

# Response Facilitation and Inhibition in Manual, Vocal, and Oculomotor Performance: Evidence for a Modality-Unspecific Mechanism

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**ABSTRACT.** In 2 experiments ( $N = 10$ , Experiment 1;  $N = 16$ , Experiment 2), the authors investigated whether evidence for response facilitation and subsequent inhibition elicited by masked prime stimuli can be observed for output modalities other than manual responding. Masked primes were followed by target stimuli that required a 2-choice manual, saccadic, or vocal response. Performance was measured for compatible trials in which primes and targets were identical and for incompatible trials in which they were mapped to opposite responses. When primes were presented centrally, performance benefits were obtained for incompatible trials; whereas for peripherally presented primes, performance benefits were found in compatible trials. That pattern of results was obtained for manual responses and for saccadic eye movements (Experiment 1), demonstrating that those effects are not mediated by specialized dorsal pathways involved in visuomanual control. An analogous pattern of effects was found when manual and vocal responses were compared (Experiment 2). Because vocal responding is controlled by the inferotemporal cortex, that result shows that prime–target compatibility effects are not primarily mediated by the dorsal stream, but appear to reflect modality-unspecific visuomotor links that allow rapid activation of motor responses that may later be subject to inhibition.

*Key words:* eye movements, inhibition, priming, response activation, vocal responses

A large amount of potentially important information continuously reaches our sense organs, but a small subset of external objects and events is used in the control of our actions. Attentional mechanisms are essential in the selection of those aspects of external information that are currently relevant for the control of behavior so that appropriate links can be established between perception and action (Allport, 1987). One problem for this sort of attentional gating of perceptuomotor links is that the selection of relevant objects takes time, whereas some events in the environment demand an immediate response. If there were additional, direct links between perception and action, those

linkages would allow some aspects of unattended information to determine response parameters before the intervention of attentional processes.

There are several lines of evidence pointing toward the existence of such direct links. The location of a target affects performance even when its location is irrelevant for response selection, as is reflected in response time (RT) benefits when stimulus and response locations correspond and RT costs when they do not (Simon effect; Simon, 1969). Electrophysiological studies have shown that task-irrelevant spatial features can activate spatially corresponding responses even when those responses are inappropriate (De Jong, Liang, & Lauber, 1994; Eimer, 1995). In noise-compatibility tasks, irrelevant items activate their corresponding responses, as reflected in performance (Eriksen & Eriksen, 1974) and in electrophysiological indicators of motor activation (Gratton, Coles, & Donchin, 1992). Those examples suggest that perceptual information can affect response-related stages directly, that is, without the intervention of attentional selection processes (see Ridderinkhof, van der Molen, & Bashore, 1995, for further evidence of direct response priming in noise-compatibility tasks). However, such fast, direct perceptuomotor links sometimes result in the activation of inappropriate response tendencies. Additional inhibitory mechanisms may be required so that response tendencies triggered by task-irrelevant information can be prevented from causing overt behavior.

Behavioral and electrophysiological evidence for the activation of direct links between perception and action, followed by response inhibition, has been found in a number

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of recent studies (Eimer, 1999; Eimer & Schlaghecken, 1998; Schlaghecken & Eimer, 1997, in press). In those experiments, participants performed manual choice RT tasks in response to simple visual target stimuli such as arrows or geometric figures. Before each target was shown, a masked prime stimulus was presented centrally. The stimulus was identical to the target on compatible trials and was mapped to a different response on incompatible trials.<sup>1</sup> Eimer and Schlaghecken assumed that the primes would activate their corresponding responses, but, because of the intervention of the mask, the activation would not be sufficient to elicit an overt response. Initially, and quite surprisingly, performance costs were found when primes and targets were identical, and benefits were obtained when they were mapped to opposite responses (negative compatibility effect): RTs were shortest and error rates were low in incompatible trials, whereas long RTs and high error rates were found in compatible trials. Further experiments revealed that the direction of those effects depended on the time interval between prime and target presentation (Schlaghecken & Eimer, 1997, in press). When the stimulus onset asynchrony (SOA) between prime and target was short, performance benefits were observed for compatible trials (positive compatibility effect; see also Klotz & Wolff, 1995; Neumann & Klotz, 1994). With increased SOA, the effect became smaller, and it eventually turned into an advantage for incompatible trials (negative compatibility effect) for intervals of 100 ms and longer.

We have argued that the reversal of prime–target compatibility effects with increased SOA occurs because an initial activation of the response assigned to the prime is later inhibited (Eimer, 1999; Eimer & Schlaghecken, 1998; Schlaghecken & Eimer, in press). Evidence for this *activation-followed-by-inhibition* hypothesis has been found in studies in which the lateralized readiness potential (LRP) has been recorded as a continuous electrophysiological measure of response activation (see Coles, 1989, and Eimer, 1998, for details on the derivation and interpretation of the LRP). Initially, the LRP showed a partial activation of the response assigned to the prime, which was then replaced by a partial activation of the opposite response (Eimer, 1999; Eimer & Schlaghecken, 1998). The early response activation reflected in the LRP shows that, initially, the response assigned to the prime is partially activated; the activation is presumably mediated by perceptuomotor links that allow information derived from the prime to directly affect response-related processing. The reversal of the effects may be caused by the subsequent inhibition of the initial activation, and we assumed that the inhibitory phase was responsible for the negative compatibility effects observed in behavioral performance when prime–target intervals were sufficiently long.

A complication for the activation-followed-by-inhibition account arises from the fact that the retinal eccentricity of masked primes has a systematic influence on the direction of priming effects. In most of the studies reported earlier,

primes were presented at fixation. When masked primes are presented peripherally, positive compatibility effects are elicited not only at short SOAs, but also at medium and long prime–target SOAs (Schlaghecken & Eimer, 1997, in press). This *central–peripheral asymmetry* suggests that masked primes activate their assigned response regardless of retinal position but that only motor activation processes triggered by foveal visual stimuli are subject to inhibition. That asymmetry may reflect basic functional differences in the impact of foveal and peripheral visual information on the motor system. Perceptual representations of foveally presented primes should be stronger than representations of peripheral primes because of the decrease in perceptual sensitivity with increasing eccentricity. If the strength of perceptual representations is directly related to the strength of the motor activation triggered by the primes and if only motor activations exceeding a certain threshold are subject to inhibition, then response inhibition would be more likely to occur with centrally presented primes (see Schlaghecken & Eimer, in press, for further details).

