# Effects of Masked Stimuli on Motor Activation: Behavioral and Electrophysiological Evidence

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Three experiments investigated the influence of unperceived events on response activation. Masked primes were presented before a target. On compatible trials, primes and targets were identical; on incompatible trials, opposite responses were assigned to them. Forced-choice performance indicated that prime identification was prevented by the masking procedure, but overt performance and motor activation as mirrored by the lateralized readiness potential (LRP) were systematically influenced by the prime. The direction of these effects was unexpected: Performance costs for compatible and performance benefits for incompatible trials were obtained relative to a neutral trial condition. The LRP revealed a sequential pattern of motor activation. A partial activation of the response corresponding to the prime was followed by a reverse activation pattern. It is argued that these effects primarily reflect an inhibition of the response initially triggered by the prime.

To adequately control their behavior, organisms must be provided with sufficient information about their surroundings. For humans, visual perception seems to be one of the most important sources of this information: Actions are planned and prepared on the basis of visual information, their execution is guided by visual information, and their effects are often monitored by means of visual information. This obvious relation between vision and action becomes problematic, however, when one tries to explicate more precisely what is meant by the term *visual perception*. It seems natural to identify visual perception with the construction of the integrated representation of objects and events that form people's conscious experience of the external world. According to this view, the conscious experience of objects and events is a necessary condition for the control of visuomotor performance. However, there is increasing evidence from different sources suggesting that this view may not be entirely correct.

Probably the most famous example of a dissociation between conscious visual perception and visually guided performance is the phenomenon of "blindsight": Patients

with cortical blindness in one hemifield caused by damage in the contralateral primary visual cortex can make use of visual information presented in their blind field (e.g., they can perform eye movements or pointing gestures toward the stimulus), although they report that they are unaware of this information (cf. Weiskrantz, Warrington, Sanders, & Marshall, 1974). Equally puzzling are cases of visual form agnosia with intact visuomotor performance. Milner et al. (1991) described a patient suffering from form agnosia caused by a lesion in the ventrolateral occipital cortex. Despite profound deficits in the recognition of object size and orientation, the patient's visuomotor performance directed at these objects was found to be similar to the performance of neurologically unimpaired control participants (cf. Milner & Goodale, 1995, for a detailed discussion).

Although these cases are fascinating in themselves, one may be inclined to interpret them as indicating bizarre deficits in accessing conscious representations that are specific to neurological patients rather than reflecting a true dissociation between conscious perception and visuomotor control. However, similar phenomena have also been reported for neurologically unimpaired participants. For example, Bridgeman, Kirch, and Sperling (1981) manipulated the perceived position of a stationary visual target by moving a surrounding frame. Although participants perceived the target as moving in a direction opposite to the frame's movement, they pointed accurately to the target's actual location. Agliotti, DeSouza, and Goodale (1995) demonstrated an analogous effect with respect to object size: Participants were asked to pick up a target disk surrounded by either smaller or larger disks. Although the same target disk was perceived as being smaller when it was surrounded by larger disks and as larger when it was surrounded by smaller disks (the so-called Titchener illusion), grasping movements were little affected by this perceptual illusion. Grip aperture was determined by the actual, not by the apparent, size of the target disk.

Observations like these have challenged the view that

visuomotor performance is exclusively guided by visual information that is present in perceptual experience. As an alternative to this view, Milner and Goodale (1995) recently advocated a "two visual systems hypothesis." On the basis of a distinction put forward, although with a different emphasis, by Ungerleider and Mishkin (1982; see also Trevarthen, 1968, for an earlier distinction between two visual systems), Milner and Goodale argued that visual perception (i.e., the construction of integrated representations necessary for the recognition of external objects) and visuomotor control (i.e., the preparation and control of actions directed toward external objects) are separate functions of the visual system that are subject to different constraints and mediated by different neural pathways. Milner and Goodale (1995) assumed that visual perception is subserved by the ventral processing stream that connects the primary visual projection areas with regions of the inferotemporal cortex, whereas visuomotor control is mediated by the dorsal stream that projects from the primary visual cortex to the posterior parietal cortex. If such a functional separation does exist within the visual system, dissociations between (conscious) visual perception and visuomotor control should not be surprising. Moreover, these dissociations should arise not only under conditions in which the visual system is impaired (as in neurological patients) or "tricked" (by using visual illusions) but also under conditions in which the conscious perception of task-relevant stimuli is completely prevented.

Such effects have indeed been observed. In an experiment by Goodale, Pellisson, and Prablanc (1986), participants were required to move a finger from a central stimulus to a target light that appeared abruptly in the periphery. In 50% of the trials, the target was displaced during a saccadic eye movement. Although participants were unable to discriminate between displacement and nondisplacement trials, the trajectory of the aiming movements was adequately corrected when targets were displaced. Instead of delivering events during saccadic suppression, Fehrer and Raab (1962) used metacontrast masking to prevent the conscious perception of a stimulus. A test stimulus was masked by adjacent stimuli that followed it with a stimulus onset asynchrony (SOA) between 0 and 75 ms. Although the test stimulus was assumed to be phenomenally absent at longer SOAs (for metacontrast masking, see Breitmeyer, 1984), simple reaction time (RT) was equally fast as simple RT to an unmasked test stimulus. Metacontrast masking may thus interfere with the conscious perception of stimuli, although it seems to be irrelevant with respect to the activation of a motor response. More recently, Neumann and Klotz (1994) demonstrated analogous effects for choice RT. Participants had to respond with a left or right keypress to a left or right box when it was marked by two horizontal bars. These targets were preceded by smaller horizontal bars (primes) that appeared inside the box at the same position as the subsequent target (compatible trials) or at the contralateral side (incompatible trials). On neutral trials, no primes were delivered. Although signal-detection analyses revealed that the primes could not be consciously discriminated, a cost-benefit pattern was found for RT, with fast responses on compatible trials and

slow responses on incompatible trials. According to Neumann and Klotz (1994), this pattern of results reflects the phenomenon of *direct parameter specification*, that is, a direct link between sensory information and response parameters without mediation by conscious perception. In terms of the model advocated by Milner and Goodale (1995), direct parameter specification may be interpreted as a function of the visuomotor control system located in the dorsal processing stream.

