmeyer, 1987). Considering these arguments, we could possibly find some evidence for shifting or spreading of facilitatory/inhibitory effects.

To answer these questions we manipulated the temporal factor (RSI) and spatial factor (location of the target) simultaneously. Specifically, we increased the number of possible locations where the target could appear. We conducted both the detection task which was a typical location task (experiment 3.1), and the color

(a)

(b)

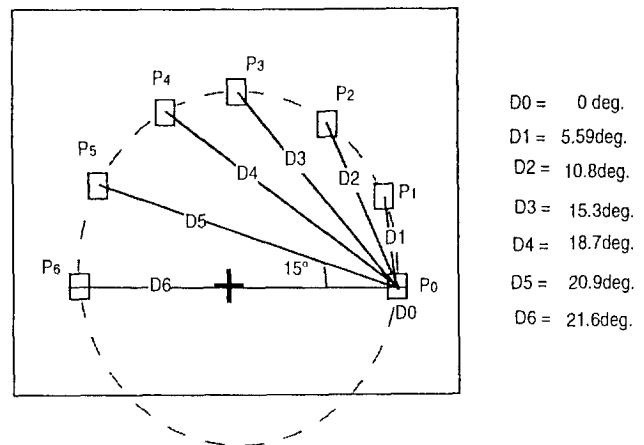| D0 =	0 deg.
D1 =	5.59deg.
D2 =	10.8deg.
D3 =	15.3deg.
D4 =	18.7deg.
D5 =	20.9deg.
D6 =	21.6deg.
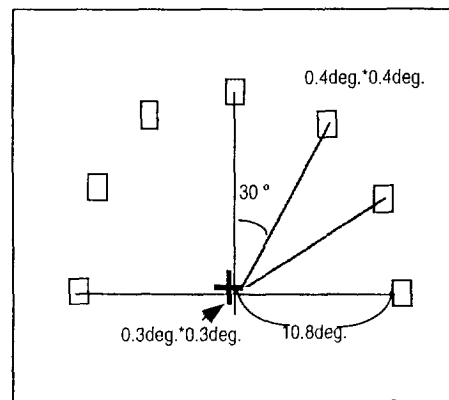
FIGURE 7. (a) Configuration of stimuli for the multiple location experiment. The target was a square (0.4 deg × 0.4 deg) presented at one of seven possible locations. The distance between the target and fixation point was constant (10.8 deg). (b) Target was randomized among the seven locations (P) across trials. Thus, the distance between the previous and the present targets randomly varied also in seven steps (D). RSIs were also randomized among 200/400/1000/2000 msec.
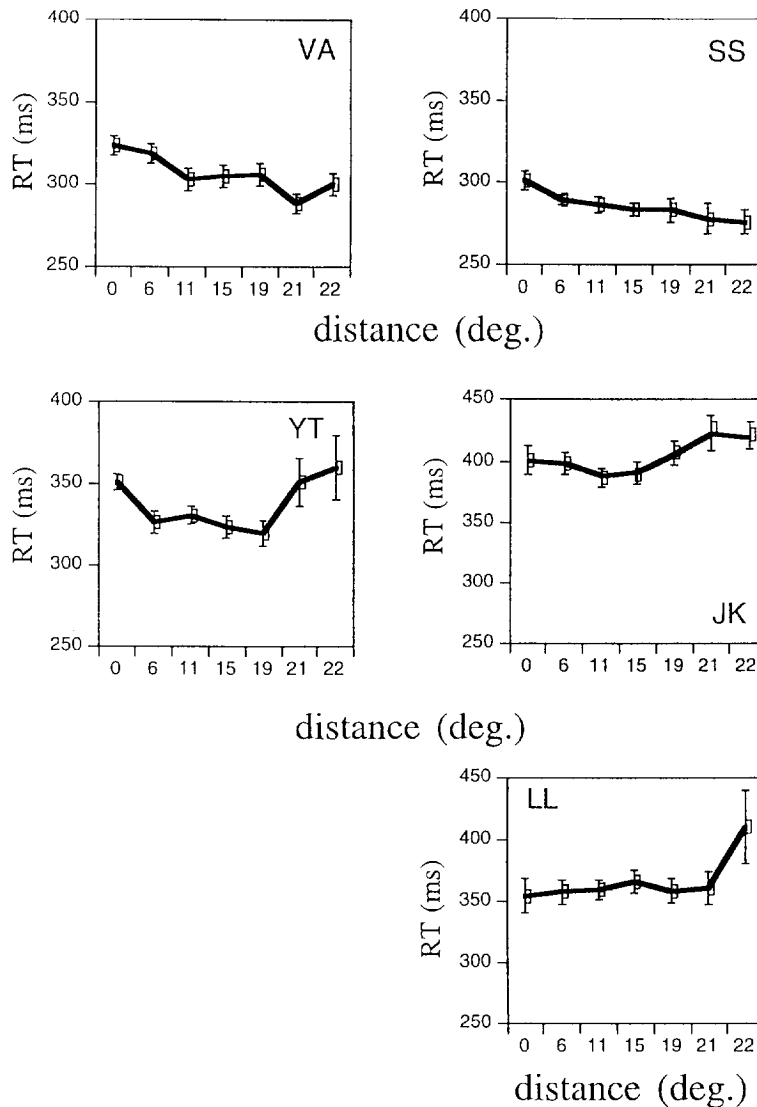
FIGURE 8. Results of the detection experiment with the multiple location experiment (periphery). The data obtained from five subjects are plotted separately in separate panels. RT is plotted against distance between the previous and present targets. The data obtained at various RSIs were pooled within each subject to see the main effect of distance. Distance 0 indicates that the present target is presented at the same location as the previous one. Vertical bars indicate standard errors.

discrimination task which was a typical feature task (experiment 3.2).

EXPERIMENT 3: IOR/FOR IN VARIOUS LOCATIONS

The purpose of experiment 3 was to determine the spatio-temporal dynamics of IOR and FOR in more detail. For this purpose, we repeated the detection (experiment 3.1) and the color discrimination (experiment 3.2) tasks with many possible locations of the target. We wanted to know whether we could duplicate the IOR and the FOR with many locations, and how large the spatial range of IOR and FOR could be.

Subjects

In experiment 3.1 four subjects [two naive (MIT students) and two non-naive (authors)] participated. The same four subjects participated also in an additional experiment with a longer observation distance in

experiment 3.1. In experiment 3.2, five subjects [three naive (MIT students) and two non-naive (authors)] participated. Naive subjects were not necessarily the same between these subexperiments. Naive subjects did not know the purpose of the experiment.