The idea that the masked primes exert their facilitatory influence on manual performance pre-attentionally was strengthened by the observation that the masking procedure was effective in preventing the conscious perception of the primes. That finding was tested in forced choice performance blocks in which participants had to detect the presence of a prime or to identify masked primes presented either with (Schlaghecken & Eimer, 1997) or without (Eimer & Schlaghecken, 1998) subsequent targets. In the tasks in which the prime was present or absent (Eimer & Schlaghecken, 1998, Experiment 2; Schlaghecken & Eimer, 1997), primes were present in 50% of all trials; and in the prime identification tasks (Eimer & Schlaghecken, 1998, Experiments 1 and 2), the two primes were presented with equal probability. Detection and identification performances were generally at chance level, and participants consistently reported their inability to respond discriminatively. That finding suggests that the masking procedure was effective in preventing subjective awareness of the primes, although the possibility of some residual perceptual sensitivity to the prime stimuli cannot be completely ruled out (see Cheesman & Merikle, 1986, for a discussion of the distinction between subjective and objective detection thresholds).

The fact that masked primes initially activate their assigned responses (regardless of retinal position) suggests that there are direct perceptuomotor links that provide access to perceptual information by the motor system independently of attentional selection processes. It is tempting to interpret those effects as an example of the dissociation of the two visual systems described by Milner and Goodale (1995). According to their view, the visual control of goal-directed action is implemented within a dorsal pathway linking primary visual cortex (V1) with posterior parietal cortex, whereas detailed attentional shape analysis and conscious visual perception are functions of a ventral pathway

that connects V1 to the inferotemporal cortex. One may explain the dissociation between the inability of participants to subjectively perceive prime stimuli that have a strong impact on performance by assuming that masking selectively impairs ventral stream processing but leaves the dorsal stream largely unaffected. We conducted the present experiments to test that idea.

According to Milner and Goodale (1995), different visuomotor control functions are implemented by independent networks within the dorsal stream. Separate parietofrontal cortical networks control reaching, grasping, and manipulating objects. The ventral intraparietal area (VIP) has strong links with area F4 in the inferior premotor cortex that represents arm and axial movements, and neuroscientists assume that this circuit controls manual reaching. The anterior intraparietal area (AIP) is linked to motor area F5ab, where different types of hand movements are represented, and that pathway may be involved in the visual control of grasping, holding, and manipulating objects (see Rizzolatti, Luppino, & Matelli, 1998, for an overview of parietofrontal circuits involved in visuomotor control).

Because different visuomotor tasks are implemented by functionally distinct dorsal circuits, prime–target compatibility effects could be restricted to specialized visuomotor networks involved in the control of manual responses. In addition, the difference between activation followed by inhibition elicited by centrally presented masked primes and activation-only in response to peripheral primes may reflect a differential sensitivity of dorsal stream mechanisms subserving manual responses to foveal and peripheral information. It is possible that visuomotor systems involved in the preparation and control of hand movements have a more direct access to information presented close to fixation whereas stimuli presented in the periphery predominantly activate visuomotor systems involved in saccade programming and execution. Whereas in all previous experiments visuomanual (button pressing) tasks have been used, in Experiment 1 of the present study we compared the impact of centrally and peripherally presented masked primes on manual responses with their effects on oculomotor performance. The control of saccadic eye movements involves dorsal stream circuits that are clearly distinct from pathways controlling visuomanual tasks. Cells in the lateral intraparietal area (LIP) shift their receptive fields prior to saccadic eye movements (Duhamel, Colby, & Goldberg, 1992), and the LIP area has strong connections with the frontal eye fields and the superior colliculus, regions involved in the control of eye movements. There is also interesting evidence that the number of retinal ganglion cells projecting to the superior colliculus increases with increasing retinal eccentricity (Bunt, Hendrickson, Lund, Lund, & Fuchs, 1975; Perry & Cowey, 1984). Because the visuomotor systems involved in saccade programming are highly sensitive to peripheral stimuli, if the central–peripheral asymmetry results from the activation of specialized

dorsal stream circuits that primarily process foveal information, then prime eccentricity may have different effects on manual and saccadic performance.

## EXPERIMENT 1

Participants were required to make left and right manual responses or left and right saccades to centrally presented targets (left-pointing or right-pointing arrows) that were preceded by masked primes. The primes were either identical to the target (compatible trials), mapped to the opposite response (incompatible trials), or response irrelevant (neutral trials), and were presented either at fixation or in the periphery. The prime–target SOA was 116 ms. For manual responses, positive compatibility effects were expected for peripheral primes and negative compatibility effects were predicted for central primes. If those effects are mediated by specialized visuomanual control circuits within the dorsal stream, they should not be found for saccadic responses. If the central–peripheral asymmetry reflects the differential sensitivity of visuomanual control systems to foveal and peripheral information, a qualitatively different pattern of prime–target compatibility effects in response to central and peripheral primes should emerge for eye movements.

## Method

### Participants

Ten paid volunteers (6 women and 4 men, aged 23–41 years [ $M = 29$  years]) participated in the experiment. Nine were right-handed, and 1 was left-handed. All had normal or corrected-to-normal vision.

### Stimuli and Apparatus

Participants were seated in a dimly lit experimental chamber, with response buttons under their left and right index fingers. We placed electrodes at the outer canthi of both eyes to record eye movements. A computer screen was placed 100 cm in front of the participant's eyes and carefully positioned so that the screen center was in the center of the participant's horizontal straight-ahead line of sight. Left- and right-pointing double arrows (<< and >>) were used as target stimuli. Primes could be left-pointing or right-pointing double arrows, or could be neutral (><). The mask consisted of left- and right-pointing double arrows superimposed upon one another. All stimuli subtended a visual angle of about  $0.8^\circ$  horizontally and  $0.35^\circ$  vertically and were presented in black in front of a white background on a computer monitor (60 Hz). Throughout the experiment, four small black dots were continuously present on the screen. Two dots were located to the left and right of the screen center at a horizontal distance of  $6.7^\circ$ . During the saccade blocks, those dots served as saccade targets (see Procedure). Two further dots were located  $0.72^\circ$  above and below the screen center. During the saccade blocks, they served as landmarks for eye movements back from the saccade target to the center of the screen in the intertrial intervals.

### Procedure

The experiment consisted of six blocks. In all trials, primes (16-ms duration), masks (100-ms duration), and targets (100-ms duration) were presented in immediate succession. The intertrial intervals were 2,000 ms. Target stimuli were always presented at the screen center. In one half of the experiment (peripheral prime condition), masked primes were presented bilaterally above and below fixation (4° eccentricity from the screen center); in the other half of the experiment (central prime condition), they were presented at the center of the screen. Half of the subjects received the peripheral prime condition first, whereas the other 5 subjects started with the central prime condition. In each experimental half, a manual response block (120 trials) was followed by an eye movement practice block (30 trials), which, in turn, was followed by an eye movement experimental block (600 trials). Trials in which primes and targets were identical were termed *compatible*, trials in which prime and target arrows pointed in opposite directions were termed *incompatible*, and trials in which a neutral prime was presented were termed *neutral*. Within each block, all combinations of prime–target compatibility (compatible, neutral, incompatible) and target identity (left arrow vs. right arrow) were delivered randomly and with equal probability, resulting in a total of 20 trials for each combination of conditions in the manual response block and a total of 100 trials in the eye movement block. A resting period of at least 18 s was included after 60 trials in the manual response block and after every 100 trials in the eye movement block. Following that interval, participants could initiate the next run of trials by pressing a button. In the eye movement blocks, the horizontal electrooculogram (HEOG) was recorded bipolarly from two electrodes at the outer canthi of both eyes. Electrode impedance was kept below 5 k $\Omega$ . Amplifier bandpass was 0.10–200 Hz. EOG data were sampled continuously with a digitization rate of 1000 Hz and stored on disk.