However, the cost-benefit pattern reported by Neumann and Klotz (1994) may at least partially be attributable to sensory priming because primes and targets were presented at identical locations in compatible trials but at contralateral sides in incompatible trials. Evidence for this was found by Neumann and Klotz (1994, Experiment 5) when a central stimulus position was included that was mapped onto the same response as one of the lateral positions. In that situation, the RT benefits for response-compatible trials were found only when primes and targets appeared at identical locations. To measure the effects of motor priming on behavioral performance independently of sensory priming, all stimuli should be presented at identical positions. In the experiments reported in this article, we used a procedure that was similar to that of Neumann and Klotz (1994) but with two major differences: First, masked primes and targets were always presented at fixation, and responses were assigned to stimulus identity. In compatible trials, primes and targets were identical; in incompatible trials, opposite responses were mapped to primes and targets. In neutral trials, an irrelevant prime was presented. Second, the mask did not serve as an imperative stimulus but was immediately followed by a target stimulus. Thus, three separate stimuli were delivered on each trial: a prime (16-ms duration), a mask (100-ms duration), and a target (100-ms duration), with no interval between them.

To investigate more directly whether masked primes would have an effect on response-related processes, we recorded the lateralized readiness potential (LRP) as a continuous electrophysiological measure of motor activation. The LRP is assumed to reflect the degree to which left- and right-hand responses are activated, and it is computed on the basis of the electroencephalographic (EEG) potentials obtained above the motor cortex areas that control right- and left-hand movements (for details, see Coles, Gratton, & Donchin, 1988; De Jong, Wierda, Mulder, & Mulder, 1988; for a discussion of the validity of the LRP as an index for response activation processes, see Coles, 1989; Eimer, 1995). If the primes have an effect on motor processes, this should be reflected in the LRP waveforms. In compatible trials, an activation of the correct response should be triggered by the primes; in incompatible trials, an activation of the incorrect response should be present; and no such effects should be found in neutral trials. In addition, these response activations should also be reflected in behavioral performance: When compared with the neutral trial condition, performance benefits (faster RTs and fewer errors) should be observed in compatible trials, whereas performance costs (slower RTs and more errors) should arise in incompatible trials.

## Experiment 1

In Experiment 1a, the targets were left-pointing and right-pointing double arrows, requiring a left- or right-hand response. The mask was created by superimposing left- and right-pointing double arrows on one another. On compatible trials, primes and targets were identical; on incompatible trials, the prime was identical to the other target. On neutral trials, inward-pointing or outward-pointing double arrows were used as primes. Experiment 1b was introduced as a control condition in which identical primes but different target stimuli were used. The letter pairs LL and RR served as targets and required a left-hand and a right-hand response, respectively. If the effects of masked primes on motor activation were attributable to the specific stimulus–response (S-R) pairings as determined by the instruction, no systematic influence of the primes should be present in Experiment 1b. If left-pointing and right-pointing arrow primes activated spatially corresponding responses independently of specific response assignments, they should have a measurable influence on motor activation and overt performance.

### Method

*Participants.* Twelve paid volunteers (7 women and 5 men) ranging in age from 21 to 38 years (mean age = 30.3 years) participated in the experiment. All participants were right-handed and had normal or corrected-to-normal vision.

*Stimuli and apparatus.* Four different prime stimuli were used: left- and right-pointing double arrows (<< and >>) and double arrows that pointed into opposite directions (<> and ><). All stimuli were presented at fixation in black in front of a white background on a computer monitor (60 Hz). The mask consisted of left- and right-pointing double arrows superimposed on one another. Target stimuli were different for Experiments 1a and 1b: In Experiment 1a, left- and right-pointing double arrows (<< and >>) were used, whereas uppercase letter pairs (LL and RR) served as targets in Experiment 1b. All stimuli were presented at the center of the computer screen and subtended a visual angle of approximately 0.8° × 0.35°. In the forced-choice performance block, the same masked prime stimuli were presented as in the regular experimental blocks, but the target stimuli were omitted.

*Procedure.* Participants were seated in a dimly lit, electrically shielded, and sound-attenuated chamber, with response buttons under their left and right index fingers. A computer screen was placed 110 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. The experiment was divided into halves (referred to as Experiments 1a and 1b), each consisting of 10 blocks. At the end of the experiment, a forced-choice performance block was added, resulting in a total of 21 experimental blocks. The regular blocks consisted of 84 trials. Each trial consisted of the presentation of a prime stimulus (16-ms duration), a mask (100-ms duration), and the target stimulus (100-ms duration), with no intervals between these stimuli. The intertrial interval was 1 s.

In Experiment 1a, left-pointing double arrows required a left-hand buttonpress, and right-pointing double arrows required a right-hand buttonpress. In Experiment 1b, the letter pair LL required a left-hand buttonpress, and the letter pair RR required a right-hand buttonpress. In Experiment 1a, primes and targets were identical on compatible trials, whereas on incompatible trials a left-pointing double arrow prime was followed by a right-pointing

double arrow target and vice versa. In Experiment 1b, trials were termed compatible when the response required by the target corresponded to the direction of the arrow primes (i.e., when the prime << was followed by the target LL or the prime >> was followed by RR). In incompatible trials, the direction of the arrow primes was opposite to the response assigned to the target. In both experimental halves, symmetrical primes (>< and <>) were presented in neutral trials. Each block consisted of 28 compatible, 28 incompatible, and 28 neutral trials. In 14 neutral trials, the prime <> was delivered, whereas the prime >< was presented in the other 14 neutral trials. Participants were asked to respond as fast and accurately as possible and to maintain central eye fixation during the trials. A short training block was run at the beginning of the experiments.

The forced-choice performance block consisted of 40 trials. Left- and right-pointing double arrow primes were presented for 16 ms and were then followed by a 100-ms presentation of the mask. No target stimulus was delivered. The intertrial interval was 2 s. Participants had to indicate with a left- or right-hand buttonpress the identity of the prime. All participants were strongly encouraged to respond in all trials irrespective of whether they were subjectively aware of the prime.

*Data recording.* EEG activity was recorded with Ag–AgCl electrodes from Fpz (according to the 10–20 system; cf. Jasper, 1958), from C3' and C4' (located 1 cm in front of C3 and C4, respectively), and from OL and OR (located halfway between O1 and T5 and between O2 and T6, respectively). Only the data from C3' and C4' that were used to compute the LRP are reported in this article. All electrodes were referenced to the right earlobe. Electrode impedance was kept below 5 kΩ. The amplifier bandpass was 0.1–40 Hz. EEG activity was sampled with a digitization rate of 200 Hz and stored on disk. RTs were recorded for each trial.

*Data analysis.* EEG activity was averaged off-line for epochs of 700 ms, starting 100 ms before prime onset and ending 600 ms after prime onset. Epochs with eyeblinks, eye movements, muscular artifacts, or incorrect buttonpress responses were excluded from analysis.

