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"Sensory and Attentional Components of Slowing of Manual Reaction Time to Non-Fixated Visual Targets by Ipsilateral Primes"

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Sensory and Attentional Components of Slowing of Manual Reaction Time to Non-Fixated Visual Targets by Ipsilateral Primes

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Reaction time (RT) for detecting extrafoveal targets is lengthened by a non-informative prime at the same location or in the same hemifield (RT inhibition). We assumed that sensory effects at primed locations should be the same for unilateral and bilateral primes, whereas systematic covert orienting to a primed location should occur only with unilateral primes. We found equal RT inhibition for both types of primes at 0.2 sec prime-target intervals (SOA), as contrasted with inhibition for unilateral but not bilateral primes at 0.6 sec SOAs. We conclude that RT inhibition involves a succession of sensory components and orienting-dependent components.

Reaction time Inhibition Covert orienting Forward masking Priming

INTRODUCTION

In classical visual psychophysics, the effects of a light flash on the response to a subsequent flash have traditionally been related to sensory processes subsumed under such headings as dark and light adaptation (e.g. Frumkes, 1990) or metacontrast and masking (e.g. Breitmeyer, 1984). In classical experimental psychology two-flash experimental paradigms have been employed for documenting the phenomenon of the psychological refractory period and for advocating the concept of a single channel for central information processing (e.g. Welford, 1980). More recently, similar paradigms have provided evidence that has a significant bearing on mechanisms of spatially selective visual attention. Consider a task that requires the emission of fast manual responses to an extrafoveal "target" flash preceded by a "cue" or "prime" flash at the same location, or at a symmetrical location in the contralateral visual hemifield. If target location is reliably predicted by a cue occurring at the same location, response speed to targets in the cued location is enhanced relative to targets in the uncued location. This effect is engendered in the cue-target interval by a deliberate spatial allocation of attention which may consist either in an overt turning of the eyes to the cued location, or in a covert orienting toward the same location unaccompanied by ocular movements (Posner, 1986). But even when cue location is by no means predictive of target location—a condition in which the term prime is preferable to cue—the speed of reactions to the target is modulated by the prime in a fashion that is again at least partly amenable to attentional explanations. When the eyes do not change fixation, the foremost effect of a non-informative prime at an extrafoveal location is a marked increase of simple manual reaction time (RT) to targets at the primed location, as well as at other locations within the same visual hemifield, over RT to targets in the opposite hemifield (Berlucchi, Di Stefano, Morelli, Marzi & Tassinari, 1981; Posner & Cohen, 1984; Maylor, 1985; Maylor & Hockey, 1985; Possamai, 1986; Tassinari, Aglioti, Chelazzi, Marzi & Berlucchi, 1987; Berlucchi, Tassinari, Marzi & Di Stefano, 1989; Tassinari, Biscaldi, Marzi & Berlucchi, 1989). It has been claimed that this RT increase may be preceded by a very short-lasting RT shortening (Posner & Cohen, 1984), but such a diphasic pattern is not a constantly and easily detectable phenomenon (Lambert & Hockey, 1991; Tassinari, Aglioti, Chelazzi, Peru & Berlucchi, 1993). In this paper we shall restrict ourselves to consideration of the conspicuous, spatially selective RT lengthening action of non-informative extrafoveal primes, which for brevity's sake will be called RT inhibition.

The interpretations of RT inhibition that have been proposed differ on many counts, but all agree on the notion that it can be related directly or indirectly to mechanisms of attention. Posner and Cohen (1984) attributed RT inhibition, which they call "inhibition of return", to an intrinsic tendency of the visual system to eschew a prolonged processing of information from the same spatial location. In their view RT inhibition is essentially a sensory phenomenon, perhaps akin to forward masking, which is bound to occur regardless of whether or not there has been an overt or covert orientation to the prime, and which biases the scanning of the visual field toward the sampling of locations avoided by

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recent stimulation. This automatic bias can of course be overcome by deliberately directing and holding attention at the inhibited location. On the other hand, Maylor (1985), Tassinari *et al.* (1987) and Berlucchi *et al.* (1989) maintain that the phenomenon of RT inhibition is preceded and in fact caused by attentional reactions. According to Maylor (1985) covert orienting to the prime temporarily pre-empts reorienting to the primed location, thus interfering with reactions to events occurring at that location over the inhibition period. Tassinari *et al.* (1987) and Berlucchi *et al.* (1989) also assume the occurrence of covert orienting to the prime, but posit that RT inhibition is the toll to be paid for dissociating such covert orienting from the normal overt attentional reaction, i.e. the turning of the eyes toward the same location. The directional imbalance associated with this veto would bias the entire motor system against emitting reactions in the general direction of the prime.

The use of bilateral priming may help decide whether RT inhibition is essentially sensory or attentional in nature. While sensory effects at primed locations are liable to be identical independent of whether priming is unilateral or bilateral, it seems obvious that the attentional mechanisms engaged in the two conditions must differ. A single salient stimulus presented at an extrafoveal location is a powerful determinant of an orienting reaction, either overt or covert, toward that location. The situation is different when two identical stimuli are presented simultaneously at mirror symmetrical locations on either side of fixation, since in this case the available evidence indicates that in the absence of eye movements attention is either maintained at fixation (Posner, Snyder & Davidson, 1980) or perhaps allocated in parallel to the two stimulus locations (Castiello & Umiltà, 1992). Thus it is reasonable to assume that whatever the effect of simultaneous bilateral primes on RT to subsequent unilateral targets, this cannot be accounted for by a selective covert orienting to one of the primed locations. It follows that if RT inhibition originates from an orienting-independent sensory process, unilateral and bilateral primes should produce the same RT inhibition; if on the contrary RT inhibition depends on covert lateral orienting, it must occur with unilateral but not bilateral primes.

Based on these expectations, two previous studies have attempted to distinguish between sensory and attentional bases of RT inhibition by comparing RT effects of unilateral and bilateral primes. The evidence afforded by these studies is controversial. Posner and Cohen (1984) reported comparable effects of RT inhibition from unilateral and bilateral primes, in keeping with a sensorial account of RT inhibition. At variance with their findings, Maylor (1985) found that RT inhibition was strongly reduced by changing from unilateral to bilateral priming, supporting the hypothesis of the dependence of inhibition on covert orienting. The present paper describes three experiments which by providing novel information on RT effects of unilateral and bilateral primes lend themselves to resolving the above controversy.