Participants were instructed to respond as fast and as accurately as possible to left or right target arrows with a left-hand or right-hand button press in the manual blocks, and with a left or right eye movement that should extend beyond the markers on the left or right side of the screen in the eye movement blocks. Participants were especially encouraged to move the eyes back to the screen center (indicated by the two central markers) as fast as possible after the execution of the outward eye movement. They were made familiar with those specific requirements during the practice block.

### Data Analysis

The HEOG was epoched off-line into intervals starting 100 ms before prime onset and ending 600 ms after target onset, separately for all combinations of compatibility (compatible, incompatible, and neutral), prime location (central vs. peripheral), and target identity (left vs. right

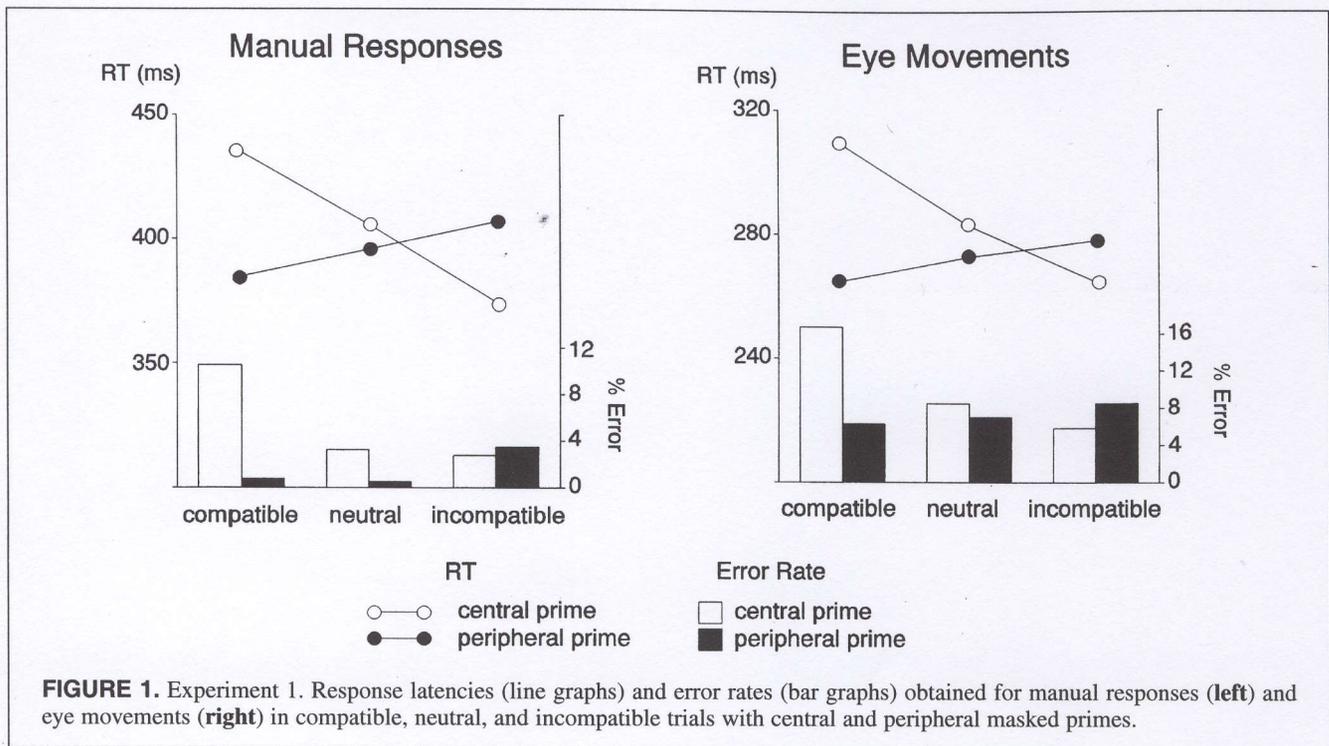
arrow). The 100-ms interval prior to prime onset served as baseline. Saccade onset was determined for individual trials in the following way. Each HEOG epoch was scanned within the 600-ms interval following target onset for the first uninterrupted positive-going or negative-going deflection, consisting of a series of at least 25 consecutive data points (equivalent to 25 ms) and exceeding an amplitude of  $\pm 25$   $\mu$ V (approximately equivalent to a 2.5° eye movement). When those criteria were met, the latency of the first data point of that time series was defined as saccade onset. The number of trials in which no reliable saccade onset time could be determined on the basis of this procedure was small, averaging 1.9% for the central prime condition and 2.2% for the peripheral prime condition. Those trials were excluded from analysis.

Repeated measures analyses of variance (ANOVAs) were conducted for correct responses on manual RTs and onset latencies of correct saccades, as well as for manual and saccadic error rates, for the variables response modality (manual vs. saccadic), prime–target compatibility (compatible vs. neutral vs. incompatible), prime location (central vs. peripheral), and target identity (left vs. right double arrow). Additional separate ANOVAs were conducted for the central and peripheral prime conditions; and with paired *t* tests, we conducted pairwise comparisons between performance measures obtained in compatible, neutral, and incompatible trials. Greenhouse–Geisser adjustments to the degrees of freedom were performed when appropriate.

### Results and Discussion

Mean RTs and error rates obtained in compatible, neutral, and incompatible trials for the central and peripheral prime conditions for manual responses (left) and saccades (right) are shown in Figure 1. The overall pattern of effects was very similar for both response modalities: In the central prime condition, benefits for incompatible trials and costs for compatible trials were obtained, whereas opposite cost–benefit effects were present in the peripheral prime condition. For central primes, mean manual RTs were 435 ms, 406 ms, and 375 ms, respectively, for compatible, neutral, and incompatible trials. The respective saccadic RTs were 309 ms, 283 ms, and 265 ms. In the peripheral prime condition, mean manual RTs were 385 ms, 396 ms, and 407 ms, respectively, for compatible, neutral, and incompatible trials. The respective saccadic RTs were 265 ms, 273 ms, and 278 ms. In Figure 2, we present grand-averaged HEOG waveforms for compatible, neutral, and incompatible trials in the central and peripheral prime conditions, including both correct and incorrect saccadic responses. Downward-going (positive) deflections indicate eye movements in the correct direction, whereas upward-going (negative) HEOG deflections indicate incorrect eye movements.

