

Motor activation with and without inhibition: Evidence for a threshold mechanism in motor control

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Masked primes presented prior to a target can trigger response activation processes that may later be subject to inhibition. Evidence for response inhibition has previously been obtained with primes presented at fixation, but not with primes presented in the periphery of the visual field. It is argued that this *central-peripheral asymmetry* reflects a threshold mechanism in motor control. Foveal masked primes give rise to stronger perceptual representations than do peripheral primes, resulting in stronger response activations. Strong response activations are actively inhibited, whereas weaker activations remain below a hypothetical inhibition threshold. Evidence in favor of this hypothesis is obtained in four experiments that manipulated the perceptual strength of foveal and peripheral primes. Experiments 1 and 2 demonstrate that when the perceptual strength of peripheral primes is gradually increased by delaying mask onset, positive prime-target compatibility effects (reflecting the absence of response inhibition) turn into negative effects (indicating the presence of response inhibition). Experiments 3 and 4 demonstrate that when the perceptual strength of foveal primes is gradually decreased by degradation, negative compatibility effects turn into positive effects. The results are discussed in terms of a simple functional model of early motor control.

In order to adaptively control its behavior, an organism must respond quickly and flexibly to rapid changes in its environment. It must be able to select relevant information and appropriate responses, while allowing for the possibility that sudden environmental changes may require an instant modification of prepared responses. To achieve these aims, sensory information not immediately relevant for present behavioral goals should still be processed up to a level at which it can potentially influence behavior. There is ample behavioral and electrophysiological evidence indicating that currently irrelevant sensory information can have a strong impact on response-related processes. Examples include effects of stimulus location under conditions in which location is irrelevant (e.g., De Jong, Liang, & Lauber, 1994; Eimer, 1995; Simon, 1969), effects of stimulus shape when another stimulus feature signals that a response has to be withheld (e.g., Miller & Hackley, 1992; Osman, Bashore, Coles, Donchin, & Meyer, 1992), and effects of irrelevant distractor stimuli presented together with relevant targets (Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Gratton, Coles, Sirevaag, Eriksen,

& Donchin, 1988; Kopp, Rist, & Mattler, 1996; Smid, Mulder, & Mulder, 1990).

It has been argued that such effects are due to a *continuous flow* of information from sensory to motor systems, resulting in an activation of motor responses prior to the completion of stimulus analysis (Coles et al., 1985; Eriksen, Coles, Morris, & O'Hara, 1985; Eriksen & Schultz, 1979; Smid et al., 1990). In line with this hypothesis, evidence has been found that even stimuli presented near or below the threshold of conscious awareness can trigger response activation processes (Dehaene et al., 1999; Klotz & Wolff, 1995; Neumann & Klotz, 1994; Schwarz & Mecklinger, 1995). These phenomena have been attributed to the existence of *direct perceptuomotor links* (Neumann, 1990), which allow perceptual information to affect the motor system directly without necessarily being consciously perceived.

If irrelevant or near-threshold stimuli can activate motor responses, the question becomes acute of how such response tendencies might be prevented from resulting in overt behavior. Numerous behavioral and electrophysiological studies have provided converging evidence that response inhibition plays a crucial role in motor control (e.g., De Jong, Coles, & Logan, 1995; De Jong, Coles, Logan, & Gratton, 1990; Eimer, 1993; Falkenstein, Hoorman, & Hohnsbein, 1999; Jodo & Kayama, 1992; Kok, 1986; Naito & Matsamura, 1994). These studies of response inhibition

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usually employ stop-signal or go/no-go tasks, in which participants are explicitly instructed to refrain from responding when presented with a specific signal. Under this condition, response inhibition is voluntary and is based on control processes activated once the respective signals are recognized (see, Logan & Cowan, 1984). This type of inhibition is assumed to be controlled centrally by executive control mechanisms in the prefrontal cortex, although it may exert its influence anywhere within the motor system (Band & van Boxtel, 1999). With response activations triggered by near-threshold stimuli, such voluntary inhibition might not be possible. Thus, it is important to know whether such activation processes are also subject to inhibitory control and whether their inhibition is based on mechanisms similar to those for the controlled inhibition of responses elicited by clearly visible signals.