EXPERIMENT 1

The two above-mentioned studies (Posner & Cohen, 1984; Maylor, 1985) employed different intervals [or stimulus-onset-asynchronies (SOAs)] between primes and targets. Posner and Cohen (1984) found that RT inhibition at primed locations was as strong after bilateral as after unilateral priming at a prime-target SOA of 0.5 sec. On the contrary, at SOAs of 0.7, 0.9 and 1.3 sec Maylor (1985) consistently observed that RT inhibition was significantly less for targets following bilateral primes than for targets at unilaterally primed locations, although RT was still somewhat longer after bilateral primes than at locations contralateral to a single prime. The apparent contradiction between Posner and Cohen (1984) and Maylor (1985) might vanish if it turns out that the relationships between the effects of unilateral and bilateral primes vary with prime-target SOA, such that RT inhibition is elicited by both unilateral and bilateral primes at relatively short SOAs, but only by unilateral primes at longer SOAs.

In Expt 1 we tested this possibility by comparing the effects of unilateral and bilateral priming on manual RT to unilateral targets at a relatively short prime-target SOA of 0.2 sec and a relatively long SOA of 0.6 sec. Our previous studies (Tassinari *et al.*, 1987, 1989; Berlucchi *et al.*, 1989) showed consistent RT inhibition effects at these SOAs. According to Posner and Cohen (1984) there should be no difference between the effects of unilateral and bilateral priming at the first SOA, whereas the results of Maylor (1985) lead to the prediction that there should be less inhibition from bilateral than unilateral priming at the second SOA. In addition we also measured, at the same prime-target SOAs, manual RT to bilateral targets following unilateral primes. Chloessy, Posner, Rothbart and Vecera (1991) found that eye movement responses to simultaneous bilateral targets preceded by a unilateral prime were biased in the direction of the unprimed location, suggesting that on bilateral target presentation the input from the primed location was less effective in eliciting oculomotor output than the input from the unprimed location. If manual RT to bilateral targets following unilateral primes is also preferentially controlled by the target in the unprimed location, it should be shorter than RT to targets in unilaterally primed locations, and as short as RT to unilateral targets opposite unilateral primes.

Methods

Subjects. Eight students and two staff members of the University of Verona served as subjects. Five were males and five females, and their ages ranged between 21 and 30 yr. All were right handed and had normal or corrected-to-normal vision. They were experienced with RT tasks but uninformed about the purpose of the experiment.

Apparatus and stimuli. Visual stimuli were delivered by two light-emitting diodes (LEDs, TIL 222) with round tips 0.5 cm in diameter, which were fastened one to the right and the other to the left of the midpoint of a

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horizontal arc perimeter. The radius of the perimeter was 57 cm and the linear distance between its midpoint and either LED was 10 cm. The LEDs were lighted by single 15 mA square pulses of current which produced flashes of light with a duration of 5 msec and a luminance of 70 cd/m^2. The luminance of the background, a white screen supporting the arc perimeter, was 0.15 cd/m^2. The response devices were two RT button-keys which were mounted on brass cylinders rigidly positioned in front and below the perimeter, one on the right and the other on the left. When pressed with a force of at least 60 g each key stopped an electronic millisecond counter. A headset driven by a pulse generator through an acoustic amplifier delivered a warning auditory signal, consisting in a 1000 Hz tone-pip having a duration of 0.1 sec and a suprathreshold but comfortable intensity.

Procedure. After placing his/her head in a chin-rest at the center of curvature of the perimeter, the subject viewed a white fixation mark on the midpoint of the perimeter and one LED in each visual hemifield. At the viewing distance of 57 cm the visual angle between the two LEDs was 20 deg, and that between the fixation mark and either LED was 10 deg. Each trial began with the warning auditory signal delivered through the headset, followed, after an interval randomly varying in a continuous manner from 1 to 3 sec, by the lighting of one LED or two LEDs simultaneously (single and double primes). After a SOA which could take one of two values, i.e. 0.2 or 0.6 sec, single primes were followed either by a single target, i.e. the lighting of only one LED, or by a double target, i.e. the simultaneous lighting of both LEDs. Double primes were always followed by single targets. The duration of primes and targets was 5 msec in all cases. Upon hearing the warning signal the subject looked at the fixation mark and maintained fixation until the end of the trial. Eye position was monitored through a TV camera. One of the subject's forearms was placed on a rigid support which allowed the hand to grasp the corresponding cylinder with the thumb resting on the button-key. The subject was to detect the single or double prime without making any overt response to it, and to press the button-key as fast as possible following the appearance of the target, either single or double, thus stopping the millisecond counter which had been started simultaneously with target onset. Each subject performed on five sessions, each of which consisted of 64 trials; with the exception of the double prime–double target combination, which was not allowed, each of all possible combinations between type of prime (single or double), type of target (single or double), position of single prime (right or left), position of single target (right or left) and the two SOAs was presented four times in each session. The different types of prime–target–SOA combinations and their repetitions were intermixed in a totally random fashion in each session. The first session was used for practice while the other four sessions provided the experimental data; each subject responded with the left hand on two of the experimental sessions and with the right hand on the other two sessions. The order of between-session hand alternations varied from subject to subject and was counterbalanced across subjects according to a Latin square design. The randomization of the different types of trials, the delivery of warning signal and visual stimuli, the control of the timing between warning signal, prime and target, and the measurement and recording of RTs were all performed with an all-purpose computer located in a room adjacent to the test room. The computer recorded but invalidated trials on which RTs were shorter than 150 msec or longer than 989 msec, or on which a key-pressing had occurred in response to the prime, and replaced each invalidated trial later in the sequence until obtaining an acceptable response. Trials on which eye fixation failed to be constantly maintained between the warning signal and the performance of the response were also discarded and replaced.

Data analysis. Statistical analysis of RT data was carried out according to a multifactor repeated-measurement design with subjects assumed to be a random-effect variable. Selected two-sample comparisons were performed by means of t-tests for paired data, using the Bonferroni correction for repeated contrasts (Myers, 1979).