Procedure

The target [a square (0.8 deg × 0.8 deg) in experiment 3.1 and a rectangle (1.0 deg × 0.8 deg) in experiment 3.2] was presented at one of the seven positions on the CRT display [see Fig. 7(a)]. The color of the target was white (luminance: 7.89 cd/m^2) in experiment 3.1 and red or green in experiment 3.2 [luminance: 6.4 cd/m^2; hue: R(0.555, 0.344) G(0.320, 0.555)]. The background was dark (luminance: 0.001 cd/m^2). The seven possible locations of the target were such that they all were equidistant from the fixation point (10.8 deg), as illustrated in Fig. 7(a). The angular distance between

TABLE 4. ANOVA results of experiments 3.1–3.3

	F Value	Pr > F
ANOVA results of experiment 3.1		
Distance	10.790	0.000001**
RSI	14.872	0.000001**
Distance × RSI	2.727	0.00012**
ANOVA results of experiment 3.2		
Distance	2.223	0.03897*
RSI	11.882	0.000001**
Distance × RSI	1.611	0.05111
ANOVA results of experiment 3.3		
Distance	4.119	0.00050**

Only the main effects and interactions which have turned out to be significant are listed here. Statistical significance at 5% level is indicated by *, and that at 1% level is indicated by **.

the adjacent targets was 30 deg. Thus, the distance of the target from that in the previous trial was 5.59, 10.8, 15.3, 18.7, 20.9 or 21.9 deg [see Fig. 7(b)]. RSIs were randomized in four steps, 200, 400, 1000, or 2000 msec. The position of the target and RSI were randomized across trials. There were seven positions × 4 RSIs × 16 repetitions, thus, the total number of trials was 448. The observation distance was fixed at 57 cm, except that an additional experiment with the detection task was run on four subjects (two non-naive and two naive) at a distance of 171 cm. This experiment was added to see the results in a finer spatial scale. The subject binocularly observed the target and performed two tasks in separate sessions: (1) simple detection (experiment 3.1); (2) color dis-

crimination (red/green) (experiment 3.2). The subject had to detect the target and to press a mouse button as quickly as possible in the detection task. The subject had to make a 2AFC judgment about color in the color discrimination task. They had to press the left mouse button when a red target appeared and press the right when a green target appeared as quickly as possible. RT was measured in each trial and the percentage of correct judgment was calculated in the discrimination task.

The subject's head was stabilized by a chin rest. The subject performed a practice session (100 trials) before each session of the experiment. RTs in error trials were eliminated from the data analysis. RT which was below 100 msec and above 1300 msec were eliminated from the analysis. Only the sessions where the error rate for discrimination did not exceed 10% are included in analysis. The data were analyzed according to the distance between the previous and the present target and RSI.

Results

The results for each subject were shown in each panel of Fig. 8, where the mean RT is plotted against the distance. The difference in RTs among RSIs were varied and not consistent among subjects, so the data were pooled among RSIs within each subject and plotted in order to see the main effect of the distance. All the subjects except for LL showed longer RTs at the distance 0, which indicated IOR. The distance for fastet RTs varied among subjects, from 11 to 22 deg. The data
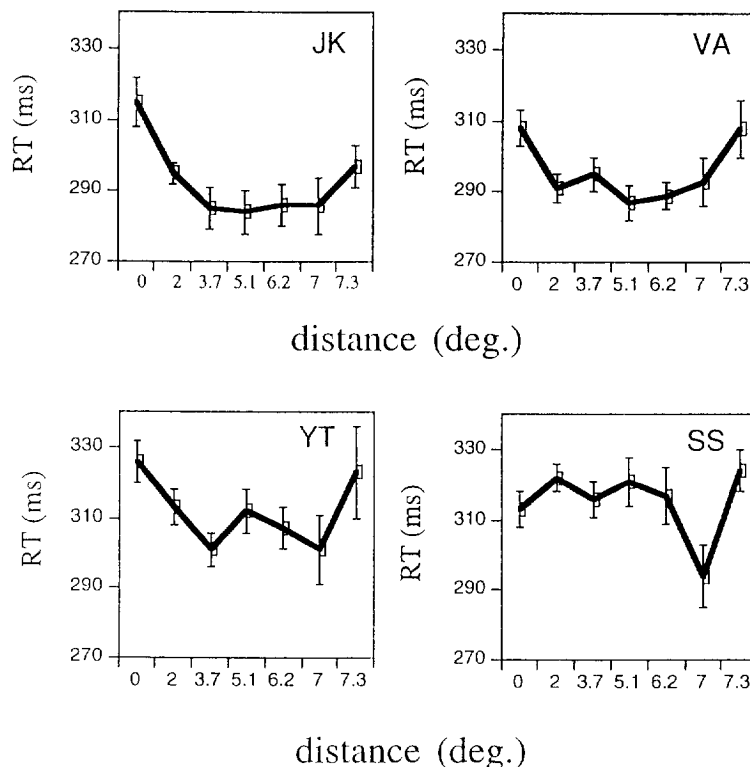

distance (deg.)

distance (deg.)

FIGURE 9. Results of the detection experiment with the multiple location experiment (fovea). The data obtained from four subjects are plotted separately in separate panels. RT is plotted against distance between the previous and present targets. Distance 0 indicates that the present target is at the same location as the previous one. Vertical bars indicate standard errors.
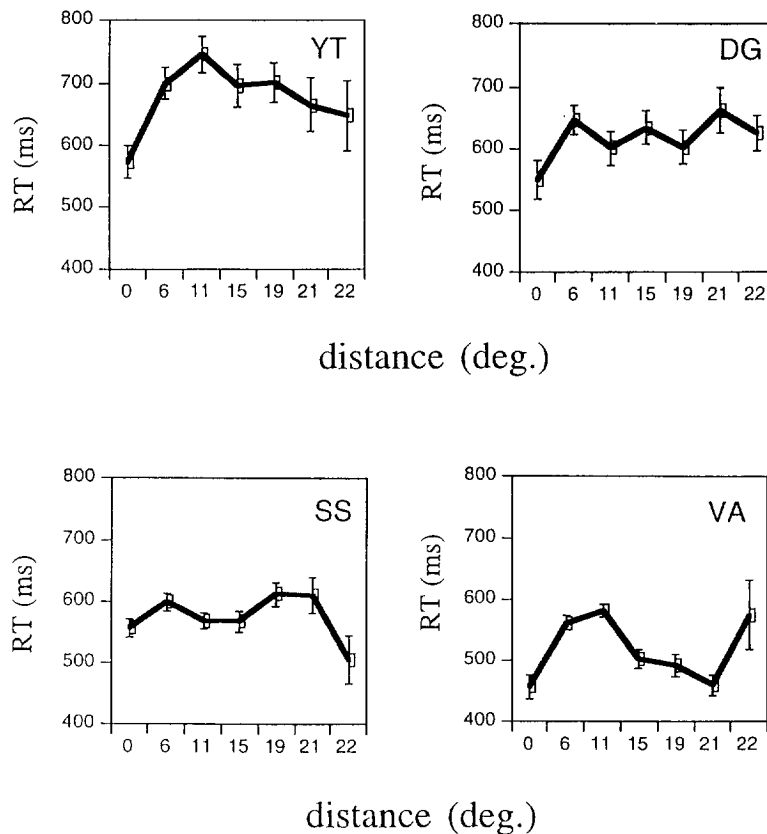
FIGURE 10. Results of the color discrimination experiment with the multiple location experiment (periphery). RT is plotted against distance between the previous and present targets. The data obtained from four subjects are plotted separately in separate panels. Distance 0 indicates that the present target is at the same location as the previous one. Vertical bars indicate standard errors.

obtained from the five subjects were combined for the statistical analysis. The mean RTs were analyzed with a two way repeated measures ANOVA (RSI × distance). The results are summarized in Table 4. The main effects of distance and RSI, and the interaction between distance × RSI were all significant in experiment 3.1. The significant interaction between distance and RSI may indicate that the spatial profile of facilitation and inhibition changed as the RSI increased, although as mentioned above, there was not necessarily a consistent pattern of change across the subjects.