EEG activity was averaged separately for each experimental half and each combination of the factors prime–target compatibility (compatible vs. incompatible vs. neutral) and response side (left vs. right). In the neutral trial conditions, trials were averaged separately for the two different prime stimuli. Because no effect of neutral prime type on LRP amplitudes was found in a preliminary analysis, we collapsed and analyzed the data obtained in response to each of the two neutral primes together. The LRP was computed separately for compatible, incompatible, and neutral trials relative to a 100-ms baseline interval before prime onset. To obtain the LRP, we subtracted the C3'–C4' difference potentials for trials with right-hand responses from the C3'–C4' difference potentials for trials with left-hand responses. As a result of this procedure, positive (downward-going) deflections in the LRP waveforms indicate the activation of a correct response (the response assigned to the target stimulus in a given trial), whereas negative (upward-going) deflections indicate incorrect response activation.

The LRP waveforms obtained for compatible, incompatible, and neutral trials were analyzed within consecutive 50-ms time windows in the interval between prime onset and 450 ms after prime onset. Repeated measures analyses of variance (ANOVAs) were conducted on the LRP mean amplitude values obtained within these time windows for the factors of experimental condition (Experiment 1a vs. Experiment 1b) and prime–target compatibility (compatible vs. incompatible vs. neutral). Separate ANOVAs were conducted for each experimental half for the factor of prime–target compatibility. Greenhouse–Geisser adjustments to the degrees of freedom were performed. When appropriate, pairwise comparisons
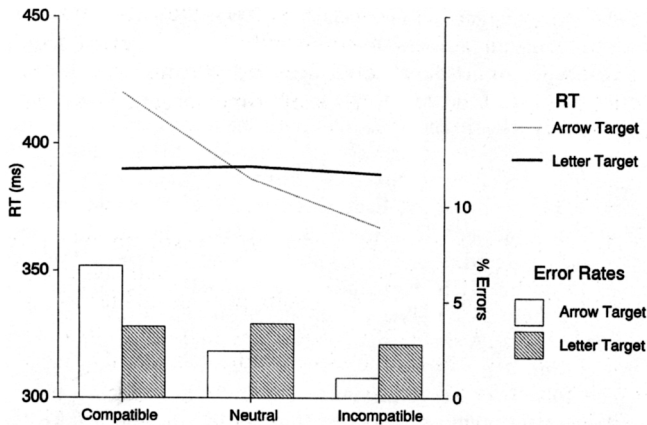
*Figure 1.* Mean response times (RTs; line graphs) and error rates (bar graphs) obtained in the compatible, neutral, and incompatible trials for arrow targets (Experiment 1a) and letter targets (Experiment 1b).

between the LRP amplitudes obtained in the compatible, incompatible, and neutral trials were conducted with paired *t* tests. Additional one-tailed paired *t* tests were used to test whether specific LRP amplitude modulations were significantly different from zero.

For the RT data, a repeated measures ANOVA was performed for the factors of experimental half, prime–target compatibility, and response side. Separate ANOVAs were performed for the factors of prime–response compatibility and response side for each experimental half. Again, Greenhouse–Geisser adjustments to the degrees of freedom were performed. Pairwise comparisons between the RTs for compatible, incompatible, and neutral trials were conducted with paired *t* tests. Additional repeated measures ANOVAs were performed on the response error rates for compatible, incompatible, and neutral trials obtained in Experiments 1a and 1b. Paired *t* tests were used for pairwise comparisons of error rates among these three conditions. For the forced-choice block, a paired *t* test was used to test whether the participants' discriminative performance was significantly different from chance.

## Results

*Behavioral performance.* Prime–target compatibility had a significant influence on RT, $F(1, 11) = 30.74, p < .001$, $\epsilon = .586; MSE = 147.5$. An interaction between compatibility and experimental condition, $F(2, 22) = 41.28, p < .001$, $\epsilon = .568; MSE = 101.5$, indicated that compatibility affected RT differently in Experiments 1a and 1b. This was confirmed by additional ANOVAs conducted separately for Experiments 1a and 1b. In Experiment 1a, in which arrows served as targets, a highly significant effect of compatibility was obtained, $F(2, 22) = 37.6, p < .001, \epsilon = .539, MSE = 231.5$. No such effect was present in Experiment 1b, in which letters served as targets. A direct comparison of the RTs obtained in the compatible, neutral, and incompatible trials confirmed that prime–target compatibility had a strong influence on RTs in Experiment 1a but that the direction of this influence was exactly opposite to what was expected (see Figure 1). RTs in the compatible, neutral, and incompatible trials were 420, 386, and 367 ms, respectively. Additional paired *t* tests revealed significant differences between

each task condition, $ts(11) > 4.8, ps < .001$. In Experiment 1b, the RTs in the compatible, neutral, and incompatible trials were 388, 391, and 390 ms, respectively, and none of these differences was significant.

The error rates observed for the three task conditions were in accordance with these unexpected RT effects (see Figure 1). In Experiment 1a, the error rates for the compatible, neutral, and incompatible trials were 6.9%, 2.5%, and 1%. This was reflected in a significant effect of prime–target compatibility on error rate, $F(2, 22) = 9.67, p < .008, \epsilon = .533, MSE = 91.2$. Paired *t* tests confirmed the presence of significant differences in error percentages between each task condition, $ts(11) > 2.8, ps < .015$. In Experiment 1b, no effect of prime–response compatibility on error rates was present.

In the forced-choice discrimination blocks, participants correctly identified the prime on 51% of all trials and made an incorrect response on 49%. A paired *t* test showed that this result was not significantly different from chance performance, $t(11) = 0.4, p > .70$.

*LRP.* Figure 2 shows the LRP waveforms obtained for the compatible, neutral, and incompatible trials in Experiment 1a (top) and Experiment 1b (bottom). Whereas no
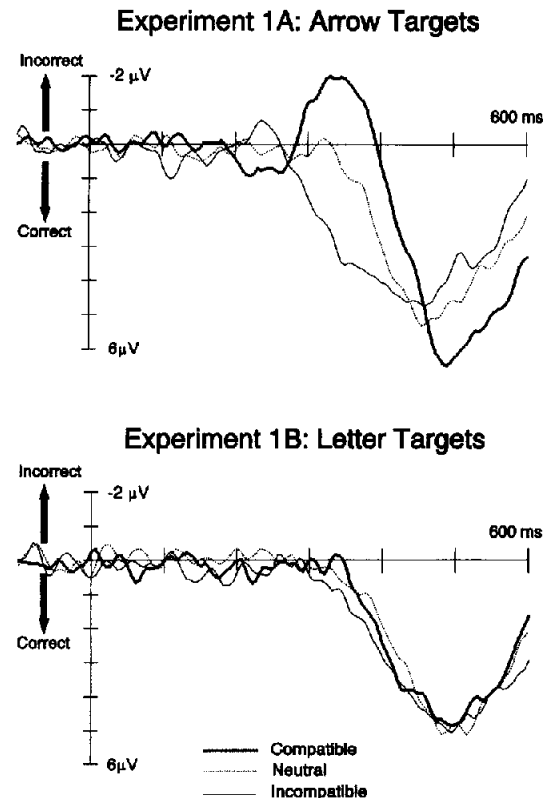
## Experiment 1A: Arrow Targets