Results

In no subject did the percentages of response errors and/or failures of fixation rise above 5%. Since the aborted trials were distributed randomly across different conditions, this aspect of the performance will not be dealt with further. For the main purpose of the study, the RTs of each subject were subdivided into four groups for each of the two SOAs: respectively, RT to single targets following single primes at the same point (same-point RT), RT to single targets following single primes at the opposite point (opposite-point RT), RT to single targets following double primes (double-prime RT), and RT to double targets following single primes (double-target RT). In each subject median RT was computed across hands and hemifields for each of the four prime-target combinations at each of the two SOAs. Thus each subject provided eight basic data which were entered into a two-way ANOVA with condition (four levels: same-point, opposite-point, double-prime and double-target) and SOA (two levels : 0.2 and 0.6 sec) as main factors.

Both main factors as well as their interaction proved highly significant [condition, $F(3, 27) = 51.67$; SOA, $F(1, 9) = 130.03$; condition/SOA interaction, $F(3, 27) = 6.32$; $P < 0.001$ in each case]. Same-point RT (289.3 msec) was significantly longer than all other RTs ($P < 0.01$ in all cases); double-prime RT (270.8 msec) was significantly longer than either opposite-point RT (252.4 msec, $P < 0.01$) or double-target RT (241.4 msec, $P < 0.01$), and opposite-point RT was significantly longer than double-target RT ($P < 0.01$). Overall RT dropped significantly from 302.5 msec at the 0.2 sec SOA to 224.5 msec at the 0.6 msec SOA ($P < 0.01$). The condition/SOA interaction is analyzed in Table 1 and illustrated in Fig. 1. The significance of the interaction is accounted for by the SOA-related slope of RT decrease being

TABLE 1. Experiment 1—differences between RTs of trials with different prime-target combinations

Differences (msec)	SOA (sec) 0.2	SOA (sec) 0.6
Same-point RT – opposite-point RT	**37.7** (9)	36.0 (10)
Same-point RT – double-prime RT	1.9 (6)	35.1 (8)
Double-prime – opposite-point RT	**35.8** (10)	0.9 (6)
Opposite-point RT – double-target RT	**16.3** (9)	5.7 (10)

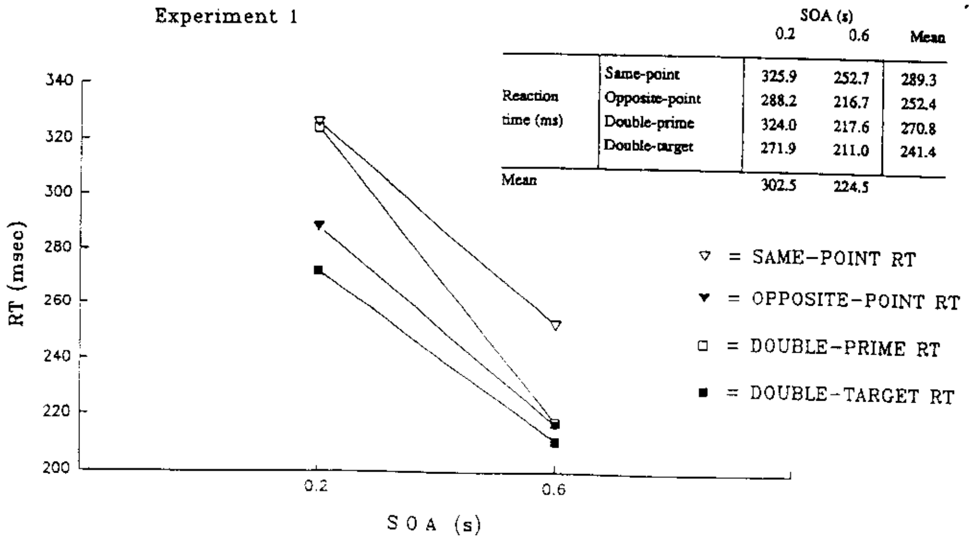
Bold underlined differences are significantly different from 0 at the $P < 0.01$ level; underlined differences in normal type are significantly different from 0 at the $P < 0.05$ level; other differences are not significantly different from 0.
In parentheses: number of subjects (out of 10) showing the difference.

steeper for the double-prime combination than for all the other combinations. RT inhibition, i.e. the difference between same-point RT and opposite-point RT, was significant and of about equal magnitude at both SOAs. The finding of major importance is that at the 0.2 sec SOA double-prime RT was virtually equal to same-point RT, while at the 0.6 sec SOA it was virtually equal to opposite-point RT. Another finding of interest is that double-target RT was slightly but significantly shorter than opposite-point RT at both SOAs.

When subjects are required to make saccadic responses to bilateral mirror-symmetric stimuli, on any trial their saccades are directed to one or the other stimulus location rather than to some intermediate point between them (Findlay, 1980; Zeevi, Wetzel & Geri, 1988). By analogy with this bistable reactivity of saccadic eye movements, bilateral primes might be expected to elicit a similar systematic pattern of response from the control for covert orienting, e.g. an alternate orienting to the right and the left, or a preferential orienting to one side. This possibility was rejected by examining the distribution shapes and variances of double-prime, same-point and opposite-point RTs. Given that target location was alternated randomly between sides, a systematic covert orienting to one or the other of the two primed locations ought to produce a bimodal distribution of double-prime RTs by conflating two different RT populations, i.e. same-point RTs and opposite-point RTs. In such a case, the variance of double-prime RTs should be greater than that of either same-point or opposite-point RT. In no subject was there evidence for a bimodal distribution of double-prime RT, as there was no significant difference between the mean across subjects of standard deviations of double-prime RTs and that of standard deviations of opposite-point RTs at both SOAs (52.9 vs 50.6 msec, and 39.1 vs 40.4 msec, respectively), while the mean across subjects of standard deviations of double-prime RTs was significantly smaller than that of standard deviations of same-point RTs at both SOAs (52.9 vs 65.2 msec, and 39.1 vs 47.6 msec, respectively: $P < 0.05$ in both cases).

Discussion

The reported RT effects of the two independent variables as well as of their interaction cannot have been caused by differences in the probability of occurrence of the different types of trials, since each experimental session included the same number of trials (eight) for same-point, opposite-point, double-prime and double-target combinations at each of the two SOAs. In keeping with several previous studies cited in the Introduction,



		SOA (s) 0.2	SOA (s) 0.6	Mean
Reaction time (ms)	Same-point	325.9	252.7	289.3
	Opposite-point	288.2	216.7	252.4
	Double-prime	324.0	217.6	270.8
	Double-target	271.9	211.0	241.4
Mean		302.5	224.5	

FIGURE 1. Experiment 1. Reaction time for same-point (▽), opposite-point (▼), double-prime (□) and double-target trials (■) as a function of SOA between prime and target.

the findings confirm the phenomenon of RT inhibition, i.e. the slowing of same-point RT relative to opposite-point RT at both SOAs tested. In the present study such RT inhibition was invariant across SOAs, regardless of the strong reduction in overall RT with increasing SOA. Such a well-known general enhancement of response speed with increasing prime-target SOA is usually attributed to the tendency of the prime to acquire the function of an additional warning signal at longer SOAs (Niemi & Näätänen, 1981).