It is often assumed that cognitive inhibition processes are activated only by above-threshold information, whereas near-threshold events result merely in passive facilitation. This has been shown in contexts as diverse as negative priming (e.g., Allport, Tipper, & Chmiel, 1985; see also Neill, Valdes, & Terry, 1995), voluntary and involuntary shifts of spatial attention (McCormick, 1997), the disambiguation of polysemous words (Marcel, 1980), and the Stroop effect (Merikle, Joordens, & Stolz, 1995). Apparently, the sensory strength of perceptual information and the presence or absence of inhibitory processes are closely linked. If this is the case not only for cognitive inhibition, but also for inhibitory processes in motor control, response inhibition should be restricted to conditions in which stimuli triggering response activations are accessible to conscious awareness.

However, results from recent studies have demonstrated that response inhibition can be elicited by near-threshold stimuli (Eimer, 1999; Eimer & Schlaghecken, 1998; Schlaghecken & Eimer, 1997, 2000, 2001). In the *masked prime paradigm*, participants performed a choice reaction time (RT) task in response to simple visual stimuli that were preceded by effectively masked primes (as evidenced by chance performance in both prime detection and prime identification tasks). Primes were mapped to the same response as the target (compatible trials), to a different response (incompatible trials), or to no response (neutral trials). When all the stimuli were presented at fixation, performance benefits (fast responses, low error rates) were found on *incompatible* trials, whereas performance costs were present on compatible trials (*negative compatibility effect*). Inspection of the lateralized readiness potential (an electrophysiological measure of unilateral response preparation) revealed an initial activation of the response assigned to the prime, which subsequently gave way to a relative activation of the contralateral motor cortex (Eimer, 1999; Eimer & Schlaghecken, 1998). This pattern suggests that masked primes initially activated their corresponding response and that this initial response activation was later inhibited. Follow-up studies have demonstrated that these effects are not due to visual-perceptual

interactions between primes, masks, and targets, since they are also found when primes and targets are physically dissimilar and appear in different locations (Eimer, 1999, Experiment 1; Schlaghecken & Eimer, 2000, Experiment 2). Also, they do not result from abstract or *semantic* processes at a central level, as is evidenced by a lack of transfer between different response modalities (Eimer, Schubö, & Schlaghecken, in press). It can thus be assumed that the behavioral and electrophysiological results observed in the masked prime paradigm reflect response activation and inhibition processes within the visuomotor system.

The fact that response activation processes triggered by masked primes are subject to inhibition seems inconsistent with previous findings suggesting that inhibition is restricted to conditions of suprathreshold perception. This discrepancy might reflect systematic differences in the mechanisms mediating inhibition in cognitive and perceptuomotor tasks. There is, however, some evidence that regularities similar to those governing cognitive inhibition also apply to inhibitory processes in motor control. Recent results suggest that the presence or absence of inhibitory processes in response to masked primes might be closely linked to the strength of the perceptual trace elicited by these stimuli. Although negative compatibility effects (reflecting response inhibition) were found when masked primes were presented at fixation, positive compatibility effects (performance benefits for compatible trials, reflecting the absence of response inhibition) occurred when primes were presented peripherally (Schlaghecken & Eimer, 1997, 2000). This *central-peripheral asymmetry* remained stable even at long (about 200 msec) prime-target intervals, suggesting that it is not due simply to a slower perceptual processing of peripheral relative to foveal information but, rather, reflects a close relationship between the presence or absence of response inhibition and retinal sensitivity (Schlaghecken & Eimer, 2000, Experiment 4): Displacing masked primes gradually from the center to the periphery of the visual field resulted in gradually decreasing negative compatibility effects (and eventually in positive effects), parallel to the decrease of perceptual sensitivity at more peripheral retinal positions (e.g., Lie, 1980). Importantly, this decrease was steeper with vertically displaced primes than with horizontally displaced primes, parallel to the faster decrease of perceptual sensitivity along the vertical relative to the horizontal meridian (Rijsdijk, Kroon, & van der Wildt, 1980).