The data obtained in the additional experiment at the longer distance (171 cm) are helpful to see the distance effect in a finer spatial scale. The results are shown in Fig. 9, where the mean RT is plotted against the distance for each of the two subjects in each panel of the figure. IOR was observed even in a very small area, especially as small as 2 deg among three subjects (YT, JK, VA) out of the four. Otherwise, the results essentially duplicated those in the main experiment. The area where the shortest RT was observed was around several degrees (3.7– 7 deg). The data obtained from the four subjects were combined for statistical analysis. The mean RTs were analyzed with a two way repeated measures ANOVA (RSI × distance). The results of the additional experiment are summarized in Table 4. The main effects of distance and RSI were significant. The interaction between distance × RSI was marginal, but not signifi-

cant. The pattern of results was basically consistent with those in the main experiment.

The results in the color discrimination task are shown in Fig. 10. The RT became longer steeply from 0 to 6.0 deg for three subjects. The range of FOR varied among subjects from 6.0 up to possibly 15.0 deg. This result confirmed that of the single target experiments (experiment 1). The data obtained from the four subjects were combined for the statistical analysis. The mean RTs were analyzed with a two way repeated measures ANOVA (RSI × distance). The results are summarized in Table 4. Only the main effect of distance was significant in experiment 3.2. Unlike the IOR in the detection task, the main effects of RSI and the interaction between distance and RSI were far from the significant level. These statistical results are again consistent with the more sustained nature of FOR.

Discussion

Even when the target was presented at various locations instead of at two restricted locations, the task difference reversed the pattern of results: the detection task led to IOR and the color discrimination task led to FOR. Thus we basically duplicated the main results of experiment 1 with many locations.

Furthermore, the detailed spatio-temporal patterns were considerably different. The spatial range of IOR in the detection task tended to change with time, thus the
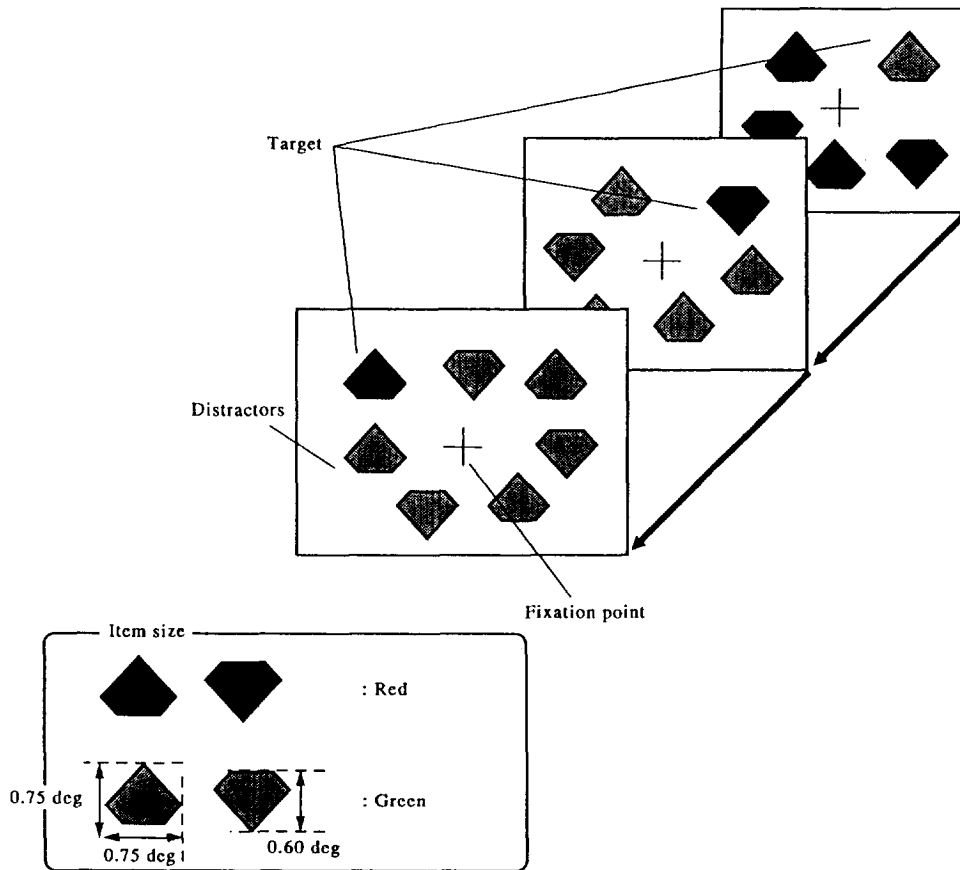
FIGURE 11. Stimulus sequence for the popout experiment. The target is defined by a color which is different from that of distractors. Each diamond was chopped off at either top or bottom. The location of the target was either top-left or top-right of the fixation point (randomized). The locations of the distractors (left/right), the color of the target (red/green), and the shape (top-chopped/bottom-chopped) were randomized across trials as well.

interaction between distance and RSI was significant. Unlike this, the spatial pattern of FOR in the color discrimination task tended to stay the same, thus there was no sign of RSI effect, nor of interaction. This could be taken as another piece of evidence for the dissociation between the IOR and the FOR.

EXPERIMENT 4: POPOUT DISPLAY

So far, the target was always single on a blank background. Is this the necessary condition for the IOR to occur? Is there a limitation in terms of stimulus complexity?

Let us now remember that the IOR is most likely to be related to sensory-guided spatial orientation. It has been commonly believed that the sensory-guided spatial orientation involves some sub-cortical loci such as the superior colliculus in its underlying neural circuit (Robinson, 1981; Hikosaka & Wurtz, 1983; Schiller et al., 1984; Weiskranz et al., 1974; Rafal et al., 1989). Considering this, it might be reasonable to assume that the neural mechanism underlying the IOR is at the sub-cortical level. However, it is too early to conclude this because most of the studies have only considered the simplest situation, where the single target was the only visible besides the fixation point. This raises a natural

question as to whether the IOR mechanism could extract the global location of the target when there are many visible distractors (Treisman & Galade, 1980; Sagi & Julesz, 1985). To answer this question, we used a popout stimuli (see Fig. 11).