The comparison of the results with unilateral primes and targets with those with bilateral primes or targets generally supports the predictions and expectations which prompted this experiment. Confirming Posner and Cohen (1984), at the 0.2 sec SOA we found the effect of bilateral priming to compare with that of unilateral same-point priming, the RTs in the two conditions being indistinguishable and thus equally increased over opposite-point RT. However, at the 0.6 sec SOA, double-prime RT was both significantly shorter than RT to unilateral targets in singly primed locations, as found by Maylor (1985) at longer SOAs, and actually equal to RT to single targets contralateral to single primes. Arguably the contrast between the results obtained at the two SOAs rules out the possibility of a unitary interpretation of all features of inhibition of simple RT to light targets in primed locations. On one hand, RT inhibition induced at short SOAs by bilateral priming and unilateral same-point priming alike is best explained by a basic sensory mechanism such as that proposed by Posner and Cohen (1984): a selective reduction in central responsiveness to input from recently stimulated visual field sites which favors the uptake of information from new locations. On the other hand, RT inhibition induced at long SOAs by unilateral same-point priming, but not by bilateral priming, is best related to mechanisms of covert orienting, and more specifically to a temporary imbalance in the spatial distribution of attention caused by unilateral visual stimulation, as proposed in different terms by Maylor (1985) and by ourselves (Tassinari *et al.*, 1987; Berlucchi *et al.*, 1989). Obviously the present results are insufficient by themselves for establishing that the sensory hypothesis of Posner and Cohen (1984) is indeed the correct interpretation of RT inhibition at short SOAs, nor do they allow to decide in favor of one or the other of the different attentional accounts of RT inhibition at long SOAs. However they do provide solid grounds for concluding that inhibition of simple visuomotor RT by local priming is a multifactorial phenomenon which can by no means be accounted for by a single mechanism. The results further indicate a general similarity between RT to bilateral targets following single primes and RT to single targets contralateral to single primes (opposite-point RT). This suggests that in trials with bilateral targets, motor output is controlled more by the target in the unprimed location than by that in the primed location, in agreement with the hypothesis that the latter location suffers from inhibition while the former benefits from facilitation (Tassinari *et al.*, 1989). This inference can also be drawn from the reduced probability of eye movements to the primed location on bilateral trials, as reported by Chloessy *et al.* (1991). It also cannot be excluded that probability summation may contribute to speed up responses to double targets compared to single targets (e.g. Marzi, Tassinari, Aglioti & Lutzemberger, 1986); such a contribution may account for our additional finding that RT to bilateral targets was slightly but significantly faster than opposite-point RT.

EXPERIMENT 2

There are valid reasons for believing that local changes in retinal sensitivity at the primed location are not responsible in any major way for RT inhibition. For example, RT inhibition has been shown to persist when there is a change in eye position beween the presentation of the prime and that of the target, such that the two stimuli are projected to different retinal regions even though they occur at the same point in space (Posner & Cohen, 1984); further, RT inhibition from ipsilateral primes has been observed with prime-target separations of as much as 29 deg (Berlucchi *et al.*, 1989). It seems clear that in these cases RT inhibition must be totally predicated on post-retinal mechanisms. If however one assumes, as we did on account of the outcome of Expt 1, that RT inhibition is a multifactorial phenomenon, one cannot exclude the possibility of a retinal contribution to its genesis when prime and target impinge on the same retinal region. For instance it can be submitted that a local retinal adaptation induced by the prime plays an at least co-factorial role in bringing about the comparable RT inhibitions seen at the 0.2 sec SOA on same-point and double-target trials in Expt 1. To test for this possibility, Expt 1 was replicated under conditions in which the prime was seen solely by one eye and the target was seen solely by the other eye, thus eliminating any local interaction between prime and target at the retina.

Methods

Subjects. Ten subjects, five males and five females, participated in the experiment. These included four medical students and six staff members of the University of Verona, ranging in age from 21 to 36 yr. They were right handed, experienced with RT tasks, and had normal or corrected-to-normal vision.

Apparatus and stimuli. Two identical photic stimulators were the sources of both primes and targets. Each stimulator contained two side-by-side miniature incandescent bulbs whose filament was focused by a lens onto one end of an optical fiber 110 mm in length and 2.5 mm in diameter. A Kodak Wratten gelatin color filter was interposed between each of the two bulbs and the end of the optical fiber. One filter was red (CAT 149 5621) and the other was green (CAT 149 5795). Each bulb in each stimulator could be independently lit by a 150 msec, 300 mA pulse of current producing a flash of light which was transmitted to the other end of the optical fiber. Due to the persistence of incandescence, the duration of the flash, measured by means of a photocell, was about 200

TABLE 2. Experiment 2—differences between RTs of trials with different prime-target combinations

Differences (msec)	SOA (sec) 0.2	0.6
Same-point RT – opposite-point RT	**55.6** (10)	**40.6** (10)
Same-point RT – double-prime RT	–12.4 (6)	39.7 (9)
Doube-prime RT – opposite-point RT	**68.0** (10)	0.9 (5)

Bold underlined differences are significantly different from 0 at the $P < 0.01$ level; underlined differences in normal type are significantly different from 0 at the $P < 0.05$ level; all other differences are not significantly different from 0.
In parentheses: number of subjects (out of 10) showing the effect.