On the basis of these findings, we have argued (Schlaghecken & Eimer, 2000) that the central-peripheral asymmetry is directly linked to the fact that the strength of sensory traces elicited by masked primes decreases with increasing retinal eccentricity. If the strength of primed response activations depends on the strength of the primes' sensory representations, motor tendencies triggered by foveal primes will be stronger than motor tendencies triggered by peripheral primes. It seems reasonable to assume that only strong partial response activations, which might eventually result in overt behavior, are subject to

active inhibition, whereas weaker activations remain below a hypothetical *inhibition threshold*. If this were the case, the central–peripheral asymmetry might reflect the fact that motor activations triggered by foveal primes are more likely to reach the inhibition threshold than are motor activations triggered by peripheral primes. Thus, similar to the inhibitory control observed in cognitive tasks, the presence or absence of response inhibition would depend on perceptual strength.

Alternatively, the central–peripheral asymmetry might result from fundamental differences in the impact of foveal and peripheral information on response-related processing stages. It is known that the amount of retinal ganglion cells projecting to the superior colliculus increases with increasing retinal eccentricity (e.g., Perry & Cowey, 1984). Specialized foveal and peripheral processing streams may mediate functionally different foveal and peripheral visuomotor links, with subsystems operative in gaze shift control (e.g., the superior colliculus and related structures) involved in the processing of peripheral information and subsystems responsible for visuomanual control more involved in processing foveal stimuli.

The aim of the present study was to decide whether the central–peripheral asymmetry observed in masked priming is due to differences in the perceptual strength of foveal and peripheral information or whether it reflects general differences in perceptuomotor pathways activated by foveal and peripheral stimuli. If the inhibition threshold account is correct, it should be possible to elicit or to eliminate response inhibition by manipulating the perceptual strength of both foveal and peripheral masked prime stimuli. More specifically, if positive compatibility effects obtained previously with peripheral primes reflect the absence of inhibition owing to below-threshold response activation, increasing the perceptual strength of peripheral primes should result in negative compatibility effects (indicating response inhibition). This was tested in Experiments 1 and 2. If the negative compatibility effects obtained previously with foveal primes reflect the presence of inhibition following above-threshold response activation, decreasing the perceptual strength of foveal primes should result in positive compatibility effects (reflecting the absence of inhibition). This was tested in Experiments 3 and 4. If the central–peripheral asymmetry is due to general differences in the impact of foveal and peripheral information on motor control processes, the polarity of the prime–target compatibility effect should be determined by the retinal location, rather than by the perceptual strength of masked primes.

EXPERIMENT 1

The perceptual strength of peripheral primes was varied by increasing prime–mask interstimulus interval (ISI) from 0 to 100 msec, while keeping prime duration constant at 17 msec. A positive compatibility effect was expected for short ISIs, reflecting the partial activation of the response assigned to the prime without subsequent inhibi-

tion of this response tendency. If increasing the strength of the sensory trace elicited by peripheral primes results in an increased motor activation that eventually crosses an inhibition threshold, negative compatibility effects should be elicited for longer prime–mask ISIs. To obtain an independent estimate of the primes' perceptual strength for different ISIs, prime identification thresholds were measured using a psychophysical staircase procedure.

Method

Participants. Twelve paid volunteers (4 male), 21–49 years of age (mean age, 30.3 years), participated in the experiment. All the participants were right-handed and had normal or corrected-to-normal vision.

Stimuli and Apparatus. Left- and right-pointing double arrows (« and ») served as prime and target stimuli, subtending a visual angle of approximately $1.2^\circ \times 0.4^\circ$. Masking stimuli were constructed from a 6×5 matrix, randomly filled with overlapping horizontal, vertical, and oblique lines of different length (0.06° to 0.3° ; width, 0.06°), resulting in a roughly rectangular array of about $1.4^\circ \times 0.9^\circ$. A new random mask was constructed on each trial.¹ All the stimuli were presented in black on a white background in the center of a 17-in. computer screen.