A main effect of response modality was obtained,  $F(1, 9) = 11.63$ ,  $p < .008$ , because saccade onsets were faster than manual responses. A main effect of prime–target compatibility,  $F(2, 18) = 22.32$ ,  $p < .001$ ,  $\epsilon = .626$ , was accompa-



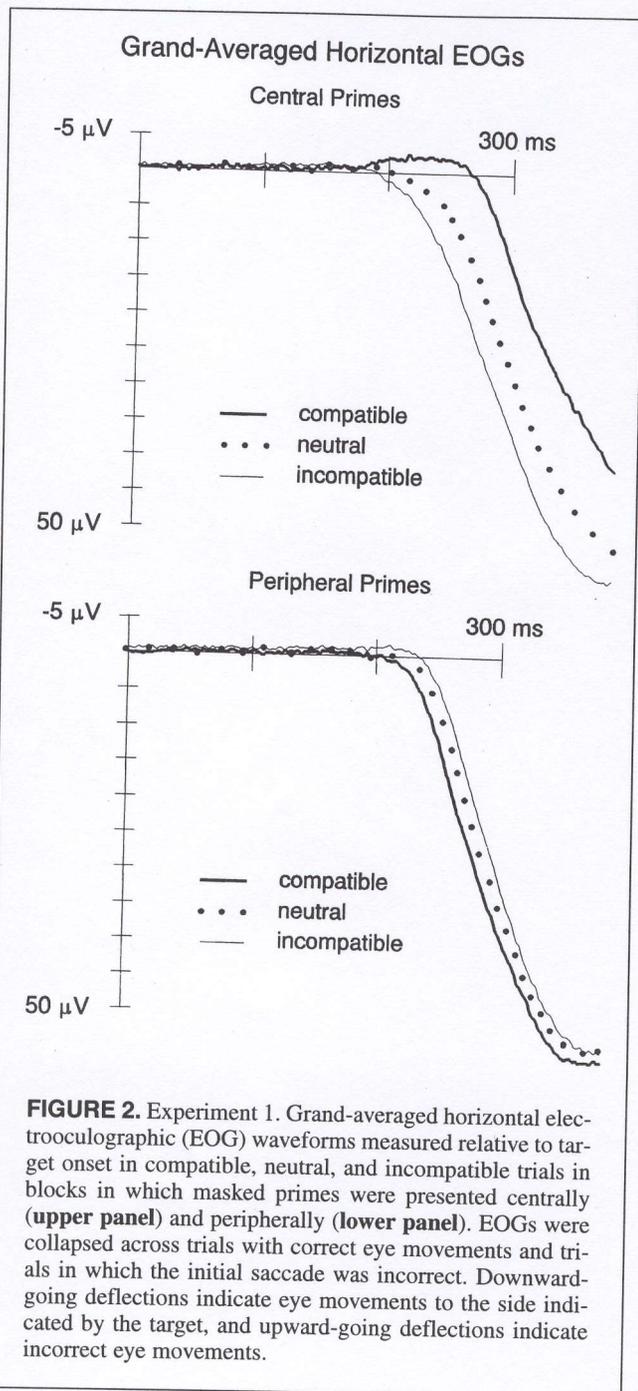
**FIGURE 1.** Experiment 1. Response latencies (line graphs) and error rates (bar graphs) obtained for manual responses (left) and eye movements (right) in compatible, neutral, and incompatible trials with central and peripheral masked primes.

nied by a highly significant Compatibility  $\times$  Prime Position interaction,  $F(2, 18) = 68.63, p < .001, \epsilon = .527$ , because compatibility effects reversed polarity for the central and peripheral prime conditions (Figure 1). Most important, no Response Modality  $\times$  Compatibility interaction was obtained. However, a significant Response Modality  $\times$  Compatibility  $\times$  Prime Position interaction was present,  $F(2, 18) = 6.17, p < .016, \epsilon = .789$ , because the overall compatible-incompatible RT differences were slightly larger for manual responses than for saccades. Two follow-up ANOVAs conducted separately for the central and peripheral prime conditions revealed highly significant prime-target compatibility effects in both prime conditions; both  $F_s(2, 18) > 20.0$ , and both  $p_s < .001$ . We further analyzed manual and saccadic RTs with paired  $t$  tests to investigate the costs and benefits of prime-target compatibility. In the central prime condition, costs in compatible trials and benefits in incompatible trials relative to neutral trials were highly significant for manual responses and saccades; all  $t_s(9) > 5.0$ , all  $p_s < .001$ . In the peripheral prime condition, reliable benefits in compatible trials and costs in incompatible trials were present for both response modalities; all  $t_s(9) > 2.4$ , all  $p_s < .04$ .

For error rates, main effects of prime location,  $F(1, 9) = 5.23, p < .048$ , and compatibility,  $F(2, 18) = 9.8, p < .007, \epsilon = .626$ , were present, because errors were more frequent in the central prime condition and for compatible trials (see Figure 1). A significant Compatibility  $\times$  Prime Position interaction was obtained,  $F(2, 18) = 14.65, p < .002, \epsilon = .590$ , indicating that error rates were differentially distributed across the compatibility conditions in the central and

peripheral prime conditions. In addition, a Response Modality  $\times$  Compatibility  $\times$  Prime Position interaction was present,  $F(2, 18) = 14.65, p < .002, \epsilon = .590$ . We further tested those effects by conducting ANOVAs separately for the central and peripheral prime conditions. For central primes, main effects of response modality,  $F(1, 9) = 8.22, p < .019$ , and compatibility,  $F(2, 18) = 12.74, p < .004, \epsilon = .578$ , were obtained, reflecting more frequent eye movement errors and a larger error rate in compatible trials. No Response Modality  $\times$  Compatibility interaction was present. For peripheral primes, a main effect of compatibility,  $F(2, 18) = 4.34, p < .042, \epsilon = .781$ , was accompanied by a Response Modality  $\times$  Compatibility interaction,  $F(2, 18) = 7.85, p < .016, \epsilon = .563$ . Additional paired  $t$  tests were conducted separately for manual and saccadic response errors in the central and peripheral prime conditions. For manual responses, significant error costs were obtained for compatible trials in the central prime condition and for incompatible trials in the peripheral prime condition as compared with the neutral condition; both  $t_s(9) > 2.7$ , and both  $p_s < .024$ . For saccadic responses, significant error costs for compatible trials and error benefits for incompatible trials were found in the central prime condition; both  $t_s(9) > 2.65$ , and both  $p_s < .026$ . In Figure 2, a residual tendency to move the eyes to the incorrect sides in response to centrally presented compatible primes is shown; that tendency resulted from the large percentage of eye movement errors in that condition. No significant differences between compatibility conditions were present for eye movement error rates in the peripheral prime condition.