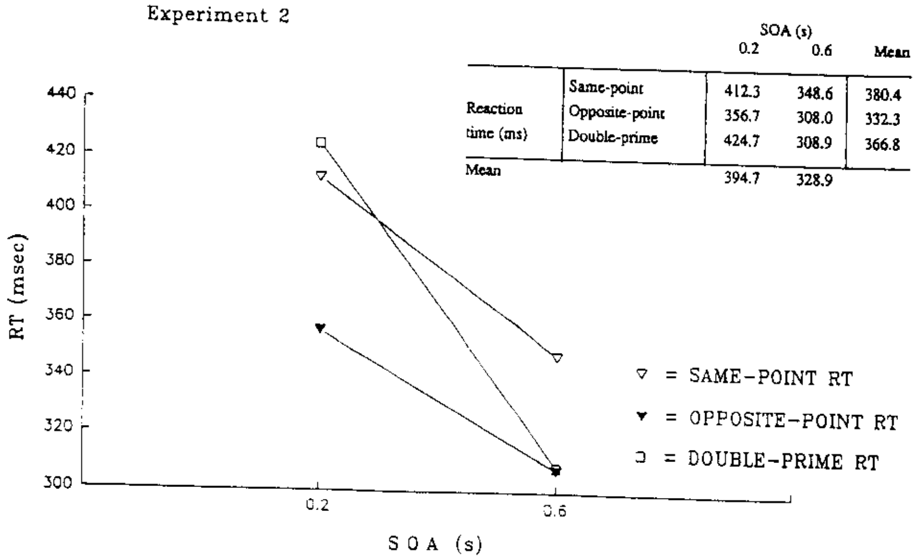
msec. The bulbs, the filters and the end of the optical fiber adjoining them were encased in a black box; an opaque plastic sheath covered the portion of the optical fiber emerging from the box so that the light could shine only through the free end of the optic fiber away from the bulbs. The two stimulators were attached 10 cm on the right and the left of midpoint of the arc perimeter used in Expt 1, the free ends of their optical fibers pointing toward the center of curvature of the perimeter. All other features of the apparatus, including the white background screen lighted at a background luminance of 0.15 cd/m^2, the response devices and the headset system for auditory stimulation were the same as in Expt 1.

Procedure. All procedural features of Expt 1 were exactly replicated, with the only difference that primes consistently differed in color from targets, and that during testing subjects wore goggles with a red glass filter in front of one eye and a green glass filter in front of the other eye. The transmittance of the eye filters matched that of the gelatin filters within the stimulators, so that a red prime or target could be seen only by the eye screened by the red filter, and a green prime or target could be seen only by the eye screened by the green filter. After the double filtering, the intensity of primes and targets was at least 100 times greater than background illumination; further, the intensity of single primes and targets was about two times that of double primes and targets. Throughout any given session the prime, whether single or double, was always one color and the target, whether single or double, was always the other color, but the colors of prime and target were alternated from session to session. The right-left position of the eye filters was exchanged every other session, so that the right eye received the prime and the left eye received the target in one session, while the reverse occurred in the next session. The orders of alternation between eye filters and colors of primes and targets were independently counterbalanced across subjects.

Data analysis. This was performed as in Expt 1, except that double-target RTs were not included in the analysis.

Results and discussion

Since the intensity of double stimuli was about half that of single stimuli, double-target RTs were longer than RTs to single targets, and therefore a two-way ANOVA was performed only on the latter RTs with condition (three levels: same-point, opposite-point, double-prime) and SOA (two levels: 0.2 and 0.6 sec) as main factors. Both main factors as well as their interaction were highly significant [condition, $F(2, 18) = 29.35$; SOA, $F(1, 9): = 55.13$; condition/SOA interaction, $F(2, 18) = 35.62$; $P < 0.001$ in each case]. Table 2 and Fig. 2 show the results for double-prime, same-point



		SOA (s) 0.2	0.6	Mean
Reaction time (ms)	Same-point	412.3	348.6	380.4
	Opposite-point	356.7	308.0	332.3
	Double-prime	424.7	308.9	366.8
Mean		394.7	328.9	

FIGURE 2. Experiment 2. Reaction time for same-point (▽), opposite-point (▼), and double-prime trials (□) as a function of SOA between prime and target.

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and opposite-point RTs, allowing a direct comparison with the corresponding findings from Expt 1.

The outcomes of the two experiments are in full agreement inasmuch as Expt 2 confirms the occurrence of comparable RT inhibitions from unilateral primes at both SOAs, as well as the statistical coincidence of double-prime RT with same-point RT at the 0.2 sec SOA and with opposite-point RT at the 0.6 sec SOA. The conclusion from Expt 1 that RT inhibition depends on different causes at different SOAs is fully supported, with the additional evidence that local retinal factors have no causal role in RT inhibition.

EXPERIMENT 3

RT inhibition caused by unilateral priming is not limited to the primed location. From our previous studies we have concluded that a prime presented in one location in the right or left visual hemifield inhibits RT to targets presented elsewhere in the same hemifield; similarly, the presentation of primes in the upper or lower hemifield results in the inhibition of RT to targets occurring at other locations within the same hemifield (Tassinari *et al.*, 1987, 1989; Berlucchi *et al.*, 1989). No study so far has assessed the possible inhibitory effects of bilateral primes on RT to subsequent unilateral targets presented away from the locations of the two primes. In Expt 3 we have compared the effects of unilateral and bilateral primes on RT to targets in non-primed locations at four prime-target SOAs.

Methods

Subjects. The group of ten subjects included three medical students and seven staff members of the University of Verona, five females and five males, aged between 22 and 57 yr. All were right handed and experienced with RT tasks, and had normal or corrected-to-normal vision.

Apparatus, procedure and data analysis. Subjects viewed the same horizontal arc perimeter as in Expt 1. Four LEDs like those used in Expt 1 were fastened to the perimeter, two on the right and two on the left of the fixation mark. From the observer's viewpoint the fixation mark lay 10 deg from the nearest (medial) LED and 30 deg from the farthest (lateral) LED on each side. Subjects performed on a practice session followed by four experimental sessions. In analogy with Expts 1 and 2 each trial involved a sequence of a warning auditory signal, a visual prime and a visual target; however, while primes could be unilateral or bilateral, targets were always unilateral, and the prime-target SOA could take one of four rather than two values, i.e. 0.2, 0.6, 1.5 or 5 sec. Unilateral primes could occur at any of the four positions, whereas bilateral primes occurred at either the two medial or two lateral positions. Targets following a single prime in a medial position could occur only at any of the two lateral positions; conversely, targets following a single prime in a lateral position could occur only at any of the two medial positions. Further, single targets following a double prime could occur only at any of the two positions not previously occupied by the prime, i.e. at a lateral position after a double medial prime, and at a medial position after a double lateral prime. The 96 trials making up each session exhausted all accepted combinations between type of prime (single or double), prime position, target position and SOA, and additionally included a repetition of each combination. Thus in each session there were, at each of the four SOAs, eight trials with bilateral primes (double-prime trials), eight trials with single primes and targets occurring in the same visual hemifield (same-field trials), and eight trials with single primes and targets occurring in opposite hemifields (opposite-field trials). The order of presentation of different types of trials and different SOAs was entirely random. In all other respects the procedure was as in Expt 1. Data analysis was shaped after those of Expts 1 and 2.