Procedure. The participants were seated in a dimly lit chamber, with response buttons under their left and right index fingers. A computer screen was placed 100 cm in front of the participants' eyes, so that the screen center was in the center of the participants' horizontal straight-ahead line of sight. The participants were instructed to maintain central eye fixation and to respond as quickly and accurately as possible with a left buttonpress to a left-pointing target arrow and with a right buttonpress to a right-pointing target arrow.

Experimental blocks consisted of 80 trials, constructed as shown in Figure 1. Each trial started with the presentation of a fixation dot at the center of the screen for 200 msec. Three hundred twenty milliseconds after the offset of the fixation dot, a prime was presented for 17 msec, randomly either 3.2° above or 3.2° below fixation. After a variable interval (0, 17, 33, 50, 67, 83, or 100 msec), a mask was presented for 117 msec 3.2° above and below fixation. Immediately after offset of the mask, a target was presented for 133 msec at the center of the screen. Intertrial interval (ITI) was 1,100 msec. Trials were termed *compatible* when the prime and the target arrows were pointing in the same direction and *incompatible* otherwise. Both conditions were equiprobable and randomized within each block. Prime–mask ISI was blocked. For each ISI condition, three blocks were run in immediate succession, and the order of these seven series was randomized for each participant. Prior to the experimental blocks, a practice block (24 trials) was run, employing a 17-msec prime–mask ISI.

At the beginning and at the end of the experiment, one staircase block was run, each consisting of two series of 50 trials, interrupted by a 20-sec break. In these blocks, primes (i.e., arrow stimuli) and masks were presented as in the experimental blocks, but no target followed the mask. ITI was 1,600 msec, and prime–mask ISI was varied. Each series started with an ISI of 133 msec. The participants had to identify the direction of the arrow and to respond with the corresponding key. They were informed that these were not speeded RT blocks but that they should try to respond spontaneously—that is, without spending too much time deciding on a response. A fixed-step, 2-up/1-down procedure was employed: After a correct response, the ISI on the next trial was reduced by 17 msec; after an incorrect response, it was increased by 33 msec, within a range of 0–133 msec. With this procedure, identification performance converges on a 66% correct level (Kaernbach, 1991).

Data analysis. Repeated measures analyses of variance (ANOVAs) were performed on RTs and error rates in the experimental blocks for the factors of prime–mask ISI (0, 17, 33, 50, 67, 83, and 100 msec)