In this display, the target was defined by a color which was different from that of distractors. This task was intriguing because the location of the "odd-ball" target could not be obtained unless vigorous, parallel feature analyses were performed across the visual field. This was presumably impossible to deal with in the sub-cortical loci (Schiller et al., 1984; Sagi & Julesz, 1985).

If the IOR occurs only in the sub-cortical process (Rafal et al., 1989), there would be no IOR in the detection task with the popout display. On the contrary, if the IOR occurs in the popout display, it would suggest that the cortical loci such as V1 should be involved in the mechanism underlying the IOR. To determine which hypothesis is more appropriate, we conducted this experiment.

Subjects

Four subjects [two naive (MIT students) and two non-naive (authors)] participated in the experiment. Naive subjects did not know the purpose of the experiment.

simple detection

false alarm: 5%

location discrimination

false alarm: 10%
percentage correct: 100%

RSI(ms)

color discrimination

false alarm: 10%
percentage correct: 93%

shape discrimination

false alarm: 5%
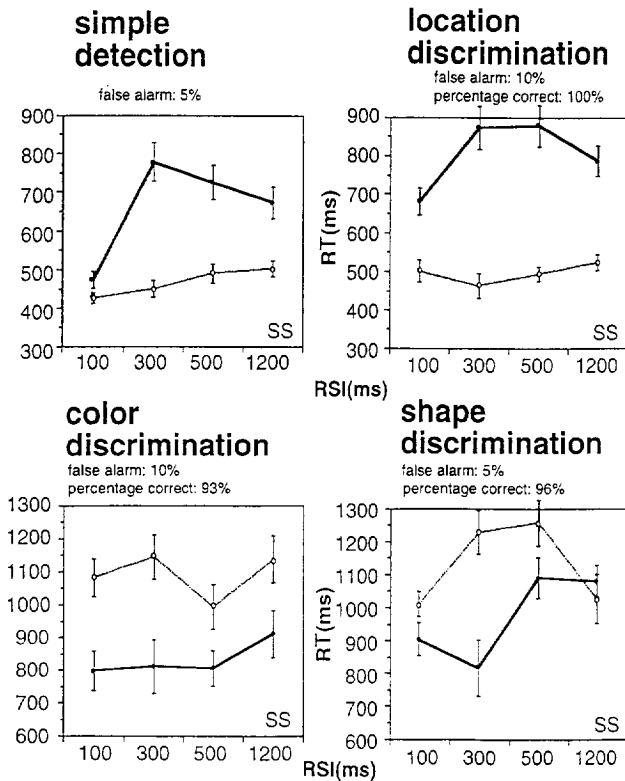percentage correct: 96%

RSI(ms)

FIGURE 12. Results of the color-based popout experiment. RT is plotted as a function of RSI. The results in four different tasks are shown separately in separate panels. Thick curve, same location; and thin curve, different location. Vertical bars indicate standard errors.

Procedure

The target (diamond) is defined by a color which is different from that of distractors (Maljkovic & Nakayama, 1994). Each diamond was chopped off at either the top or the bottom. The size of the target/distractor was 0.75 × 0.60 deg (see Fig. 11). The size of the fixation point was 0.1 × 0.1 deg. The distance between the target and fixation point was 5.20 deg. The luminance of the target/distractor item was 5.18 cd/m^2 when it was red and 12.6 cd/m^2 when it was green [hue: R(0.555, 0.344), G(0.320, 0.555)]. The luminance of the background was 0.01 cd/m^2.

The location of the target was randomized across trials between top-left and top-right of the fixation point. The locations of the distractors and the color of the target were also randomized (red/green) across trials. The number of distractors was fixed at 15. There were catch trials (20% of the overall trials) where red and green items were mixed and presented at random locations. In this case, no target popped out and the subject should not respond. This was just to make sure that the subject really responded to the popout stimulus, rather than to a local feature. The viewing distance was 114 cm.

Tasks were similar to those in experiment 1; simple detection, location discrimination (left or right), color discrimination (red or green) and shape discrimination (the top or the bottom of the target chopped off). In discrimination tasks, the subject made a 2AFC judgment.

In the case of shape discrimination, the subject had to judge whether the top or the bottom corner of the diamond-shaped target was chopped off. The total number of trials was 380 in each session.

The data were again analyzed in terms of the positional relationship between the previous and the present trial (same/different). RTs in error trials were eliminated from the data analysis. RTs below 100 msec and above 1300 msec were omitted the analysis. Sessions where the error rate for discrimination exceeded 10% were also eliminated. The subject's head was stabilized by a chin rest.

Results

The results for each subject are shown in Fig. 12. Once again, we found the IOR in the simple detection and the location discrimination tasks, whereas the FOR in the color and the shape discrimination tasks in all subjects.

The difference between the results of this experiment and the results of experiment 1 was the amount of IOR and FOR. Surprisingly, the magnitude of both IOR and FOR (difference of RT at the same and different location) were exaggerated, even when the elevation of overall RTs were taken into account. They were roughly 15–20% of the mean RT in experiment 1, whereas they were 30–50% in this experiment, depending on the subjects.

The data obtained from the four subjects were combined for the statistical analysis. They were analyzed with a four-way repeated measures ANOVA (RSI × location × color × shape) in each subexperiment. The results are summarized in Table 5. As indicated in Table 5, only the main effect of location was significant. The rest of the main effects and the interactions were not significant in experiment 4.1 (detection). This was also true for experiment 4.2 (location discrimination). The main effects of location, shape, and RSI were significant, and the interactions between location × shape, loca-

TABLE 5. ANOVA results of experiments 4.1–4.4

	F Value	Pr > F
ANOVA results of experiment 4.1		
Location	6.24	0.01236*
ANOVA results of experiment 4.2		
Location	6.13	0.0115*
ANOVA results of experiment 4.3		
Location	8.27	0.0042**
Shape	5.78	0.0166*
RSI	9.52	0.0022**
Location × Shape	6.23	0.0129*
Location × RSI	8.91	0.0030**
Color × Shape	4.87	0.0278*
Color × RSI	5.12	0.0241*
Shape × RSI	6.09	0.0140*
Location × Shape × RSI	5.89	0.0156*
Color × Shape × RSI	4.83	0.0285*
ANOVA results of experiment 4.4		
Location	6.25	0.0134*