Results

A preliminary inspection of the data evinced no systematic difference between RTs of the two hands, or to targets in the two hemifields. RT to targets in medial positions was significantly faster than RT to targets in lateral positions, as expected on the basis of the well known relation between retinal sensitivity and stimulus eccentricity (e.g. Haines & Gilliland, 1973). However this was true for all types of trials. Thus double-prime, same-field and opposite-field RTs were obtained in each subject by averaging median RTs across right and left hands and hemifields, as well as across medial and lateral target positions.

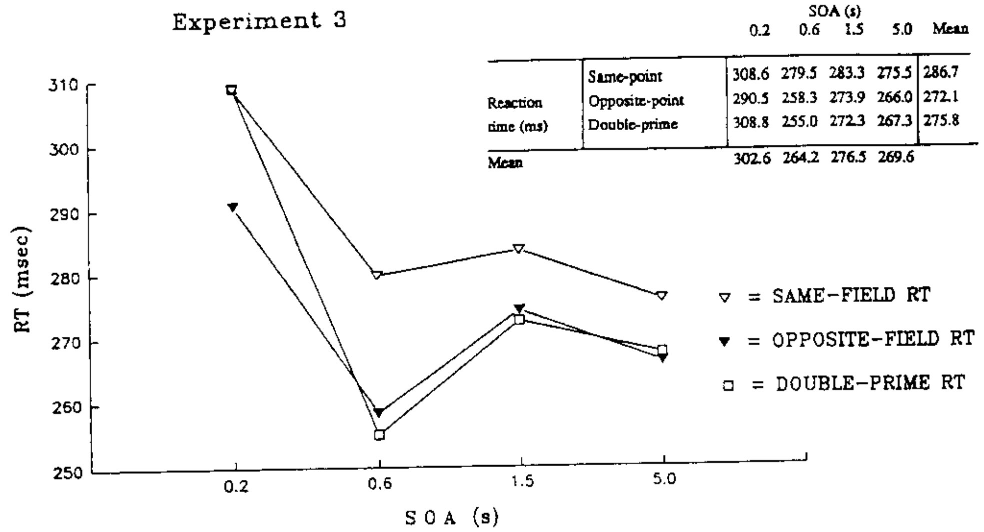
A two-way ANOVA with condition (three levels: same-field, opposite-field and double-prime) and SOA (four levels) as main factors demonstrated significant

TABLE 3. Experiment 3—differences between RTs of trials with different prime-target combinations

Differences (msec)	SOA (sec) 0.2	0.6
Same-field RT – opposite-field RT	**18.1** (10)	**21.2** (9)
Same-field RT – double-prime RT	0.2 (5)	**24.5** (10)
Double-prime RT – opposite-field RT	18.3 (9)	−3.3 (5)

Bold underlined differences are significantly different from 0 at the $P < 0.01$ level; underlined difference in normal type is significantly different from 0 at the $P < 0.05$ level; all other differences are not significantly different from 0.

In parentheses: number of subjects (out of 10) showing the effect.



		SOA (s)				
		0.2	0.6	1.5	5.0	Mean
Reaction time (ms)	Same-point	308.6	279.5	283.3	275.5	286.7
	Opposite-point	290.5	258.3	273.9	266.0	272.1
	Double-prime	308.8	255.0	272.3	267.3	275.8
Mean		302.6	264.2	276.5	269.6	

FIGURE 3. Experiment 3. Reaction time for same-field (▽), opposite-field (▼), and double-prime trials (□) as a function of SOA between prime and target.

effects from both factors as well as from their interaction [condition, $F(2,18) = 19.25$; SOA, $F(3,27) = 13.23$; condition/SOA interaction, $F(6,54) = 4.62$; $P < 0.001$ in each case]. Same-field RT was significantly longer than both double-prime RT and opposite-field RT ($P < 0.01$ in both cases) which did not differ from one another ($P > 0.05$). The significance of the SOA factor is accounted for by RT at the shortest SOA being slower than RTs at the other SOAs. The condition/SOA interaction is analyzed in Table 3 and Fig. 3. Table 3 shows that at the 0.2 sec SOA, double-prime RT was virtually equal to same-field RT, and both RTs were significantly slower than opposite-field RT. By contrast, at the 0.6 sec SOA double-prime RT was virtually equal to opposite-field RT, and both RT were significantly faster than same-field RT. These relationships between the three RTs also obtained at the two longest SOAs, although at the 5.0 sec SOA there was a clear tendency for the different types of trials to yield the same RT.

Discussion

The inhibitory action of unilateral primes on speed of reaction to ipsilateral targets can be inferred from the finding of slower RTs on same-field trials compared to opposite-field trials. RT inhibition inferred from this difference is fully apparent from the findings, even though such same-field inhibition is clearly smaller than the same-point inhibition demonstrated in Expts 1 and 2. It may be argued that in the present experiment RT inhibition depended on differences in the prime-target distance rather than on the primes being ipsilateral or contralateral to the targets. According to the experimental design the prime-target distance was indeed consistently smaller on same-field trials (20 deg) than on opposite-field trials (40 deg). However in a previous study (Berlucchi *et al.*, 1989) we have proven that RT inhibition arises when primes and targets occur on the same side of the main meridians of the visual field, quite independent of the distance separating their locations. On these grounds, the present results can be taken to conform with the notion that unilateral primes produce RT inhibition not only at the primed location, but also at other locations within the same visual hemifield. The novel finding emerging from Expt 3 is the evidence that a similar inhibition can be elicited by bilateral priming at a prime-target SOA of 0.2 sec, but not at SOAs $\geqslant 0.6$ sec. The resemblance between this finding and the results from Expts 1 and 2 intimates that the conclusions drawn from those experiments can be generalized to the present case. More explicitly, same-field as well as same-point inhibitions can be considered to be independent from lateral orienting at short prime-target SOAs, insofar as either inhibition is caused by both unilateral and bilateral primes. By contrast, lateral orienting appears to be required for inhibition to arise at either same-field or same-point locations at longer SOAs, as can be argued from the parallel presence of inhibition at each of these locations on unilateral priming, and from the parallel absence of inhibition at both locations on bilateral priming. If the overall phenomenon of RT inhibition at primed locations is thought to depend on a sequence of a sensory component and an orienting component, as as been inferred from the results of Expts 1 and 2, then the results of Expt 3 imply that RT inhibition at unprimed location within the primed hemifield can similarly be divided into two components. Further, the results support those of Expt 2 to the extent that local prime-target interactions at the retina can hardly be invoked to account for RT inhibition effects at unprimed locations at a distance of as much as 20 deg from primed locations.