## Experiment 1B: Letter Targets



*Figure 2.* Grand mean lateralized readiness potential waveforms recorded in the interval between prime onset and 600 ms after prime onset for the compatible, neutral, and incompatible trials in Experiment 1a (arrow targets, top graph) and Experiment 1b (letter targets, bottom graph). Downward-going deflections indicate the activation of the correct response (the response assigned to the target stimulus), and upward-going deflections indicate the activation of the incorrect response.

obvious difference between these conditions was present in Experiment 1b, strong effects of prime–target compatibility on the LRPs were observed for Experiment 1a. A first marked difference between the three task conditions was seen 200–270 ms after prime onset. Within this time interval, the LRPs revealed an activation of the correct response in compatible trials, an activation of the incorrect response in incompatible trials, but no systematic response activation in neutral trials. This initial response activation reversed around 280 ms after prime onset, giving way for an activation of the incorrect response in compatible trials and an activation of the correct response in incompatible trials.

These observations were substantiated by statistical analyses. No significant effect of prime–target compatibility was obtained before 200 ms after prime onset. Between 200 ms and 250 ms after prime onset, the interaction between prime–target compatibility and experimental condition approached significance, $F(2, 22) = 2.84, p < .083, \epsilon = .960$, $MSE = 0.76$. In Experiment 1a, but not in Experiment 1b, an almost significant effect of prime–target compatibility was present, $F(2, 22) = 3.67, p < .071, \epsilon = .608, MSE = 1.09$. One-tailed paired $t$ tests showed that the LRP for incompatible trials was significantly more negative than the LRP measured in neutral and compatible trials, $ts(11) > 1.8, ps < .05$, and that the difference between the LRP measured in compatible and neutral trials approached significance, $t(11) = 1.7, p < .059$. Additional paired $t$ tests showed that the LRP amplitude for compatible trials was significantly positive, $t(11) = 2.03, p < .034$, whereas for the incompatible trials the LRP amplitude tended to be below zero, $t(11) = 1.75, p < .055$.[1]

No significant effects of prime–response compatibility were observed in the 250- to 300-ms time interval. Between 300 ms and 350 ms after prime onset, a significant effect of compatibility was again observed, $F(2, 22) = 22.47$, $p < .001, \epsilon = .676, MSE = 1.73$, accompanied by an interaction between compatibility and experimental condition, $F(2, 22) = 9.56, p < .003, \epsilon = .745, MSE = 2.12$. No significant effect of prime–response compatibility was found for Experiment 1b. In contrast, compatibility had an effect in Experiment 1a, $F(2, 22) = 19.3, p < .001, \epsilon = .569, MSE = 2.99$. A paired $t$ test revealed significant differences in LRP amplitude between each task condition, $ts(11) > 3.1, ps < .009$. The LRP waveforms elicited in compatible trials were significantly larger than zero, $t(11) = 3.61, p < .002$, and the LRP amplitudes elicited in incompatible trials were significantly smaller than zero, $t(11) = 4.75, p < .001$.

A similar pattern was observed between 350 ms and 400 ms after prime onset. Effects of prime–response compatibility were observed, $F(2, 22) = 11.86, p < .005, \epsilon = .533$; $MSE = 3.43$, as well as an interaction between compatibility and experimental condition, $F(2, 22) = 7.81, p < .011, \epsilon = .633, MSE = 3.31$, reflecting the fact that compatibility had a significant effect in Experiment 1a, $F(2, 22) = 10.81, p < .006, \epsilon = .536, MSE = 5.95$, but not in Experiment 1b. In Experiment 1a, significant differences between each task condition were again present, as evidenced by paired $t$ tests, $ts(11) > 2.95, ps < .007$. Although the LRPs for the neutral and incompatible trials showed a significant activation of the

correct response, $ts(11) > 4.3, ps < .001$, the LRP obtained for compatible trials was not significantly different from zero within this time window. Beyond 400 ms after prime onset, no significant LRP effects of prime–target compatibility were obtained.

## Discussion

Our aim in Experiment 1 was to investigate whether masked visual stimuli would affect motor activation and behavioral performance. The results provide evidence that this is indeed the case. Participants' discriminative performance in the forced-choice blocks indicated that the masking procedure was effective in preventing the perceptual identification of the prime stimuli. Identification performance was at chance level, and all participants reported their inability to perceive the masked stimulus in both the regular and forced-choice blocks. Nevertheless, prime–target compatibility was found to have a profound impact on both behavioral measures and LRP waveforms in Experiment 1a. However, the direction of the behavioral effects found in Experiment 1a was exactly opposite of what had been predicted at the beginning of the experiment. Instead of observing performance benefits for compatible trials and performance costs in incompatible trials (as reported by Neumann & Klotz, 1994), we observed delayed responses and high error rates in compatible trials and the fastest responses and the lowest error rates in incompatible trials.

Which processes are responsible for these unexpected cost-benefit effects? The LRP waveforms revealed that the prime stimuli initially activated their corresponding responses, with an activation of the correct response in compatible trials and an activation of the incorrect response in incompatible trials. No systematic response activation was present within this time window in neutral trials. This initial activation of the response corresponding to the primes' direction was later reversed. For compatible trials, the LRPs indicated an activation of the incorrect response. At the same time, the correct response was already partially activated on incompatible trials. In neutral trials, the onset of the correct response activation started considerably later than in incompatible trials, but earlier than in compatible trials.

The LRP effects observed for the compatible, neutral, and incompatible trials conformed nicely with the behavioral results. Given that the target stimulus was identified and the corresponding response selected around 300 ms after prime onset (about 200 ms after target onset), the state of motor activation within this critical time period differed among the three compatibility conditions: Whereas the correct response was already activated on incompatible trials, the incorrect response seemed to be partially activated on compatible

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[1] An additional analysis was conducted on the LRP waveforms measured between 220 and 270 ms after prime onset. Within this interval, the LRP amplitudes for compatible trials were significantly positive, whereas the LRP amplitudes obtained for incompatible trials were significantly negative: $ts(11) = 1.86$ and $2.1, ps < .045$ and $0.30$, one-tailed, respectively.

trials. Under these conditions, fast responses and few response errors should be expected for incompatible trials, whereas delayed responses and more erroneous reactions should be found for compatible trials, with the performance in neutral trials falling in between performance for these two conditions.

No systematic effects of prime–response compatibility on behavioral and electrophysiological measures were found in Experiment 1b, in which letters were used as targets. The fact that no early effects of the arrow primes on the LRP waveforms were observed indicates that these effects were not elicited automatically by the primes, but only when specific responses were assigned to these stimuli. However, it is not yet clear whether any response assignment is sufficient to trigger this early response activation. It is conceivable that it will be elicited only under conditions of high spatial S-R compatibility between primes and responses. This was investigated in Experiment 2.