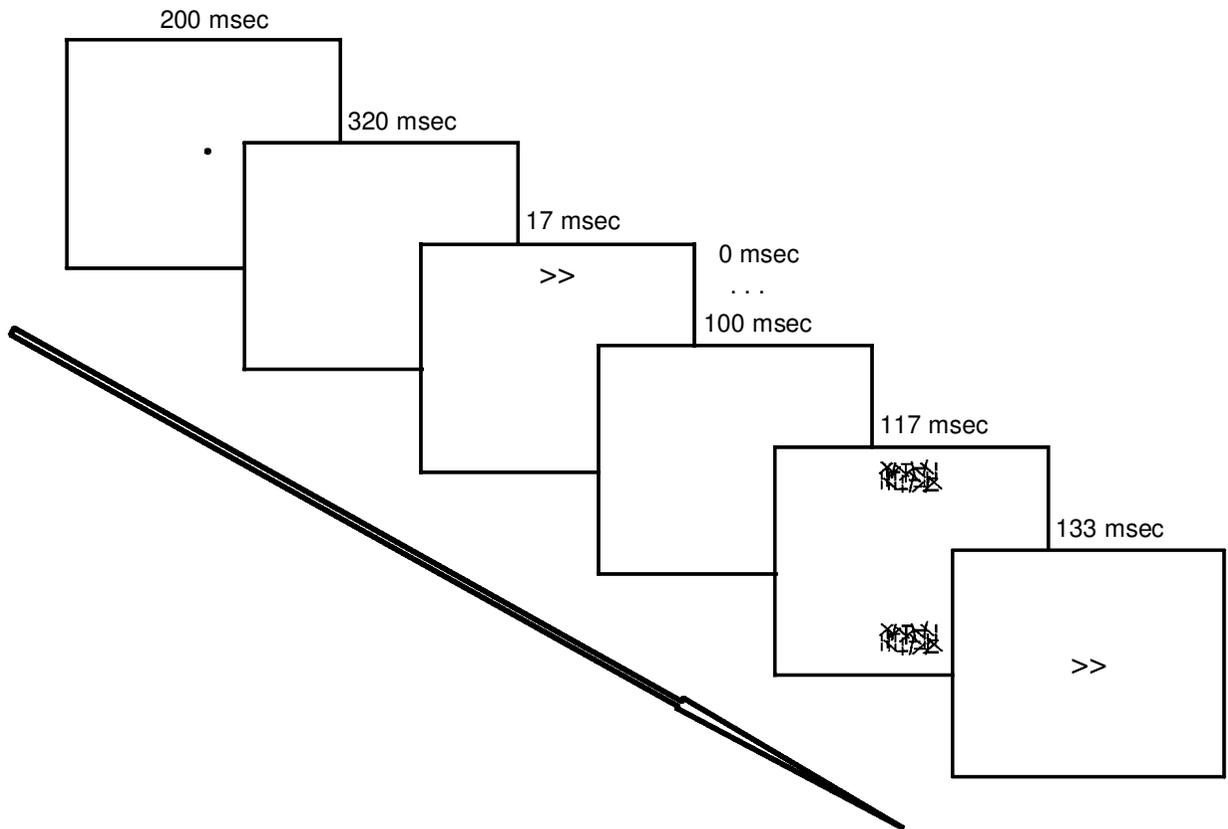


Figure 1. Schematic representation of the stimulus material and trial structure in Experiment 1.

and compatibility (compatible, incompatible). Where appropriate, Greenhouse–Geisser adjustments to the degrees of freedom were performed (indicated in the Results section by ϵ). From the staircase data, the first 10 trials of each series were discarded. From the remaining 2×40 trials, mean prime–mask ISI on correct–incorrect turns (i.e., first incorrect response after one or more correct responses) was computed and served as a conservative estimate of overall identification performance.

Results and Discussion

Prime identification thresholds (estimated as mean mask–target ISI on correct–incorrect turns) were 30 msec in the preexperimental staircase and 28 msec in the post-experimental staircase [$t(11) < 0.4$, n.s.].

In the masked priming blocks, no main effects of compatibility or prime–mask ISI were obtained for RTs (both $F_s < 1.5$, both $p_s > .25$). However, a highly significant compatibility \times ISI interaction was present [$F(6,66) = 4.93$, $p < .008$, $\epsilon = .466$]. As can be seen from Figure 2, positive compatibility effects obtained with short ISIs turned into negative compatibility effects with longer ISIs. Subsequent t tests revealed a significant positive compatibility effect for the 0-msec conditions [$t(11) = 3.33$, $p < .007$] and significant negative compatibility effects for the 83-msec and the 100-msec conditions [$t(11) = 3.76$, $p < .003$, and $t(11) = 2.41$, $p < .035$, respectively]. No other differences were significant. Mean error rate was 2.7%.

Although inspection of Figure 2 suggests that error rates showed a similar pattern of results as RTs, none of the effects reached statistical significance (all $F_s < 2.4$, all $p_s > .088$).

These results are entirely in line with the inhibition threshold hypothesis. Although a positive compatibility effect was obtained when the mask followed the prime immediately, increasing the perceptual strength of the prime by increasing the prime–mask ISI resulted in the reduction and ultimate reversal of this effect. This is the first time that negative compatibility effects have been found in response to masked primes presented peripherally. These results are inconsistent with the hypothesis that retinal eccentricity as such is responsible for the central–peripheral asymmetry observed in previous studies but, rather, provide strong support for the inhibition threshold account.