GENERAL DISCUSSION

Inhibition of RT to extrafoveal targets following ipsilateral primes has previously been described either as a passive, orienting-independent aftereffect of visual stimulation, or as a consequence of an active covert orienting toward the prime. Based on our demonstration of different relationships between the effects of unilateral and bilateral primes at different prime-target intervals, we submit that these two explanations of RT inhibition need not be mutually exclusive. The coincidence between the inhibitory effects of unilateral and bilateral primes at a relatively short prime-target interval is evidence for a passive, stimulus-dependent nature of these effects. On the other hand, at the longer prime-target interval the active, orienting-dependent character of RT inhibition is substantiated by the occurrence of inhibition with unilateral but not bilateral primes. These dissociations, as demonstrated in Expts 1–3, lead us to propose that RT inhibition derives from at least two sequential effects of the prime, i.e. an early component linked to afferent stimulation, and a late component linked to covert orienting. The results of Expt 2 show that neither component depends on local prime-target interactions at the retina, because both are present on dichoptic delivery of primes and targets; and the results of Expt 3 suggest that the effects of both components spread throughout the hemifield containing the primed location, insofar as unprimed locations within that hemifield also show the early and late inhibitory effects. By generalizing from these results and those of other experiments on distribution of attention in visual space (e.g. Tassinari *et al.*, 1987; Hughes & Zimba, 1987; Rizzolatti, Riggio, Dascola & Umiltà, 1987), it can be surmised that the spread of inhibitory effects from the primed location is limited by the main meridians of the visual field. In the studies just cited, a similar sorting of RT effects according to hemifield has been reported to occur in tasks involving the deliberate direction of attention to a location in one hemifield, whereby the cost of such attentional selection manifests itself chiefly as a reduction in reactivity to stimuli delivered to the opposite hemifield.

There is limited information on the putative post-retinal neural mechanisms of the two proposed components of RT inhibition. Effects which may possibly underlie the early component of RT inhibition have been observed with single neurons of the primary visual cortex (Judge, Wurtz & Richmond, 1980) and superior colliculus (Wurtz, Richmond & Judge, 1980) of behaving monkeys. In both cortex and midbrain the response of neurons to appropriate stimulation of their receptive field centers is attenuated by previous stimulation at the same locations. However, neurons in the superior colliculus also show response attenuation by previous stimulation of locations remote from the receptive field, an effect ordinarily observable within a 0–100 msec interval between conditioning and test stimuli. This response attenuation is especially relevant to our findings inasmuch as it is induced by remote stimuli lying in the hemifield ipsilateral to the receptive field, much less so or even not at all with contralateral remote stimuli, in general keeping with the pattern of ipsilateral RT inhibition described here and elsewhere. By suggesting that their response attenuation effect in the superior colliculus depends on the stimulus conditions rather than on an attentive reaction to the remote stimulus, Wurtz *et al.* (1980) give an interpretation of such phenomenon similar to the one we have proposed for the early passive component of RT inhibition. On the other hand Rizzolatti, Camarda, Grupp and Pisa (1974) have described in the superior colliculus of curarized unanesthetized cats a response attenuation by remote stimuli which is more likely to be linked to attention, since this effect is absent when the remote stimulus is presented repeatedly in an habituation-inducing fashion. As in monkeys (Wurtz *et al.*, 1980), the response attenuation of superior collicular neurons of cats is induced by remote stimuli in the hemifield ipsilateral to the receptive field, but not by contralateral remote stimuli. In contrast with the findings in monkeys, Rizzolatti *et al.* (1974) obtained attenuation effects with interstimulus intervals up to 3 sec, in agreement with the long duration of the late attentional component of RT inhibition described here.

If it is conceded that the remote inhibitions found by Rizzolatti *et al.* (1974) and Wurtz *et al.* (1980) constitute two different effects, one attentional and the other merely input-dependent, then it is reasonable to assume that the superior colliculus may contain a common substrate for both components of RT inhibition. The superior colliculus has long been implicated in both visual attention and oculomotor behavior, and recent evidence suggests that it may also directly participate in skeletomotor reactivity to visual stimuli (Werner, 1992). Its hypothetical involvement in RT inhibitory effects must of course be substantiated by recording from single neurons in the superior colliculi of unanesthetized animals performing the simple behavioral tasks described here. It should be mentioned, in this respect, that attentional effects limited to one hemifield have been found with single-neuron recordings in other visual areas of the brain, such as, for example, the inferotemporal cortex (Sato, 1988). These effects may originate in the inferotemporal cortex itself, but they may also arise upstream of the inferotemporal cortex along the visual pathways.

The term "forward masking" has been used in the perceptual literature to allude to the decrease in the subjective visibility of a stimulus that is brought about by previous visual stimulation (Kahneman, 1968; Breitmeyer, 1984). Typical forward masking phenomena are usually considered to be subject to time constraints, the effective mask-targets intervals ranging between 0 and < 500 msec, as well as to space constraints, with the best effects depending on an overlap or close contiguity of mask and target. While the early component of RT inhibition described here may be identified as a forward masking phenomenon, we are wary to suggest such an identification for two reasons. First, typical forward masking effects do not appear to spread to a whole hemifield, as seems instead to be the case for all components of RT inhibition. Second, motor reactions to masked stimuli are at least partially dissociable from phenomenal visibility, as indicated by the observation of measurable RTs to visual targets which are denied access to conscious experience by masking (Taylor & McCloskey, 1990). Whatever its relation to classical forward masking, the early component of RT inhibition suggests itself as an attention-independent phenomenon possibly associated with rapid loss of visual sensitivity on repeated stimulation (Frome, MacLeod, Buck & Williams, 1981), or with the equalization of information intake from different locations (Posner & Cohen, 1984), or with the attenuation of visual input necessary to prevent image blurring during saccadic eye movements (Judge *et al.*, 1980). By contrast, the later, long-lasting component of RT inhibition appears to be best accounted by the consequences of a selective covert orientation toward the location of a single prime.