Only the main effects which have turned out to be significant are listed here. Statistical significance at 5% level is indicated by *, and that at 1% level is indicated by **.
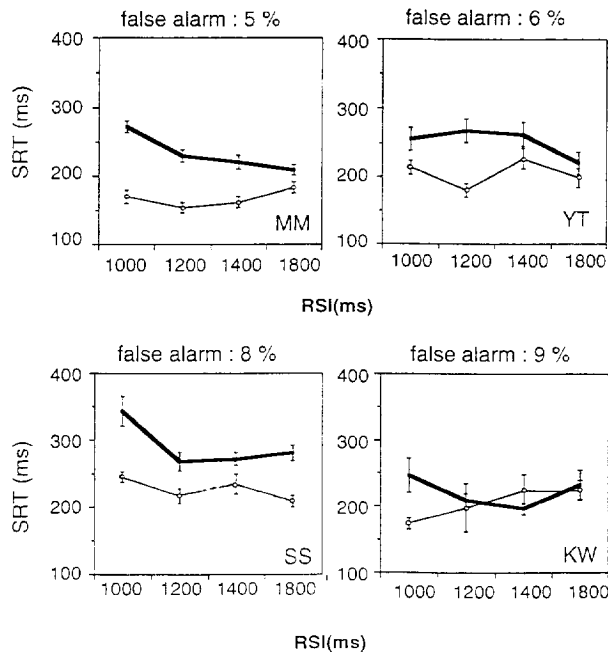
FIGURE 13. Results of the saccadic eye-movement experiment with a single target experiment. SRT is plotted as a function of RSI. The data obtained from four subjects are plotted in each panel. Thick curve, same location; thin curve, different location. Vertical bars indicate standard errors.

tion × RSI, color × shape, color × RSI, shape × RSI, location × shape × RSI, and color × shape × RSI were all significant in experiment 4.3 (color discrimination). Only the main effect of location was significant, and the rest of the main effects and all the interactions were not significant in experiment 4.4 (shape discrimination).

Discussion

The results were consistent with our hypothesis that the task difference leads to different patterns of result (IOR and FOR). Moreover, there was a surprising tendency for both the IOR and the FOR to be larger than in the simple condition. We have obtained basically the same patterns of result in another type of popout display where the target was defined by orientation of the bar stimulus, that is, the target was horizontal when the distractors were vertical, and vice versa (Tanaka & Shimojo, 1994). These results reject the hypothesis that the mechanism underlying the IOR involves only the sub-cortical process. Rather, it indicates the availability of output from the global texture analysis for the IOR mechanism, suggesting significant involvement of cortical areas such as V1 and V2 (Sagi & Julesz, 1985; Lamme, 1994). This might be related to the activation of V1 neurons by the texture segregation stimuli in the extra-receptive field (Lamme, 1994; Zipser et al., 1994).

Another aspect of the results worth noting was that color-related interactions turned out to be mostly significant. This may be related to the cumulative memory effects based on color repetitions in the popout

display, which has been reported by Maljkovic and Nakayama (1994).

So far we have only used the button pushing as a response. There still is the question about the nature of the response. Could the findings about IOR be generalized to other motor responses? There is some indication that the IOR is generated in the visual motor process of the saccadic programming (Rafal et al., 1989). Weiskranz et al. (1974) also found the "blind sight" in visual motor tasks such as a saccadic eye movement and pointing tasks. To investigate the robustness and generality of IOR, we employed more typical tasks of visually-guided orientation, saccadic eye-movement task (experiment 5.1) and arm-reaching task (experiment 5.2). We expected that these motor tasks would also lead to IOR.

EXPERIMENT 5: SACCADIC EYE-MOVEMENT TASK AND ARM-REACHING TASK

Subjects

Four subjects [two naive (MM, KS) and two non-naive (authors)] participated in experiment 5.1 and four subjects [two naive (MIT students) and two non-naive(authors)] participated in experiment 5.2. Naive subjects did not know the purpose of the experiment.

Procedure

In the saccadic eye-movement task (experiment 5.1), we employed both the single target version (experiment 5.1.1) and the popout display version (experiment 5.1.2). The configuration of target and fixation point were identical to experiment 1 (experiment 5.1.1, experiment 5.2) or to experiment 4 (experiment 5.1.2). The target's location, color, and shape were again randomized across trials. In the popout display, the location of distractors were also randomized (experiment 5.1) and the RSI was also randomized among 1000/1200/1400/1800 msec (experiment 5.1) or 100/300/500/1200 msec (experiment 5.2).

The task was to move the eyes to the target (experiment 5.1), or to move the cursor and press the button (experiment 5.2; see Fig. 14) as quickly as possible. The target's color, orientation or shape should be neglected. In experiment 5.1, saccade reaction time (SRT) was measured as the time from the target's onset to the initiation of the eye movement. Ober 2 (Permobil Inc.) was used to measure SRT. Its temporal resolution was 120 Hz and the spatial resolution was at, or better than 0.31 deg. In experiment 5.2, the performance time (PT; the time from the onset of the target to the moment of button pressing) were measured. SRTs below 50 msec and above 1000 msec were eliminated from the analysis. PTs below 100 msec and above 2500 msec were also eliminated from the analysis. In these eliminated trials, a feedback visual signal, "too fast" or "too slow" was presented. The subject's head was stabilized by a chin rest.

Results

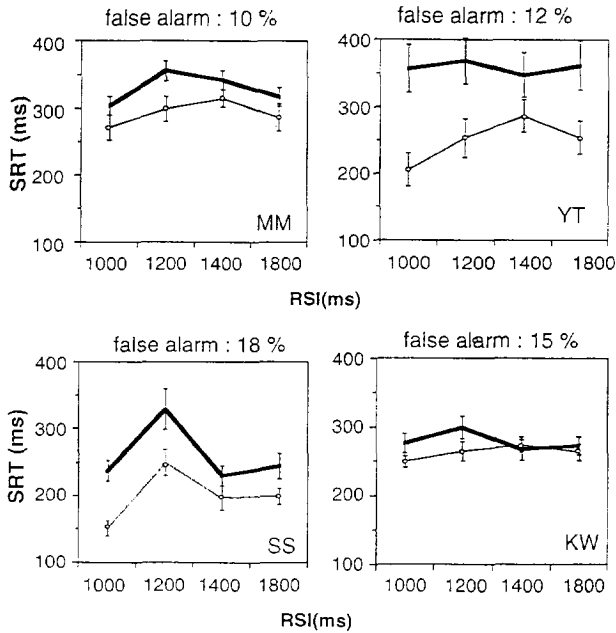In experiment 5.1, the results indicated a strong IOR

FIGURE 14. Results of the saccadic eye-movement experiment with a popout display. SRT is plotted as a function of RSI. The data obtained from four subjects are plotted in each panel. Thick curve, same location; thin curve, different location. Vertical bars indicate standard errors.

across all RSIs in both the single target (Fig. 13) and the popout display (Fig. 14) of all the subjects except at 1400 msec RSI in KW. In experiment 5.2, the results also indicated a clear IOR: the PT at the same location as in the previous trial was longer than that at a different location (see Fig. 15). The data obtained from the subjects were combined for the statistical analysis in experiment 5.2. Then the data in both experiments 5.1 and 5.2 were analyzed with a four-way repeated measures ANOVA (RSI × location × color × shape) in each subexperiment. The results are summarized in Table 6. The main effects of location and RSI were significant in experiment 5.1.1 (single target, detection). The main effects of location and RSI were significant in experiment 5.1.2 (popout, detection). The main effects of location and shape, the interaction between color × shape were significant in experiment 5.2 (single target, reaching).