Before accepting this conclusion, a potentially confounding factor needs to be considered. Because mask duration was held constant, prime–mask ISI covaried with prime–target ISI. Therefore, evidence for response inhibition was found when the interval between the prime and the target was long (200 msec and more), but not when it was short (117 msec). Thus, it might have been the time interval between the prime and the target that determined whether or not an inhibition process was elicited. However, previous results from Schlaghecken and Eimer (1997,

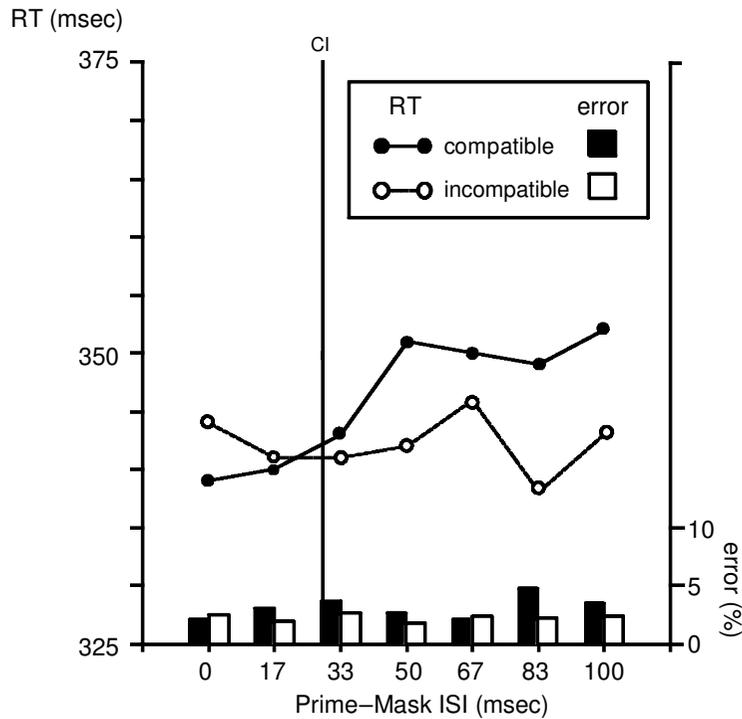


Figure 2. Experiment 1: Reaction times (RTs, line graphs) and error rates (bar graphs) in compatible trials (black) and incompatible trials (white) for the seven prime-mask interstimulus interval (ISI) conditions. Vertical solid line marked "CI" indicates mean level of identification performance in the staircase blocks.

2000, Experiment 1) clearly show that this is not the case. In those experiments, peripheral primes were immediately followed by a mask, whereas prime-target ISI was varied. Substantial *positive* compatibility effects were observed for prime-target ISIs of about 200 msec, indicating that the time interval between the prime and the target in itself does not determine whether or not an inhibition process will be elicited.²

It should be noted that reliable negative compatibility effects were obtained under conditions in which, according to identification performance in the staircase blocks, the prime stimuli were above identification threshold. This indicates that presenting primes below or near threshold may not be a necessary condition to obtain negative compatibility effects. One could argue, however, that owing to the different task demands, identification performance in the staircase blocks might not be a valid indicator of awareness of the primes in the experimental blocks.³ Because attention was focused on the foveal targets, peripheral primes that were identified with above-chance frequency in the staircase blocks might still have been near threshold in the experimental blocks. Therefore, the threshold estimate obtained on the basis of staircase performance might have seriously underestimated the prime identification threshold for the experimental blocks. Inspection of Figure 2 also suggests that the negative compatibility

effect obtained with the 100-msec ISI was smaller than the effect obtained with the 83-msec ISI. Although this difference was not significant, it might indicate that masked primes presented well above identification threshold with even longer prime-mask ISIs may eventually fail to elicit negative compatibility effects. Experiment 2 was conducted to investigate this issue.

EXPERIMENT 2

Prime-target compatibility effects were measured for peripherally presented primes with prime-mask ISIs between 83 and 183 msec. The 83-msec ISI condition was included to replicate the finding from Experiment 1 that perceptually strong peripheral primes give rise to a negative compatibility effect. The other ISI conditions were used to test whether this effect would continue to be present even when the primes are clearly above the identification threshold.

Method

Participants. Eight paid volunteers (3 male), 19–42 years of age (mean age, 27.6 years), participated in the experiment. All the participants were right-handed and had normal or corrected-to-normal vision.