Which factors are responsible for the behavioral effects and the successive LRP deflections observed in Experiment 1a? The first LRP phase (the activation of the response assigned to the prime) probably reflects that sort of direct link between visual information and response parameters postulated by Neumann and Klotz (1994). With respect to the second phase (presumably indicating an activation of the response opposite to the one initially activated), different interpretations are conceivable. On the one hand, it is possible that the second "activation" phase actually reflects an inhibition of the response that was initially activated. This was further investigated in Experiment 3. On the other hand, the LRP waveforms may truly reflect the successive activation of two opposite response tendencies, and the specific prime–mask configuration realized in Experiment 1 may be responsible for this. Because the mask resulted from the superimposition of two double arrows pointing in different directions, presenting left- or right-pointing double arrows as primes that were then followed by the mask was equivalent to presenting double arrows pointing in opposite directions in rapid succession. One possibility is that this stimulus sequence resulted in an induced motion in the direction opposite to the prime arrow's direction, which in turn may have triggered a corresponding response activation. If induced motion was a critical factor, similar prime–target compatibility effects should have been obtained in Experiments 1a and 1b, which was clearly not the case. To finally rule out this possibility, in Experiment 2 we investigated whether the effects observed in Experiment 1a could be replicated in a situation in which prime stimuli that would not give rise to induced motion were used.

## Experiment 2

In this experiment, symmetrical primes and targets were used to prevent any induced motion to the left or right from being elicited by the sequential presentation of primes and masks. Moreover, this set of stimuli made it possible to investigate whether the initial activation of the response assigned to the prime can also be observed in a situation in which all S-R mappings are noncompatible. In contrast to

Experiment 1, only compatible and incompatible trials were included.

### Method

*Participants.* Twelve paid volunteers participated in this experiment. One of them had to be excluded because of excessive eyeblink activity, leaving 7 women and 4 men (aged 22–38 years; mean age = 29.4 years) in the sample. All participants were right-handed and had normal or corrected-to-normal vision.

*Stimuli, apparatus, and procedure.* In contrast to Experiment 1, symmetrical arrow stimulus arrays (<> and ><) were used as primes and targets, and no neutral trials were included. The mask was identical to that used in Experiment 1. The experiment consisted of 10 regular blocks, followed by 2 forced-choice discrimination blocks. The regular blocks consisted of 80 trials (40 compatible trials and 40 incompatible trials) and had a duration of about 97 s. The stimuli <> and >< served as primes and targets, and participants were instructed to respond to the target <> with a left-hand buttonpress and to the target >< with a right-hand buttonpress. In all other respects, the procedure in the regular blocks was identical to that in Experiment 1.

In one forced-choice block (identity condition), the stimuli <> and >< were presented and subsequently masked, and participants were instructed to make a left-hand response to the former stimulus and a right-hand response to the latter stimulus. In the second forced-choice block (present–absent condition), these stimuli were presented on only 50% of all trials, and no stimulus was presented on the other half of the trials. Participants were instructed to make a left-hand response when a stimulus was present and a right-hand response when no stimulus was presented before the mask. In all other respects, the procedure was identical to that used in Experiment 1.

*EEG recording and data analysis.* EEG recording and data analysis were equivalent to those used in Experiment 1 except that the experimental condition factor was omitted.

### Results

*Behavioral performance.* Again, prime–target compatibility had a significant effect on RT, $F(1, 10) = 32.67$, $p < .001$, $MSE = 549.6$. The RTs in the compatible and incompatible trials were 462 and 422 ms, respectively. In addition, compatibility had a significant influence on error rates, $F(1, 10) = 16.1, p < .002, MSE = 33.6$, with 4.1% errors in compatible trials and only 1.6% errors in incompatible trials (see Figure 3). In the forced-choice blocks, participants responded correctly on 50.2% of all trials in the identity condition and on 51.6% of all trials in the present–absent condition. Paired $t$ tests showed that the discriminative performance in both conditions was not significantly different from chance, $ts(10) < 0.7, ps > .5$.

*LRP.* Figure 4 shows the LRP waveforms obtained for the compatible and incompatible trials. The pattern of results was very similar to that in Experiment 1a. An initial activation of the response indicated by the prime was later replaced by an activation of the contralateral response, which resulted in an incorrect response activation in the case of compatible trials. Statistical analyses confirmed these observations. No significant effect of compatibility was observed up to 250 ms after prime onset. Between 250 ms and 300 ms after prime onset, compatibility had an effect on

the LRP waveforms, $F(1, 10) = 5.64$, $p < .039$, $MSE = 1.44$. One-tailed paired $t$ tests showed that within this time interval, the LRP elicited in the compatible trials was significantly larger than zero, $t(10) = 1.98$, $p < .038$, whereas the LRP elicited in incompatible trials was smaller than zero, $t(10) = 2.28$, $p < .023$. No effect was observed in the next time interval (300–350 ms), but between 350 ms and 400 ms after the onset of the prime, another significant effect of prime–target compatibility was present, $F(1, 10) = 14.11$, $p < .004$, $MSE = 1.18$. Within this time range, the LRP elicited in compatible trials was significantly negative, $t(10) = 3.49$, $p < .003$, whereas the LRP amplitude obtained for incompatible trials was larger than zero, $t(10) = 2.34$, $p < .021$. Between 400 ms and 450 ms, this effect of compatibility on LRP waveforms still approached significance, $F(1, 10) = 4.37$, $p < .063$, $MSE = 2.68$. In this time range, the LRP mean amplitude obtained for compatible trials was not different from zero, whereas the LRP amplitude recorded for incompatible trials was significantly positive, $t(10) = 3.6$, $p < .002$.

## Discussion

The results obtained in Experiment 2 were clear-cut. The effects observed in Experiment 1a were essentially replicated in a situation in which no induced motion should have been produced by the sequential presentation of primes and masks. Again, performance in incompatible trials was superior to the performance measured in compatible trials, and the LRP revealed an initial activation of the response assigned to the prime that was later replaced by a contralateral response activation. This pattern of results also demonstrated that the initial activation of the response mapped to the prime could also be observed when this mapping was not spatially compatible but entirely arbitrary.