The pattern of results obtained in Experiment 1 shows



**FIGURE 2.** Experiment 1. Grand-averaged horizontal electrooculographic (EOG) waveforms measured relative to target onset in compatible, neutral, and incompatible trials in blocks in which masked primes were presented centrally (**upper panel**) and peripherally (**lower panel**). EOGs were collapsed across trials with correct eye movements and trials in which the initial saccade was incorrect. Downward-going deflections indicate eye movements to the side indicated by the target, and upward-going deflections indicate incorrect eye movements.

that prime–target compatibility effects can be obtained in tasks that do not involve visuomanual couplings. For manual responses, the results obtained in previous studies were replicated. Positive compatibility effects were observed when primes were presented peripherally, and negative compatibility effects were found when primes were presented at fixation. The central–peripheral asymmetry was not restricted to manual responding but was also observed for saccades. Similar results were found for error rates, except that no significant positive compatibility effects were present for saccadic responses in the peripheral prime

condition. It is thus unlikely that the central–peripheral asymmetry reflects the differential sensitivity of dorsal stream circuits responsible for the control of manual responses to foveal and peripheral information. More generally, the presence of qualitatively similar patterns of priming effects for manual and saccadic responses rules out the idea that those effects are mediated by specialized dorsal stream circuits involved in visuomanual control. It should be noted that saccades were about 120 ms faster than manual responses. In spite of the large baseline difference in response latencies between modalities, the overall pattern of prime–target compatibility effects was sufficiently similar to warrant the conclusion that masked primes have equivalent effects on manual responses and on eye movements; the effects involve not only different effectors but also different cortical and subcortical control circuits.

Given the present results, one should critically re-evaluate the general idea that the effects of masked primes on performance effects reflect dorsal stream processing. According to Milner and Goodale (1995), the dorsal stream controls prehensile and other skilled movements by continuously updating visual object features (size, shape, orientation, and location) and integrating them with ongoing movement sequences. In contrast, responding to the shape of a visual stimulus with a left or right button press or saccade in a masked prime experiment involves much simpler, fixed, and largely arbitrary stimulus–response mappings. It is not at all obvious that this type of motor task should primarily be controlled by the dorsal stream. A direct way to show that prime–target compatibility effects are not produced by dorsal stream processes is to demonstrate their presence for a task that is clearly not controlled by the dorsal stream.

In Experiment 2, we compared prime–target compatibility effects in a manual response task and in a vocal response task. Vocal responses to visual stimuli are controlled by inferior temporal (ventral) rather than parietal (dorsal) brain areas (Peterson, Fox, Posner, Mintun, & Raichle, 1988). Visual information is transmitted from striate and extrastriate cortex via inferior temporal cortex to Broca's area (Büchel, Price, & Friston, 1998; Kioysawa et al., 1996) and further to motor and supplementary motor cortex. The relevance of inferior temporal pathways for the control of vocal responses to visual stimuli is underlined by the observation that a lesion in that region results in impaired naming of visually presented objects (Ferreira, Giusiano, Ceccaldi, & Poncet, 1997). If prime–target compatibility had had qualitatively similar effects on vocal and manual responses in Experiment 2, the hypothesis that those effects are primarily produced within the dorsal stream would have been seriously undermined.

## EXPERIMENT 2

Effects of masked primes on performance were compared for a manual task and for a task in which vocal responses (left or right) to target stimuli were required.

Masked primes were presented either centrally or peripherally. For manual responses, prime–target compatibility effects of opposite polarity should be found in those two presentation conditions. Because links between visual stimulation and vocal responses are mediated by ventral rather than dorsal brain areas, the presence of qualitatively analogous effects for vocal performance would show that masked primes do not selectively affect visual processing within the dorsal stream.

### Participants

Sixteen paid volunteers participated in the experiment. Two participants were excluded because their overall response error rate exceeded 10%; therefore, 14 participants (8 women and 6 men), aged 18–25 years ( $M = 21$  years), took part in the experiment. Thirteen participants were right-handed, and 1 was left-handed. All had normal or corrected-to-normal vision.

### Stimuli, Apparatus, and Procedure

Prime, mask, and target stimuli were identical to those in Experiment 1, except that no neutral primes were included. The overall procedure was similar to Experiment 1, but vocal responses instead of eye movements were required in half of the blocks, and the intertrial interval was reduced to 1,200 ms. A head-worn microphone was positioned about 2 cm in front of the participants' mouth. Verbal responses triggered a voice key through the microphone and were recorded on a tape recorder.

The experiment consisted of 12 blocks. In manual response blocks, left-pointing double arrows signaled a left-hand button press, and right-pointing double arrows signaled a right-hand button press. In vocal response blocks, participants were instructed to respond by saying "left" or "right" to left-pointing and right-pointing target arrows, respectively. In one half of all blocks (central prime condition), all stimuli were presented at fixation. In the other half (peripheral prime condition), targets were presented at fixation, and primes and masks were presented bilaterally to the left and right of fixation at a horizontal distance of  $4^\circ$  from the screen center. Each of the four combinations of response modality (manual vs. vocal) and prime location (central vs. peripheral) was realized in 3 successive blocks, which were preceded by 1 practice block. The order in which those combinations of conditions were delivered was randomized across participants. Each block consisted of 80 trials. Compatible and incompatible trials and trials with left-pointing and right-pointing target arrows were delivered randomly and with equal probability, resulting in 20 trials per block for each combination of prime–target compatibility and target identity.

### Data Analysis

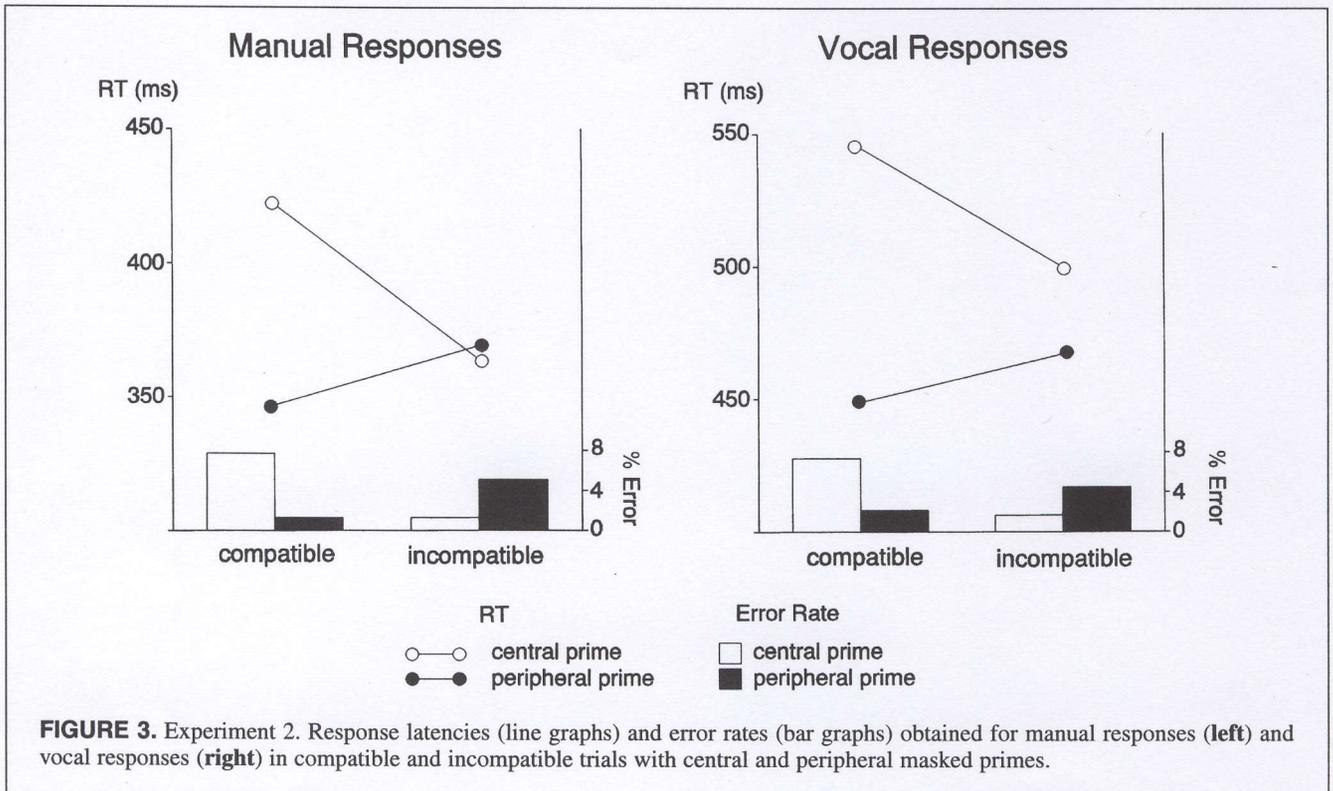
Vocal responses were categorized off-line as correct or incorrect on the basis of the tape recordings. Vocal response errors were classified as *full* when they were left uncorrect-