TABLE 6. ANOVA results of experiments 5.1.1, 5.1.2 and 5.2

	F Value	Pr > F
ANOVA results of experiment 5.1.1		
Location	48.027	0.000001**
RSI	6.083	0.0005**
ANOVA results of experiment 5.1.2		
Location	28.316	0.00001**
RSI	7.128	0.0001**
ANOVA results of experiment 5.2		
Location	5.03	0.0253*
Shape	99.69	0.0001**
Color × Shape	15.47	0.0001**

Only the main effect and interactions which have turned out to be significant are listed. Statistical significance at 5% level is indicated by *, and that at 1% level is indicated by **.
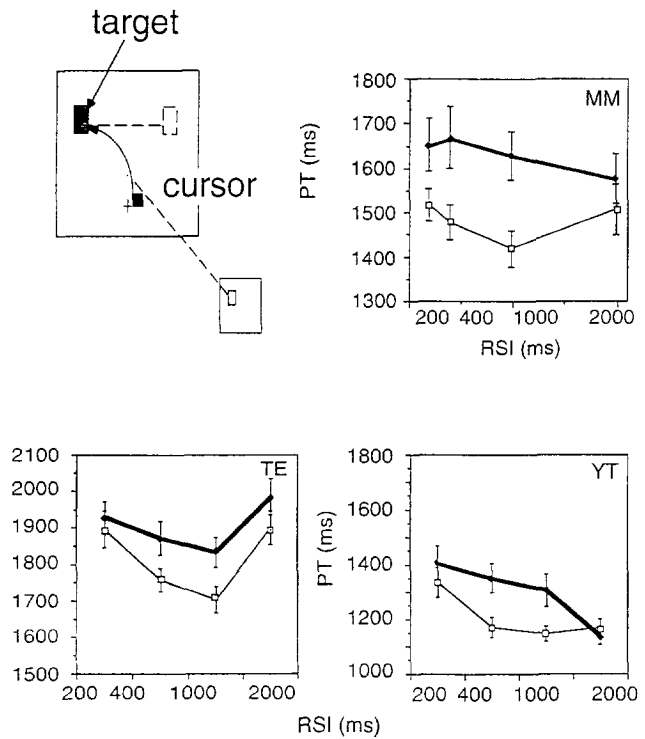

FIGURE 15. Stimulus configuration (top-left) and results of the arm-reaching experiment. RT is plotted as a function of RSI. The data obtained from three subjects are plotted separately in separate panels. Thick curve, same location; thin curve, different location. Vertical bars indicate standard errors.

Discussion

The IOR was generalized to different types of visual stimuli (experiment 5.1). It was also generalized to both the saccadic eye-movement and the arm-reaching tasks. This suggests that IOR reflects a common process among spatial orienting tasks (Posner, 1980; Rafal et al., 1989). More specifically, it indicates the general mechanism of spatial attention which is common both in visual and motor processes. In this regard, it is interesting to note that the amount of IOR was exaggerated especially when RSI was 400 and 1000 msec compared to the location discrimination task in experiment 1. This suggests that the attentional modulation is not only in the initial visual stage, but all through the following stages relevant to the motor performance.

In experiment 5.1 (saccadic eye-movement task), the overall levels of SRTs were somewhat slower than in the previous studies (Fischer & Ramsperger, 1984), presumably because of the randomization of location and the presence of catch trials.

GENERAL DISCUSSION

To summarize, the results all together indicate a clear dissociation between two types of visual task. One is the spatial orientation task which requires information about the presence and global location of the target. The simple detection, location discrimination, saccadic eye-movements, the arm-reaching tasks are examples. In such tasks IOR is commonly observed. The other is the feature

analysis task which requires information about fine features of objects. The color/luminance discrimination, shape/orientation discrimination, vernier/size discrimination tasks are the examples. In such tasks FOR is commonly observed (see Table 7).

Our results are consistent with the well-known neurophysiological distinction between two visual pathways, the ventral-parietal and the dorsal-temporal pathways. They have been characterized as "where" vs "what " by Schneider (1969) in the rat, by Ungerleider and Mishkin (1982) in the primate, by Weiskranz et al. (1974) and Duncan (1993) in the human, or as "action" vs "recognition" by Goodale and Milner (1992) in human brain-damaged cases (see Fig. 16). Location related global tasks are thought to be processed through V1 to the A7 (parietal) or through SC via pulvinar to A7 (Weiskranz et al., 1974). Thinking together with the result of popout display, SC and V1 or V2 could be the candidates for the neural correlate of the IOR. On the other hand, features such as color, orientation, luminance, and vernier offset could be processed in the pathway through V1 via V2 or V4 to IT (Livingstone & Hubel, 1988). What we found are clear psychophysical correlates in RT to these neurophysiological dissociation.

Moreover, we eliminated the nature of the task (detection/discrimination) and the difference of motor response (button pressing, saccadic eye-movement, and arm-reaching) as a decisive factor for IOR. In contrast, we identified types of information which the task demands (global location/fine characteristics of objects) as a more specific condition to generate IOR or FOR.

The results in experiment 3 indicate that the IOR and the FOR have not only the opposite polarity but also different spatio-temporal characteristics. This suggests that transient mechanisms of attention are closely related to the IOR, whereas its sustained mechanisms are closely related to the FOR. These two components of attention have been argued to be different (Nakayama & Mackeben, 1989; Hikosaka et al., 1993).

It is important to note that IOR was observed even in the popout display of experiment 4. As we suggested before, this may indicate some involvement of early cortical processes in the mechanism underlying the IOR.

The FOR which was found in the popout experiment may be related to visual learning (Karni & Sagi, 1991, 1993; Maljkovic & Nakayama, 1994; Poggio et al., 1992, McKee & Westheimer, 1978; Ramachandran & Braddick, 1973). It has been claimed that some type of
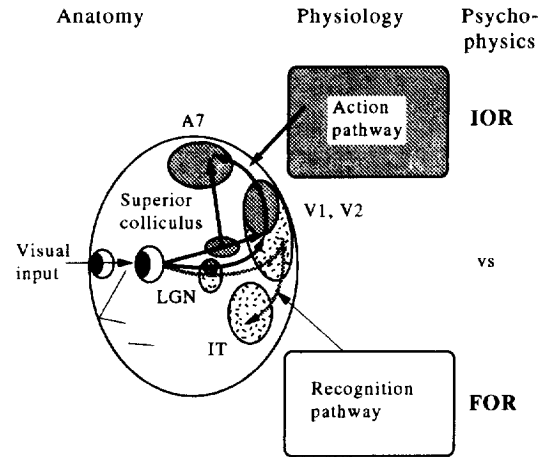

FIGURE 16. Schematized diagram for distinct visual pathways and functions. "where" vs "what" or "action" vs "recognition" dichotomy in the neural pathways are neatly corresponding to the psychophysical distinction between IOR and FOR.

perceptual learning is in an earlier stage (Karni & Sagi, 1991; Ramachandran & Braddick, 1973), modular specific (Poggio et al., 1992), retinotopically location-specific (Karni & Sagi, 1991) and temporally specific (McKee & Westheimer, 1978; Poggio et al., 1992). Both the FOR in the present study and their findings indicate that repeated presentations of objects at the same location lead to facilitation, though the time spans are somewhat different in their and our cases (Maljkovic & Nakayama, 1994; Tanaka & Shimojo, 1993). It would be interesting to examine cumulative, facilitatory/inhibitory effects more systematically in terms of repetition in location and/or attributes (color, shape and size) and tasks (location related tasks and feature related tasks). Preliminarily, we found the comulative facilitation effect corresponding to the FOR (Tanaka & Shimojo, 1995; Shimojo et al., 1996).