However, there is another way in which the effects observed in Experiments 1 and 2 may have resulted from the specific masking procedure. In the compatible and incompatible trials, the presentation of the mask was always equiva-
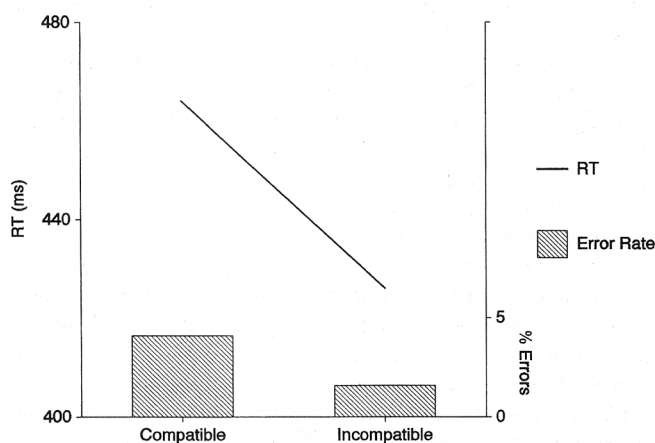


*Figure 3.* Mean response times (RTs; line graph) and error rates (bar graphs) obtained for compatible and incompatible trials in Experiment 2.
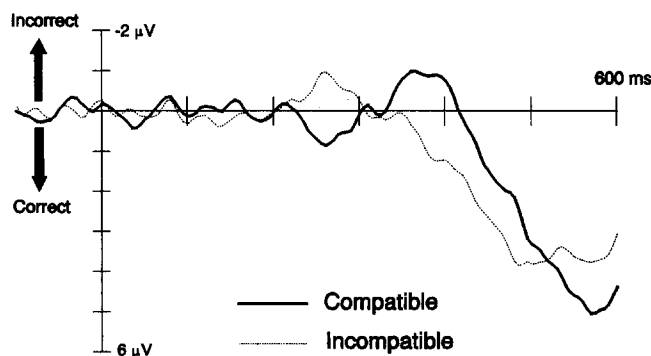


*Figure 4.* Grand mean lateralized readiness potential waveforms recorded for compatible and incompatible trials in Experiment 2.

lent to adding the opposite target stimulus to the prime, and this may have resulted in an activation of the opposite response. An obvious way to test this possibility is to use masking stimuli that are different from both targets. This was done in an RT experiment that followed the general procedure described earlier but used different primes, masks, and targets. The stimuli oo and + + were used as primes and targets and were mapped to left- and right-hand responses. In different blocks, the primes were masked by the superimposed letter pairs SS and ZZ (letter mask) or by the superimposed character strings ## and &&. Ten participants were tested, and effects analogous to those described before were obtained. For the pattern mask, RTs for compatible and incompatible trials were 407 and 390 ms, $F(1, 9) = 9.83$, $p < .012$; $MSE = 284.0$; for the letter mask, the respective RTs were 410 and 384 ms, $F(1, 9) = 25.8$, $p < .001$, $MSE = 250.9$. In addition, errors again occurred more frequently on compatible trials than on incompatible trials.

If the effects observed in Experiments 1 and 2 cannot be attributed to the specific masking procedure used, the possibility that they reflect an inhibition of the response initially activated by the prime should be considered. Unfortunately, the LRP data cannot provide unambiguous evidence with respect to this issue. Because of the way it is derived, the LRP is an index for the *relative* activation of left- and right-hand responses. A negative-going LRP deflection (as observed for the compatible trials in Experiments 1 and 2) thus may be attributable to (a) a selective activation of the incorrect response, (b) a selective inhibition of the correct response, or (c) a combination of both processes. We conducted Experiment 3 to further investigate these alternative possibilities.

## Experiment 3

If the effects observed in the first two experiments reflected the successive activation of both effectors (hands), they should be smaller or even absent when two alternative responses are mapped to the same hand. If they reflected the successive activation of two potentially relevant responses, they should not be observed when only a single overt response is to be executed in a given block. If they were due

to response inhibition processes, however, these factors should not be of critical importance. This was investigated in Experiment 3, in which only behavioral performance was measured.

In the single-hand condition, two target stimuli were mapped to the left middle and index fingers, and the right index and middle fingers, in separate blocks to investigate whether the effects observed before are critically dependent on a between-hands S-R mapping. In the single-finger condition, go and no-go target stimuli were delivered with equal probability. Go targets mapped to left- or right-hand responses were presented in separate blocks, so that the response was fixed in any given block. On compatible trials primes and targets were identical (i.e., two go or no-go stimuli were delivered), whereas on incompatible trials a no-go prime was followed by a go target or vice versa. On neutral trials, an irrelevant prime was presented before a go or no-go stimulus. If a response activation initially triggered by go primes was later inhibited, RTs should be slow for compatible go trials and only a few false alarms should be observed for incompatible no-go trials (i.e., for trials on which a no-go target was preceded by a go prime).

In addition, the forced-choice procedure was varied in Experiment 3. In the previous experiments, participants consistently reported their total inability to detect any masked stimulus in the forced-choice blocks. This subjective failure to conform to the experimental instructions may have had the unwanted consequence that participants switched to a random guess strategy. To prevent this, we varied the duration of masked stimuli in the forced-choice blocks of Experiment 3. If participants were able to successfully detect the masked stimulus at least on some forced-choice trials, this should have helped them keep their attention focused on the discrimination task.

## Method

*Participants.* Twelve paid volunteers (8 women and 4 men aged 21–38 years; mean age = 29.5 years) participated in the experiment. All participants were right-handed and had normal or corrected-to-normal vision.

*Stimuli, apparatus, and procedure.* In contrast to the first two experiments, response buttons were located under the participants' left and right index and middle fingers. Two different task conditions (single hand and single finger, each consisting of 6 blocks) were delivered successively, and these 12 regular blocks were followed by 1 forced-choice block. The order in which the single-hand and single-finger conditions were delivered was balanced between participants. Each regular block consisted of 96 trials.

In the single-hand condition, the prime, mask, and target stimuli were identical to those in Experiment 1a, but all responses were to be executed with one hand within a single block. In half the blocks, left-hand responses were required, and the target stimulus << required a response with the left middle finger, whereas the target stimulus >> required a response with the left index finger. In the other three single-hand blocks, these stimuli were mapped onto the right index and right middle fingers, respectively. Thirty-two trials per block were compatible, incompatible, and neutral, and both target stimuli were equiprobable. In the neutral trials, the prime stimuli >< and <> were delivered with equal probability.

In the single-finger blocks a no-go target stimulus (<>) was presented on 50% of the trials, whereas on the remaining half of the trials one go target stimulus (either << or >>) was presented. This stimulus was mapped to a response with the left or right index finger. On three blocks, << served as the go stimulus, whereas >> was used as the go stimulus on the other three blocks. As a result, only one response (left or right index finger) was to be performed in a given block. Go and no-go trials were classified with respect to prime–target compatibility: On compatible trials, primes and targets were identical (left-pointing or right-pointing arrows presented as prime and target on go trials, or two <> stimuli presented as prime and target on no-go trials). On incompatible trials, a go target was preceded by a no-go prime, or a no-go target was preceded by a go prime. On neutral trials, the stimulus >< preceded the go or no-go target stimuli. All six possible combinations of conditions (go and no go; compatible, incompatible, and neutral) were delivered 16 times per block. In all other respects, the stimulus conditions were equivalent to those used in the first two experiments.