REFERENCES

Berlucchi, G., Tassinari, G., Marzi, C. A. & Di Stefano, M. (1989). Spatial distribution of the inhibitory effect of peripheral non-informative cues on simple reaction time to non-fixated visual targets. *Neuropsychologia, 27,* 201–221.

Berlucchi, G., Di Stefano, M., Marzi, C. A., Morelli, M. & Tassinari, G. (1981). Direction of attention in the visual field as measured by a reaction time paradigm. *Behavioural Brain Research, 2,* 244–245.

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

Castiello, U. & Umiltà, C. (1992). Splitting focal attention. *Journal of Experimental Psychology: Human Perception and Performance, 18,* 837–848.

Chloessy, A. B., Posner, M. I., Rothbart, M. K. & Vecera, S. P. (1991). The development of inhibition of return in early infancy. *Journal of Cognitive Neuroscience, 3,* 345–350.

Findlay, J. M. (1980). The visual stimulus for saccadic eye movements in human observers. *Perception, 9,* 7–21.

Frome, F. S., MacLeod, D. I. A., Buck, S. L. & Williams, D. R. (1981). Large loss of visual sensitivity to flashed peripheral targets. *Vision Research, 21,* 1323–1328.

Frumkes, T. E. (1990). Classical and modern psychophysical studies of dark and light adaptation and their relationship to underlying retinal function. In Leibovic, K. N. (Ed.), *Science of vision* (pp. 172–210). New York: Springer.

Haines, R. F. & Gilliland, K. (1973). Response times in the full visual field. *Journal of Applied Psychology, 58,* 289–295.

Hughes, H. C. & Zimba, L. D. (1987). Natural boundaries for the spatial spread of directed visual attention. *Neuropsychologia, 25,* 5–18.

Judge, S. J., Wurtz, R. H. & Richmond, B. J. (1980). Vision during saccadic eye movements. I. Visual interactions in striate cortex. *Journal of Neurophysiology, 43,* 1133–1155.

Kahneman, D. (1968). Method, findings and theory in studies of visual masking. *Psychological Bulletin, 70,* 404–425.

Lambert, A. & Hockey, R. (1991). Peripheral visual changes and spatial attention. *Acta Psychologica, 76,* 149–163.

Marzi, C. A., Tassinari, G., Aglioti, S. & Lutzemberger, L. (1986). Spatial summation across the vertical meridian in hemianopics: A test of blindsight. *Neuropsychologia, 24,* 749–758.

Maylor, E. A. (1985). Facilitatory and inhibitory components of orienting in visual space. In Posner, M. I. & Marin, O. S. M. (Eds), *Attention and performance XI* (pp. 89–104). Hillsdale, N. J.: Erlbaum.

Maylor, E. A. & Hockey, R. (1985). Inhibitory component of externally controlled covert orienting in visual space. *Journal of Experimental Psychology: Human Perception and Performance, 11,* 777–787.

Myers, J. L. (1979). *Fundamentals of experimental design.* Boston, Mass.: Allyn & Bacon.

Niemi, P. & Näätänen, R. (1981). Foreperiod and simple reaction time. *Psychological Bulletin, 89,* 133–162.

Ottes, F. P., Van Gisbergen, J. A. M. & Eggermont, J. J. (1984). Metrics of saccade responses to visual double stimuli: Two different modes. *Vision Research, 24,* 1169–1179.

Posner, M. I. (1986). *Chronometric explorations of mind.* New York: Oxford University Press.

Posner, M. I. & Cohen, Y. (1984). Components of visual orienting. In Bouma, H. & Bouwhuis, G. G. (Eds), *Attention and performance X* (pp. 531–556). Hillsdale, N. J.: Erlbaum.

Posner, M. I., Snyder, C. R. R. & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General, 109,* 160–174.

Possamaï, C. A. (1986). Relationship between inhibition and facilitation following a visual cue. *Acta Psychologica, 61,* 243–258.

Rizzolatti, G., Camarda, R., Grupp, L. A. & Pisa, M. (1974). Inhibitory effect of remote visual stimuli on visual responses of cat superior colliculus: Spatial and temporal factors. *Journal of Neurophysiology, 37,* 1262–1275.

Rizzolatti, G., Riggio, L., Dascola, I. & Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia, 25,* 31–40.

Sato, T. (1988). Effects of attention and stimulus interaction on visual responses of inferior temporal neurons in macaque. *Journal of Neurophysiology, 60,* 344–364.

Tassinari, G., Biscaldi, M., Marzi, C. A. & Berlucchi, G. (1989). Ipsilateral inhibition and contralateral facilitation of simple reaction time to non-foveal visual targets from non-informative visual cues. *Acta Psychologica, 70,* 267–291.

Tassinari, G., Aglioti, S., Chelazzi, L., Marzi, C. A. & Berlucchi, G. (1987). Distribution in the visual field of the costs of voluntarily allocated attention and of the inhibitory after-effects of covert orienting. *Neuropsychologia, 25,* 55–71.

Tassinari, G., Aglioti, S., Chelazzi, L., Peru A. & Berlucchi, G. (1993). Do peripheral non-informative cues induce early facilitation?

Taylor, J. L. & McCloskey, D. I. (1990). Triggering of preprogrammed movements as reactions to masked stimuli. *Journal of Neurophysiology, 63,* 439–446.

Welford, A. T. (1980). The single-channel hypothesis. In Welford, A. T. (Ed.), *Reaction times* (pp. 215–252). New York: Academic Press.

Werner, W. (1992). Activity of primate superior colliculus neurons during arm movements. *European Journal of Neuroscience (Suppl.), 5,* 279.

Wurtz, R. H., Richmond, B. J. & Judge, S. J. (1980). Vision during saccadic eye movements. III. Visual interactions in monkey superior colliculus. *Journal of Neurophysiology, 43,* 1168–1181.

Zeevi, Y. Y., Wetzel, P. A. & Geri, G. A. (1988). Preferences and asymmetries in saccadic responses to delayed bihemifield stimuli. *Vision Research, 28,* 1145–1155.

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