ed and as *corrected* when an initially incorrect vocal response was replaced by a correct response, usually prior to the completion of the incorrect utterance. Because the total number of uncorrected vocal response errors was small, both error types were collapsed for analysis. Repeated measures ANOVAs were conducted for manual and vocal RTs and for manual and vocal error rates for the variables response modality (manual vs. vocal), prime–target compatibility (compatible vs. incompatible), prime location (central vs. peripheral), and target identity (left vs. right double arrow). Additional ANOVAs were conducted separately for the central and peripheral prime conditions, and with paired  $t$  tests we conducted pairwise comparisons between performance measures obtained in compatible and incompatible trials.

## Results and Discussion

In Figure 3 are shown mean RTs and error rates obtained in compatible and incompatible trials with central and peripheral primes for manual responses (left) and for vocal responses (right). With central primes, responses were slower and error rates were higher in compatible trials than in incompatible trials. With peripheral primes, responses were faster and error rates were lower in compatible trials. That pattern was found for manual responses as well as for vocal responses. For RT, main effects of response modality,  $F(1, 13) = 527.78, p < .001$ , and prime location,  $F(1, 13) = 52.86, p < .001$ , reflected faster manual responses and faster responses in the peripheral prime condition. A main effect of compatibility,  $F(1, 13) = 22.21, p < .001$ , was accompanied by Prime Location  $\times$  Compatibility,  $F(1, 13) = 139.87, p < .001$ , and Response Modality  $\times$  Prime Location  $\times$  Compatibility,  $F(1, 13) = 8.19, p < .013$ , interactions. Whereas the former interaction reflected negative compatibility effects with central primes, turning into positive compatibility effects with peripheral primes, the latter interaction resulted from the slightly larger overall size of those effects for manual than for vocal responses. No Response Modality  $\times$  Compatibility interaction was present. For error rates, a main effect of compatibility,  $F(1, 13) = 10.31, p < .007$ , was accompanied by a Prime Location  $\times$  Compatibility interaction,  $F(1, 13) = 28.27, p < .001$ , because the direction of prime–target compatibility effects on error rates reversed with prime location. No interaction involving response modality was present for error rates.

Follow-up analyses showed that with central primes, main effects of response modality,  $F(1, 13) = 188.50, p < .001$ , and compatibility,  $F(1, 13) = 82.88, p < .001$ , were present for RT. Mean RTs were 422 ms and 364 ms for compatible and incompatible manual responses, and 545 ms and 500 ms for compatible and incompatible vocal responses. A Response Modality  $\times$  Compatibility interaction was obtained,  $F(1, 13) = 6.52, p < .024$ , because negative compatibility effects were larger for manual responses (58 ms) than for vocal responses (45 ms). Additional  $t$  tests revealed, however, that RT in incompatible trials was significantly



**FIGURE 3.** Experiment 2. Response latencies (line graphs) and error rates (bar graphs) obtained for manual responses (left) and vocal responses (right) in compatible and incompatible trials with central and peripheral masked primes.

faster than RT in compatible trials both for manual and for vocal responses; both  $t(12) > 6.8$ , both  $p < .001$ . For error rates, a main effect of compatibility,  $F(1, 13) = 23.93$ ,  $p < .001$ , reflected the greater number of errors made in compatible trials than in incompatible trials. Error rates did not differ between manual and vocal responses, and no Response Modality  $\times$  Compatibility interaction was obtained.

With peripheral primes, main effects of response modality,  $F(1, 13) = 169.57$ ,  $p < .001$ , and compatibility,  $F(1, 13) = 40.52$ ,  $p < .001$ , were present for RT. Mean RTs were 347 ms and 369 ms for compatible and incompatible manual responses and 449 ms and 467 ms for compatible and incompatible vocal responses, respectively. No Response Modality  $\times$  Compatibility interaction was present. Response errors were more frequent in incompatible trials than in compatible trials, as reflected in a main effect of compatibility,  $F(1, 13) = 21.35$ ,  $p < .001$ . Error rates did not differ between manual and vocal responses, and no Response Modality  $\times$  Compatibility interaction was obtained.

The pattern of results obtained in the second experiment seriously challenges the idea that masked primes affect performance by acting on visuomotor processes within the dorsal stream. With masked primes presented at fixation, negative compatibility effects were present, because both manual and vocal responses were faster and error rates were lower in incompatible trials. With peripheral primes, RTs were faster and error rates lower for compatible trials, both for manual and vocal responses. Although the effects of

prime–target compatibility on response latencies tended to be somewhat larger for manual than for vocal responses, the overall pattern of priming effects was very similar for both response modalities. Visuomotor control depends primarily on dorsal pathways, whereas vocal responses to visual stimuli are predominantly controlled by ventral (inferotemporal) brain regions. The fact that qualitatively similar patterns of prime–target compatibility effects were observed for manual and vocal responses strongly suggests that those effects do not result from a selective impact of the masked primes on dorsal stream processing.