After the regular blocks, one forced-choice block was delivered in which the prime stimuli << or >> were presented with equal probability but different durations and were immediately followed by the mask stimulus (100-ms duration). Participants were instructed to press the right response button whenever a prime was present and the left button when no prime was present. Prime duration was varied randomly (48, 32, 16, and 0 ms), and all four durations were equiprobable. Participants were told that the prime would be absent in 25% of all trials. The forced-choice block consisted of 80 trials and included a short break after 40 trials.

*Data analysis.* The analysis of the behavioral data was equivalent to the procedure described before. The single-hand and single-finger conditions were analyzed separately.

## Results

*RTs and error rates.* A main effect of prime–target compatibility on RTs was found for the single-hand condition, $F(2, 22) = 47.47, p < .001, \epsilon = .568, MSE = 1,024.2$, and for the single-finger condition, $F(2, 22) = 23.80, p < .001, \epsilon = .643, MSE = 247.7$. As can be seen from Figure 5, RTs were faster in incompatible trials and slower in compat-
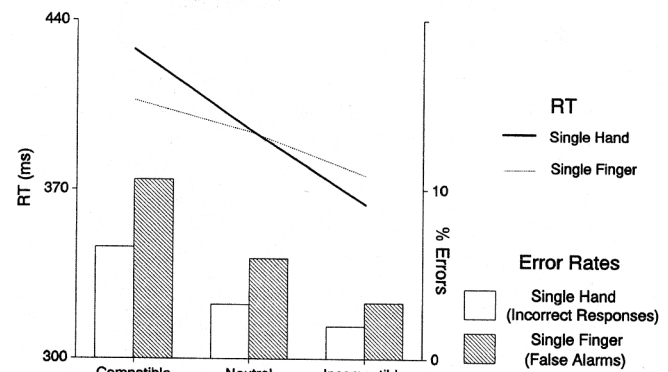


*Figure 5.* Mean response times (RTs; line graphs) and error rates (bar graphs) obtained for the compatible, neutral, and incompatible trials in the single-hand and single-finger conditions of Experiment 3. For the single-hand condition, the error rates (white bars) refer to overt response errors. For the single-finger condition, the error rates (hatched bars) refer to false alarms on no-go trials.

ible trials relative to neutral trials in both task conditions. The respective RTs for the incompatible, compatible, and neutral trials were 364, 428, and 395 ms in the single-hand condition and 376, 407, and 394 ms in the single-finger condition. Additional paired $t$ tests revealed significant differences between each task condition for the single-hand condition, $ts(11) > 5.8$, $ps < .001$, as well as for the single-finger condition, $ts(11) > 3.33$, $ps < .007$.

In the single-hand condition, prime–target compatibility also influenced error rate, $F(2, 22) = 12.26$, $p < .002$, $\epsilon = .643$, $MSE = 21.6$. Figure 5 (white bars) reveals the same cost-benefit pattern on error rates for compatible and incompatible trials that was observed in Experiment 1a. The respective error rates for the compatible, neutral, and incompatible trials were 6.6%, 3.2%, and 1.7%. Paired $t$ tests showed that more errors were made in the compatible than the neutral and incompatible trials, $ts(11) > 3.5$, $ps < .005$, and that the difference in error rate between neutral and incompatible trials was almost significant, $t(11) = 2.16$, $p < .054$.

In the single-finger condition, in which the response was fixed for an entire experimental block, no response errors were observed in go trials, and participants failed to respond on less than 0.2% of all go trials. However, a high percentage of false alarms was observed in no-go trials (as shown in Figure 5 by the hatched bars). Prime–target compatibility had an effect on the false-alarm rate in no-go trials, $F(2, 22) = 7.03$, $p < .008$, $\epsilon = .832$, $MSE = 21.5$. The respective false-alarm rates for the compatible, neutral, and incompatible trials were 10.6%, 5.9%, and 3.3%. Paired $t$ tests revealed a significant difference in false alarms between compatible and incompatible trials, $t(11) = 3.39$, $p < .006$, and an almost significant difference between compatible and neutral trials, $t(11) = 2.12$, $p < .057$. The difference between the neutral and incompatible trials was not significant, $t(11) = 1.78$, $p < .103$.
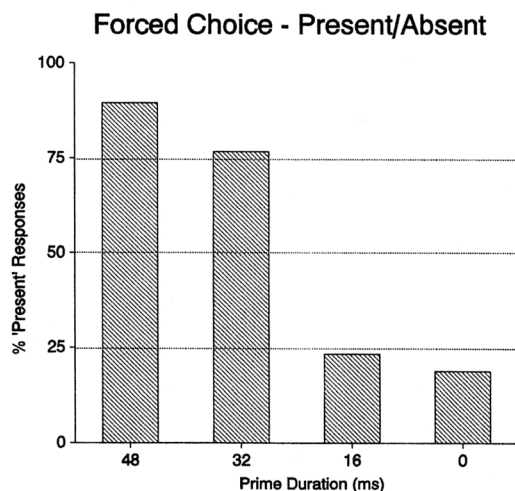
## Forced Choice - Present/Absent



*Figure 6.* Percentage of target-present responses in the forced-choice performance blocks of Experiment 3 for the four different prime durations (48, 32, 16, and 0 ms).

*Forced-choice performance.* Figure 6 shows the forced-choice performance (the percentage of "present" responses) for the different prime stimulus durations, with "present" being the incorrect response for the 0-ms prime duration condition. Forced-choice performance was affected by prime duration, $F(3, 33) = 34.87$, $p < .001$, $\epsilon = .499$, $MSE = 62.2$. If chance level is set to 75% target-present responses (because participants were informed that the probability of target-absent trials was only 25%), above-chance performance was observed only for the 48-ms presentation condition, $t(11) = 3.24$, $p < .008$. However, the fact that the overall percentage of target-present responses was only 52.1% suggested that the information about the a priori probabilities of target-present trials did not affect performance. If 50% target-present responses are defined as chance level, the target-present response percentage was above chance level in the 48- and 32-ms prime duration conditions, $ts(11) > 3.5$, $ps < .005$, and below chance level in the 16- and 0-ms conditions, $ts(11) > 4.9$, $ps < .001$. No significant difference in the percentage of target-present responses was found between the 16- and 0-ms conditions, $t(11) = 1.33$, $p < .211$.

## Discussion

The effects of prime–target compatibility on performance that were observed in the first two experiments were replicated in a situation in which both responses were mapped to a single hand. The costs for compatible trials and the benefits for incompatible trials relative to neutral trials were observed for RTs as well as for error rates. This shows that the processes responsible for these effects are not restricted to situations in which alternative responses are mapped to separate hands but that they can also be obtained when responses are to be executed with two fingers of the same hand.