We would like to consider a possible account of IOR/ FOR by masking. One might argue that a masking could affect RT to the target (Coenen & Eijkman, 1972; Pease & Sticht, 1965; Breitmeyer et al., 1981; Breitmeyer, 1984). Suppose, for instance, that the masking effect from the previous target has more influence on detection than on a local discrimination of the following target at the same location. In this case, presumably, the detection threshold of the following target would be higher than the

TABLE 7. Summary of results in all the experiments

IOR	Simple detection (popout)	Location discrim. (popout)	Saccadic eye-movement (popout)	Arm reaching		Orienting tasks
FOR	Color discrim. (popout)	Orientation discrim. (popout)	Luminace discrim.	Size discrim.	Vernier discrim.	Feature tasks

IOR occurred in orienting tasks (simple detection, location discrimination, saccadic eye-movement, and arm-reaching tasks) and FOR occurred in the feature tasks (color/luminance discrimination and vernier/size discrimination tasks). "popout" indicates that the effect was observed in the popout display as well as the single target display.

discrimination threshold, which could lead to a relative inhibition of RT for the target detection at the same location. However, this masking account is unlikely in our experiments.The reason is because:

1. ISI (the interval between one target to the other, calculated by RT+RSI) was relatively long (around 400–1600 msec). The masking effects are very much attenuated in this range as compared to the shorter ISI (Breitmeyer, 1984; Foley & Boynton, 1993).
2. The duration of the stimulus was relatively longer as well (around 400 msec in simple detection), which also attenuates the forward masking effect (Foley & Boynton, 1993).
3. The range of ISI and duration also seems too long to obtain the Troxler effect (Breitmeyer et al., 1980).
4. In another experiment, we employed the detection task in which target duration is much shorter (17 msec) (subjects YT and SS). In this case, a relatively stronger masking effect would be expected, which could cause stronger IOR (Foley & Boynton, 1993).

The result showed the absolute magnitude of inhibition in terms of RT was not significantly different (50–100 msec) from the previous experiments, suggesting IOR is independent of forward masking effect. These also hold for the local feature discrimination task. Thus, it is unlikely that the results are explained by the masking effect alone.

Finally, does the dissociation that we discovered have any value from a biological or ecological viewpoint? We think it does. Let us accept the assumption, for the time being, that there are indeed two functional pathways. The "where" or "action" pathway is allegedly for orienting to a new stimulus or event in the visual field. Its main purpose is to prepare for an unexpected and unpredictable event somewhere other than the currently attended object, and to respond to it as quickly as possible. Thus, it would make sense if this pathway increases sensitivity at new locations while sacrificing sensitivity at the same location. On the other hand, the "what" or "recognition" pathway is allegedly for identifying finer details of the concerned object. Its main purpose is to do feature analysis as much and as deeply as possible for the currently attended object. Thus, it would make biological sense if it increases efficiency at the same location while sacrificing it at different locations. The former may correspond to the mechanism for the transient attention shift, i.e. the disengagement/engagement of attention (Posner et al., 1984; Fischer & Breitmeyer, 1987), while the latter presumably has more sustained characteristics (Hikosaka et al., 1993). This expectation is consistent with our data in that RTs were in general faster when IOR was observed, while RTs were in general slower when FOR was observed.

It is as yet unclear at what stage IOR and FOR occur. Do they occur at the sensory (Hikosaka et al., 1993), or the visual-motor stage (Rafal et al., 1989)? It is also unknown whether the retinotopic or object-bound locations (Tipper & Bruce, 1991; Gibson & Egeth, 1994; Tipper et al., 1994) are critical for these effects. Further research is necessary to resolve these issues.

REFERENCES

Broadbent, D. E. (1958). Perception and communication. Boston, Pergamon Press.

Breitmeyer, B. G. (1984). Visual masking: An integrative approach. New York, Oxford University Press.

Breitmeyer, B. G. Levi, D. M. & Harwerth, R. S. (1981). Flicker-masking in spatial vision. Vision Research, 21, 1377–1385.

Breitmeyer, B. G. Valberg, A. Kurtenbach, W. & Neumeyer, C. (1980). The lateral effect of oscillation of peripheral luminance gratings on the foveal increment threshold. Vision Research, 20, 799–805.

Coenen, A. M. L. & Eijkman, E. H. J. (1972). Cat optic tract and geniculate init responses corresponding to human visual masking effects. Experimental Brain Research, 15, 441–451.

Duncan, J. (1993). Coordination of what and where in visual attention. Perception, 22, 1261–1270.

Fischer, B. & Breitmeyer, B. G. (1987). Mechanisms of visual attention revealed by saccadic eye movements. Neuropsychologia, 25, 73–83.

Fischer, B. & Ramsperger, E. (1984). Human express saccades: Extremely short reaction times of goal directed eye movements. Experimental Brain Research, 57, 191–195.

Foley, J. M. & Boynton, G. M. (1993). Forward pattern masking and adaptation: Effects of duration, interstimulus interval, contrast, and spatial and temporal frequency. Vision Research, 33, 959–980.

Gibson, B. & Egeth, H. (1994). Inhibition of return to object-based and environment-based locations. Perception and Psychophysics, 55, 323–339.

Goodale, M. A. & Milner, A. D. (1992). Separate visual pathways for perception and action. Trends in Neuroscience, 15, 20–25.

Helmholtz, H. (1910). Hundbuch der Physiologischen Optik Verlag, Hamburg.

Hikosaka, O. Miyauchi, S. & Shimojo, S. (1993). Focal visual attention produces illusory temporal order and motion sensation. Vision Research, 33, 1219–1240.

Hikosaka, O. & Wurtz, R. H. (1983). Effects on eye movements of a GABA agonist and antagonist injected into monkey superior colliculus. Brain Research, 272, 368–372.

James, W.(1890). The principles of psychology. Dover Publications Inc. New York.

Kahneman, D. & Treisman, A. M. (1984). Changing views of attention and automaticity. In Parasuraman R. and Davis D. R., (Eds) Varieties of Attention. New York: Academic Press.