## GENERAL DISCUSSION

Our aim in this study was to investigate the relations between response priming effects elicited by masked stimuli (Eimer, 1999; Eimer & Schlaghecken, 1998; Klotz & Wolff, 1995; Neumann & Klotz, 1994; Schlaghecken & Eimer, 1997, in press) and the activity of specialized perceptuomotor circuits by investigating the generality of those effects across different output modalities (manual, oculomotor, and vocal responses). In Experiment 1, we compared prime–target compatibility effects on manual and saccadic responses. Although visuomotor and oculomotor control are implemented by separate parietofrontal pathways, masked primes affected manual responses and eye movements in a qualitatively similar way, suggesting that those effects are not mediated by a selective influence of the primes on dorsal pathways specialized for visuomotor control. In Experiment 2, we compared priming effects on manual and vocal performance and found the same pattern of prime–target

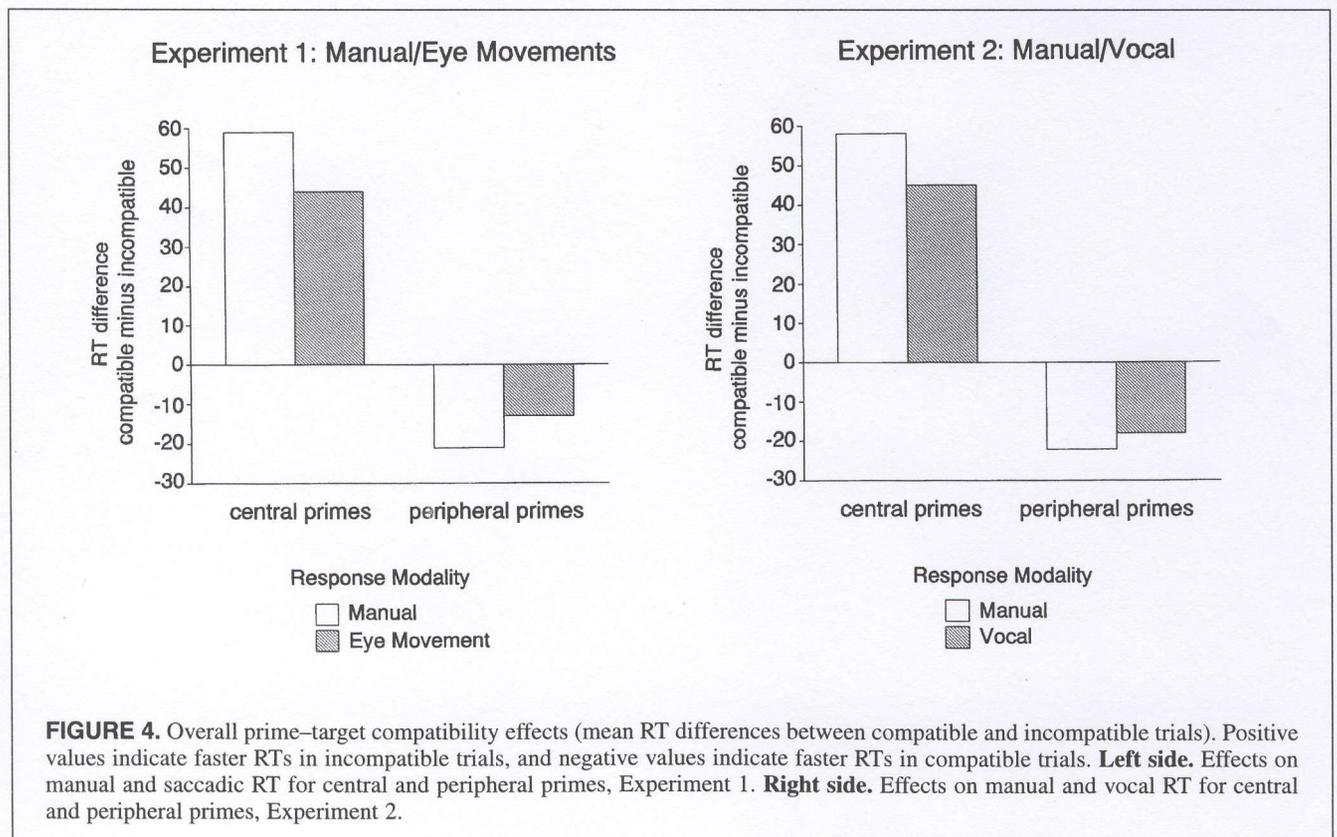
compatibility effects for both response modalities. Because it is assumed that vocal responses to visual stimuli are controlled by ventral brain areas, that finding demonstrates that the masked primes do not affect performance by selectively acting on dorsal stream processing.

For all three response modalities investigated in these studies, negative compatibility effects were found with centrally presented primes, whereas positive compatibility effects were elicited by peripheral primes. Figure 4 illustrates the presence of central-peripheral asymmetry across response modalities by showing the net compatible-incompatible RT differences obtained for central and peripheral primes. As can be seen from Figure 4, the overall size of the asymmetry was slightly larger for manual responses than for eye movements or vocal responses, and that finding was reflected in significant Response Modality  $\times$  Prime Location  $\times$  Compatibility interactions. The fact that those three-way interactions were reliably obtained in Experiment 1 as well as in Experiment 2 indicates that these experiments were sensitive enough to enable us to detect the presence of modality-specific differences in prime-target compatibility effects. The fact that the pattern of those effects remained remarkably robust in spite of variations in output modalities therefore seriously challenges the idea that the effects are mediated by specialized perceptuomotor pathways.

The central-peripheral asymmetry observed in the present study may reflect activation-followed-by-inhibition for central primes, and activation-only for peripheral primes.

Alternatively, one could argue that the different pattern of prime-target compatibility effects observed with central and peripheral primes was the result of attentional processes rather than response-related factors. Because masked primes appeared at the same location as subsequent targets in the central prime conditions, whereas they were located at irrelevant positions in the peripheral prime conditions, peripheral primes may have been more effectively filtered out, leading to reduced priming and a delayed inhibitory response. However, findings reported by Schlaghecken and Eimer (in press) indicate that attentional factors cannot fully account for the central-peripheral asymmetry. In that study, we found that the asymmetry continued to be present even when prime-target SOA was increased to more than 200 ms; that finding is inconsistent with the idea that response inhibition is merely delayed for peripheral primes. In addition, we manipulated visuospatial attention in a trial-by-trial cueing paradigm and found positive compatibility effects not only in response to peripheral masked primes at uncued (unattended) locations, but also to primes at cued (attended) locations. That result suggests that the location of masked primes relative to the current focus of spatial attention does not determine the direction of prime-target compatibility effects.