The data obtained in the single-finger condition provide evidence in favor of the response inhibition hypothesis. The observation that RTs were slower when the go target was preceded by a go prime than when it was preceded by a neutral or no-go prime indicates an inhibition of the response that was initially activated by the prime. No other response was to be executed in this condition, so this effect can hardly be explained in terms of an activation of a different, potentially relevant response. The inhibition hypothesis is also supported by the false-alarm rates observed for no-go trials: The false-alarm rate was smaller on incompatible no-go trials (on which a no-go target was preceded by a go prime) than on compatible trials (on which the no-go target was preceded by a no-go prime), indicating an inhibition of the initial response activation triggered by the go prime. Moreover, in addition to the RT costs observed for compatible go trials, an RT benefit was found for incompatible go trials (on which a no-go stimulus was delivered as prime) relative to neutral trials. The no-go primes thus seemed to have had an effect on motor activation and overt performance that was distinct from that of the neutral primes.

## General Discussion

In the present research, we investigated dissociations between conscious visual perception and visuomotor control by studying how masked primes that are delivered before the appearance of target stimuli would affect overt performance and electrophysiological indicators of response activation. Conscious perception of the masked primes was assessed in forced-choice blocks in which the participants' discriminative performance with respect to the presence or the identity of these stimuli was at chance level.[2] Nevertheless, the masked primes were found to have profound effects on behavioral performance and motor activation in all three experiments. This finding may be taken as additional evidence in favor of the assumption put forward by Neumann and Klotz (1994) and Milner and Goodale (1995) that sensory information may affect response parameters directly (i.e., without mediation by conscious perception).

It is interesting that the direction of this impact of masked prime stimuli on overt performance was contrary to what we expected. On compatible trials, on which identical stimuli were delivered as primes and targets, responses were slower and more errors occurred than on neutral trials, whereas on incompatible trials, on which primes and targets were mapped to opposite responses, responses were faster and fewer errors occurred. These effects on overt performance were accompanied by a multiphasic LRP pattern. Initially, the LRP waveforms revealed an activation of the response assigned to the prime stimuli that started around 200 ms after prime onset. This early response activation is likely to reflect the impact of the visual information conveyed by the prime on response activation and may thus be attributable to a direct specification of response parameters by sensory information (cf. Neumann & Klotz, 1994) that might be mediated by visuomotor control structures in the dorsal processing stream (cf. Milner & Goodale, 1995). However, this initial activation of the response assigned to the prime was replaced by LRP deflections of opposite polarity around 300 ms after prime onset (i.e., in an interval in which the target was identified and the appropriate response selected). This was reflected in a fast activation of the correct response (resulting in performance benefits) for incompatible trials and in a delayed activation of the correct response (and performance costs) for compatible trials.

These behavioral and electrophysiological effects may reflect a selective inhibition of the response that was initially triggered by the prime or a successive activation of both potentially relevant responses. The fact that they were replicated with incompatible S-R mappings (Experiment 2) and perceptually different primes, masks, and targets demonstrated that these effects were not produced by the specific prime–mask configuration used. Experiment 3 (the single-finger condition) brought evidence in favor of the assumption that the response initially triggered by the prime was in fact inhibited. Performance costs for compatible go trials were obtained in a situation in which no alternative, potentially relevant response was present. Moreover, few false alarms were observed when no-go stimuli were pre-

ceded by go primes, presumably indicating that the response mapped to the go prime was partially inhibited.

The assumption that responses initially triggered by the masked prime are later inhibited can account not only for the RT costs obtained for compatible trials but also for the performance benefits observed for incompatible trials. When one of two equiprobable responses has to be executed on each trial, the general readiness to respond should be high, so that both possible responses will be latently activated at the start of each trial. If one of these alternative responses is inhibited, this should give the other response a competitive advantage (relative to neutral trials). On incompatible trials, correct responses will profit from this competitive advantage. In addition, low error rates will be observed on incompatible trials because it is unlikely that the (initially activated, but then inhibited) incorrect response will be erroneously executed. On compatible trials, however, the correct response will be activated and then inhibited, which should give a competitive advantage to the incorrect response, eventually resulting in higher error rates (relative to neutral trials).[3]

In summary, the results of our experiments have again demonstrated that stimuli that are not consciously perceived nevertheless can have a strong influence on motor activation and behavioral performance. A new aspect of the present findings is that this influence may include an inhibitory component. One could assume that response activation processes are generally subject to inhibition (cf. MacKay, 1987) and that this inhibition is particularly pronounced whenever a partial response activation is not immediately followed by the execution of this response. Alternatively, it is possible that the inhibitory effects observed in the present research are specific for the visuomotor control system. Milner and Goodale (1995) pointed out that visual parameters that are relevant for the control of action may change continuously. Because of that, the visuomotor system in the dorsal stream is assumed to operate almost completely on-line, without any long-time storage of these parameters. In our experiments, the prime initially activated a response, but because it was immediately followed by a mask, on-line sensory evidence accounting for this response activation was no longer available to the visuomotor system. It is conceivable that whenever continuous on-line sensory evidence is suddenly removed, the visuomotor control system will consequently interrupt any ongoing response activation processes.

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[2] Of course, more sophisticated signal-detection techniques are needed to more precisely determine the perceptual sensitivity parameters for the different masked primes used in the present research. Nevertheless, the forced-choice performance observed in these experiments indicated that the identification of the prime stimuli was successfully prevented by the masking procedure.

[3] In Experiment 3 (the single-finger condition), RTs were faster when a go stimulus was preceded by a no-go prime than when it was preceded by a neutral prime, and most false alarms were observed on trials in which a no-go prime was delivered before a no-go target. One way to interpret these findings is to assume that "no response" was in fact treated as a regular response alternative and was also subject to inhibitory processes.

Although this type of inhibition might be specific for visuomotor control, inhibitory mechanisms have also been invoked to explain other effects such as negative priming (Tipper, 1985), the attentional blink (Raymond, Shapiro, & Arnell, 1992), or repetition blindness (Kanwisher, 1987, 1991). For example, the inhibition account of negative priming (cf. Tipper & Cranston, 1985) assumes that responses mapped to currently irrelevant items are actively inhibited and that this inhibition causes delayed responses when such an item becomes relevant on subsequent trials. Future research will have to clarify whether the phenomena reported in this study are similar to other types of inhibitory processes or whether they reflect mechanisms that are specific to the visuomotor control system. Moreover, the pattern of behavioral and electrophysiological results obtained in the present research will have to be replicated in different experimental situations in order to learn more about the boundary conditions for the presence of these effects.

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