Karni, A. & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. Proceedings of the National Academy of Science, 88, 4966–4970.

Karni, A. & Sagi, D. (1993). The time course of learning a visual skill. Nature, 365, 250–252.

Kwak, H. W. & Egeth, H. (1992). Consequences of allocating attention to locations and to other attributes. Perception and Psychophysics, 51, 455–464.

Lamme, V. (1994). Neural correlates of figure–ground segregation in primary visual cortex. Investigative Ophthalmology and Visual Science (Supplement), 35, 1489.

Livingstone, M. & Hubel, D. (1988). Segregation of form, color, movement and depth: Anatomy physiology and perception. Science, 240, 740–749.

Maljkovic, V. & Nakayama, K. (1994). Priming of popout: I role of features. Memory and Cognition, 226, 657–672.

Maylor, E. (1985). Facilitatory and inhibitory components of orienting in visual space. Attention and Performance, 11, 189–194.

McKee, S. P. & Westheimer, G. (1978). Improvement in vernier acuity with practice. Perception and Psychophysics, 24, 258–262.

Nakayama, K. & Mackeben, M. (1989). Sustained and transient

components of focal visual attention. *Vision Research, 29,* 1631–1647.

Pease, V. P. & Sticht, T. G. (1965). Reaction time as a function of onset and offest stimulation of the fovea and periphery. *Perception & Motor Skills, 20,* 549–554.

Poggio, T. Fahle, M. & Edelman, S. (1992). Fast perceptual learning in visual hyperacuity. *Science, 256,* 1018–1021.

Posner, M.I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology, 32,* 3–25.

Posner, M. I. & Cohen, Y. (1984). Components of visual orienting. *Attention and Performance, 10,* 531–556.

Posner, M. I. Walker, J. A. Frienfrich, F. J. & Rafal, R. D. (1984). Effects of parietal injury on covert orienting of attention. *Journal of Neuroscience, 4,* 1863–1874.

Rafal, R. D. Calabresi, P. A. & Scioltio, T. K. (1989). Saccade preparation inhibits reorienting to recently attended locations. *Journal of Experimental Psychology: Human Perception and Performance, 15,* 673–685.

Ramachandran, V. S. & Braddick, O. (1973). Orientation-specific learning in stereopsis. *Perception, 2,* 371–376.

Remington, R. & Pierce, L. (1984). Moving attention: Evidence for time-invariant shifts of visual selective attention. *Perception and Psychophysics, 35,* 393–399.

Sagi, D. & Julesz, B. (1985). " Where" and "what" in vision. *Science, 228,* 1217–1219.

Schiller, P. H. Sandall, J. H. & Maunsell, J. H. R. (1984). The effect of superior colliculus and frontal eye field lesions on saccadic latency in the monkey. *Neuroscience Abstract, 10,* 60.

Schneider, G. E. (1969). Two visual systems. *Science, 164,* 895–902.

Shimojo, S. Tanaka, Y. Hikosaka, O. & Miyauchi, O. (1996). Vision, attention, and action—inhibition and facilitation in sensory-motor links revealed by the reaction time and the line motion. *Attention and Performance, 16,* in press.

Tanaka, Y. & Shimojo, S. (1993). Location priming and probability priming are isolatable in detection and discrimination. *Investigative Ophthalmology and Visual Science (Supplement), 34,* 1234.

Tanaka, Y. & Shimojo, S. (1994). Location vs. feature: Two visual functions separated by reaction time in the popout display. *Investigative Ophthalmology and Visual Science (Supplement), 35,* 1619.

Tanaka, Y. & Shimojo, S. (1995). Facilitation induced by color- and shape repetition but not by location-repetition. *Investigative Opthalmology and Visual Science (Supplement), 36,* 902.

Tassinai, G. Aglioti, L. Chelatti, A. Peru, A. & Belucchi, G. (1994). Do peripheral non-informative cues induce early facilitation of target detection? *Vision Research, 34,* 179–189.

Terry, K. M. Valdes, L. A. & Neill, T. (1994). Does "inhibition of return" occur in discrimination tasks? *Perception and Psychophysics, 55,* 279–286.

Tipper, J. D. & Bruce, W. (1991). Short report: Object-centered inhibition of return of visual attention. *Quarterly Journal of Experimental Psychology, 43A,* 289–298.

Tipper, S.P. Weaver, B. Jerreat, L.M. & Burak, A.L. (1994). Object- and environment-based inhibition of return of visual attention. *Journal of Experimental Psychology: Human Perception and Performance, 20,* 478–499.

Treisman, A. & Galade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12,* 97–136.

Ungerleider, L. G. Mishkin, M., Ingle, D. J. G. & Mansfield, J. W. (1982). *Analysis of visual behavior,* (pp. 549–586) MIT Press Cambridge, MA.

Weiskranz, L. Warrington, E. E., Sanders, M. D. & Marshall, J. (1974). Visual capacity in the hemianomic field following a restricted occipital ablation. *Brain, 97,* 704–728.

Zipser, K. Lee, T. S. Lamme, V. A. F. & Schiller, P. H. (1994). Invariance of figure–ground segregation in V1 for depth, orientation, luminance, and chrominance cues. *Investigative Ophthalmology and Visual Science (Supplement), 35,* 1973.

APPENDIX

One could possibly argue that a part of the results might be explained by the so-called "stimulus–response (S-R) compatibility". To examine this as a possibility, we have to consider at least three aspects:

1. the locations of the stimuli (left/right);
2. the task (either location-correlated or not); and
3. the response (either location-correlated or not).

For a direct test, we need to manipulate the relationship among these dimensions. It would be interesting to try different kinds of response measurements, such as pressing buttons which align perpendicular to the stimuli, or a voice key. Yet, it seems already unlikely that the results could be explained by the S-R compatibility, for reasons which we list below.

1. Among the detection, location discrimination (button-pressing) and saccade tasks, there was a significant difference between the first one and the other two in terms of stimulus–response correlation. The target location was irrelevant (because there was only one kind of response allowed) in the detection task, whereas it is 100% correlated with correct responses in the latter two. Yet, we obtained the same type of IOR, which would be difficult to explain from the viewpoint of S–R compatibility.
2. More simply, the fact of IOR itself would not be expected from the S–R compatibility. The reason is that from this viewpoint, why should one expect the RT to be faster when there was always a simple detection and a single response required, or when there was 1.0 correlation between the target location and the correct response?
3. It is certainly true that the subject had to neglect the target location in order to respond correctly only in the discrimination tasks where we found the FOR. (This was not true at all in the tasks where we found the IOR, because the subject was allowed just a single response in the detection task, and he/she had to respond accordingly to the target location in the location discrimination and the saccade tasks.) However, the locations of the target and of the correct response button were compatible with 0.5 chance, at both the same and the opposite location. Thus, there was no particular reason to expect that the RT was faster at the same location. The situation would be the same even when the S–R compatibility is analyzed in terms of being the same or different relative to the stimulus and the response in the previous trial.