The presence of qualitatively similar central-peripheral asymmetries in prime-target compatibility effects on manual, saccadic, and vocal responses suggests a modality-unspecific locus for those effects. Voluntary action requires



**FIGURE 4.** Overall prime-target compatibility effects (mean RT differences between compatible and incompatible trials). Positive values indicate faster RTs in incompatible trials, and negative values indicate faster RTs in compatible trials. **Left side.** Effects on manual and saccadic RT for central and peripheral primes, Experiment 1. **Right side.** Effects on manual and vocal RT for central and peripheral primes, Experiment 2.

visuomotor links that can be flexibly established so that largely arbitrary stimulus–response mappings can be implemented. Once such links are established, masked prime stimuli can partially activate their assigned responses even when they are presented too briefly to be accessible to attentional control and subjective awareness,<sup>2</sup> indicating that thresholds for visual information to directly affect motor stages are lower than thresholds for response selection controlled by attentional mechanisms. Masking can keep the primes below the latter threshold without preventing them from directly triggering motor activation processes. Low thresholds for sensory information to affect motor processes will allow maximally fast responses to sudden environmental changes. That advantage in speed comes at a cost, however, because motor activation tendencies will sometimes be rendered irrelevant by simultaneously or subsequently available information. The efficient control of voluntary action therefore requires inhibitory mechanisms that enable unwanted activity to be shut down. The cessation of activity may be achieved by self-inhibitory circuits triggered by motor activation; the circuits operate to facilitate a return of motor activity to baseline level. If perceptual information relevant to the activated response is currently available, that information will sustain ongoing motor activation processes in spite of inhibitory feedback (see Houghton, Tipper, Weaver, & Shore, 1996, for similar ideas). In the present experiments, a masking stimulus that arrived immediately after a prime wiped out the sensory information that previously activated a response, and as a result the continuous sensory evidence needed to counteract response inhibition was no longer available. That account fits well with the pattern of effects observed for centrally presented masked primes, and the fact that those effects were very similar across response modalities suggests that self-inhibition is a general principle in the control of different output systems. However, further research is necessary to enable us to understand the dynamics of response-activation processes triggered by peripheral events.

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#### NOTES

1. Different types of primes, masks, and targets were employed in those studies, including alphanumerical characters followed by pattern masks (see Eimer & Schlaghecken, 1998), left-pointing and right-pointing arrows masked by superimposed arrow stimuli (Eimer, 1999; Eimer & Schlaghecken, 1998), or square and diamond shapes followed by a metacontrast mask (Eimer, 1999, Experiment 3; see also Klotz & Wolff, 1995).

2. It should be noted that no separate forced choice tests were included in the present study. The masking procedure employed in these experiments was identical to the procedure used in previous experiments (see introductory discussion); in those investigations,

forced choice tests clearly showed that participants could not consciously detect or discriminate centrally or peripherally presented masked primes. In post-experimental interviews, no participants in the present study ever reported that they were aware of the presence of prime stimuli.

#### REFERENCES

- Allport, A. (1987). Selection for action: Some behavioral and neurophysiological considerations of attention and action. In H. Heuer & A. F. Sanders (Eds.), *Perspectives on perception and action* (pp. 395–419). Hillsdale, NJ: Erlbaum.
- Büchel, C., Price, C., & Friston, K. (1998). A multimodal language region in the ventral visual pathway. *Nature*, *394*, 274–277.
- Bunt, A. H., Hendrickson, A. E., Lund, J. S., Lund, R. D., & Fuchs, A. F. (1975). Monkey retinal ganglion cells: Morphometric analysis and tracing of axonal projections, with a consideration of the peroxidase technique. *Journal of Comparative Neurology*, *164*, 265–285.
- Cheesman, J., & Merikle, P. M. (1986). Distinguishing conscious from unconscious perceptual processes. *Canadian Journal of Psychology*, *40*, 343–367.
- Coles, M. G. H. (1989). Modern mind-brain reading: Psychophysiology, physiology, and cognition. *Psychophysiology*, *26*, 251–269.
- De Jong, R., Liang, C. C., & Lauber, E. (1994). Conditional and unconditional automaticity: A dual-process model of effects of spatial stimulus-response compatibility. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 731–750.
- Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, *255*, 90–92.
- Eimer, M. (1995). Stimulus-response compatibility and automatic response activation: Evidence from psychophysiological studies. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 837–854.
- Eimer, M. (1998). The lateralized readiness potential as an on-line measure of central response activation processes. *Behavioural Research Methods, Instruments, & Computers*, *30*, 146–156.
- Eimer, M. (1999). Facilitatory and inhibitory effects of masked prime stimuli on motor activation and behavioural performance. *Acta Psychologica*, *101*, 293–313.
- Eimer, M., & Schlaghecken, F. (1998). Effects of masked stimuli on motor activation: Behavioural and electrophysiological evidence. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 1737–1747.
- Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in visual search. *Perception & Psychophysics*, *16*, 143–149.
- Ferreira, C. T., Giusiano, B., Ceccaldi, M., & Poncet, M. (1997). Optic aphasia: Evidence of the contribution of different neural systems to object and action naming. *Cortex*, *33*, 499–513.
- Gratton, G., Coles, M. G. H., & Donchin, E. (1992). Optimizing the use of information: Strategic control of activation of responses. *Journal of Experimental Psychology: General*, *121*, 480–506.
- Houghton, G., Tipper, S. P., Weaver, B., & Shore, D. I. (1996). Inhibition and interference in selective attention: Some tests of a neural network model. *Visual Cognition*, *3*, 119–164.
- Kiyosawa, M., Inoue, C., Kawasaki, T., Tokoro, T., Ishii, K., Ohyama, M., Senda, M., & Soma, Y. (1996). Functional neuroanatomy of visual object naming: A PET study. *Graefes Archive of Clinical and Experimental Ophthalmology*, *234*, 110–115.
- Klotz, W., & Wolff, P. (1995). The effect of a masked stimulus on the response to the masking stimulus. *Psychological Research*, *58*, 92–101.

- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.
- Neumann, O., & Klotz, W. (1994). Motor responses to nonre-reportable, masked stimuli: Where is the limit of direct parameter specification? In C. Umiltà & M. Moskvitch (Eds.), *Attention and performance XV* (pp. 123–150). Cambridge, MA: MIT Press.
- Perry, V. H., & Cowey, A. (1984). Retinal ganglion cells that project to the superior colliculus and pretectum in the macaque monkey. *Neuroscience*, *12*, 1125–1137.
- Peterson, S. E., Fox, P. T., Posner, M. I., Mintun, M., & Raichle, M. E. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature*, *331*, 585–589.
- Ridderinkhof, K. R., van der Molen, M. W., & Bashore, T. R. (1995). Limits on the application of additive factor logic: Violations of stage robustness suggest a dual-process architecture to explain flanker effects on target processing. *Acta Psychologica*, *90*, 29–48.
- Rizzolatti, G., Luppino, G., & Matelli, M. (1998). The organization of the cortical motor system: New concepts. *Electroencephalography and Clinical Neurophysiology*, *106*, 283–296.
- Schlaghecken, F., & Eimer, M. (1997). The influence of subliminally presented primes on response preparation. *Sprache & Kognition*, *16*, 166–175.
- Schlaghecken, F., & Eimer, M. (in press). A central/peripheral asymmetry in subliminal priming. *Perception & Psychophysics*.
- Simon, J. R. (1969). Reactions toward the source of stimulation. *Journal of Experimental Psychology*, *81*, 174–176.

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