Stimuli and Apparatus, Procedure, and Data Analysis. The stimuli, apparatus, procedure, and data analysis were identical to

those in Experiment 1, except that the prime–mask ISI was 83, 117, 150, or 183 msec. Correspondingly, the ISI factor now consisted of only four levels. No staircase blocks were run.

Results and Discussion

Negative compatibility effects were obtained with mean RTs of 364 msec on compatible trials and 353 msec on incompatible trials [$F(1,7) = 6.53, p < .038$] and mean error rates of 3.7% and 1.9%, respectively [$F(1,7) = 5.24, p < .056$]. There was no main effect of ISI on either RTs or error rates (both $F_s < 2.6$, both $p_s > .12$). Although an inspection of Figure 3 suggests that negative compatibility effects were smaller for longer ISIs than for shorter ones, the interaction of compatibility and ISI approached significance only for error rates [$F(1,7) = 2.95, p < .087$] and was not significant for RTs [$F_s < 1.1, p_s > .36$]. The results thus replicate the central finding of Experiment 1 that sufficiently strong peripheral primes will elicit negative compatibility effects, thereby suggesting that the response activation triggered by these primes is subject to active inhibition.

Since the second aim of this experiment was to further investigate whether negative compatibility effects would continue to be present when peripheral primes are well above identification threshold, additional paired t tests were conducted for each ISI condition separately. Reliable negative compatibility effects on RTs were found only for the 83-msec and the 117-msec ISI conditions [both

$ts(7) > 3.0$, both $p_s < .02$], but not for the 150-msec and the 183-msec ISI conditions [both $ts(7) < 1.3$, both $p_s > .25$]. For error rates, there was a significant negative compatibility effect only in the 83-msec ISI condition [$t(7) = 2.95, p < .021$; all other $ts(7) < 1.4$, all other $p_s > .22$]. However, since the overall reduction in effect size with increasing ISI was not reflected in a significant compatibility \times ISI interaction, there is no unequivocal statistical evidence that masked primes have to be close to identification threshold to trigger negative compatibility effects.

Taken together, Experiments 1 and 2 provide conclusive evidence that response activation processes triggered by peripherally presented masked primes will be subject to inhibition, given that their perceptual quality is high enough to have a sufficiently strong impact on the motor system. This pattern of results supports the inhibition threshold hypothesis as outlined above and clearly contradicts the idea that the central–peripheral asymmetry is due to functional differences between specialized visuo-motor pathways. Experiments 3 and 4 address the same issue with respect to foveally presented primes.

EXPERIMENT 3

Foveally presented primes are normally strong enough to elicit response activations followed by inhibition, as reflected by negative compatibility effects. According to the inhibition threshold hypothesis, reducing the perceptual strength of foveal primes reduces their ability to trigger a strong response activation, so that sufficiently weak foveal primes will result in response activations below inhibition threshold. Therefore, positive compatibility effects similar to those previously observed for peripheral primes with short prime–mask ISIs should be found under conditions in which weak foveal primes are employed.

In Experiment 3, the perceptual strength of foveal primes was manipulated by presenting them in front of random-dot degradation fields of different density. Increasing random-dot density should decrease the primes' perceptual salience and, therefore, their impact on the motor system. According to the threshold account, negative compatibility effects obtained for undegraded foveal primes should turn into positive effects with increased degradation. To obtain an independent estimate of the perceptual salience of undegraded and degraded primes, staircase blocks similar to those employed in Experiment 1 were included.

Method

Participants. Fourteen paid volunteers (3 male), 18–36 years of age (mean age, 24.2 years), participated in the experiment. All the participants but 1 were right-handed, and all had normal or corrected-to-normal vision.

Stimuli and Apparatus. The stimuli and apparatus were similar to those in the previous experiments, with one addition: A rectangular random-dot area, subtending a visual angle of approximately $2.6^\circ \times 1.3^\circ$, served as degradation field. In the medium degradation condition, approximately 25% of the pixels in this area were set; in the maximum degradation condition, 50% were set. For

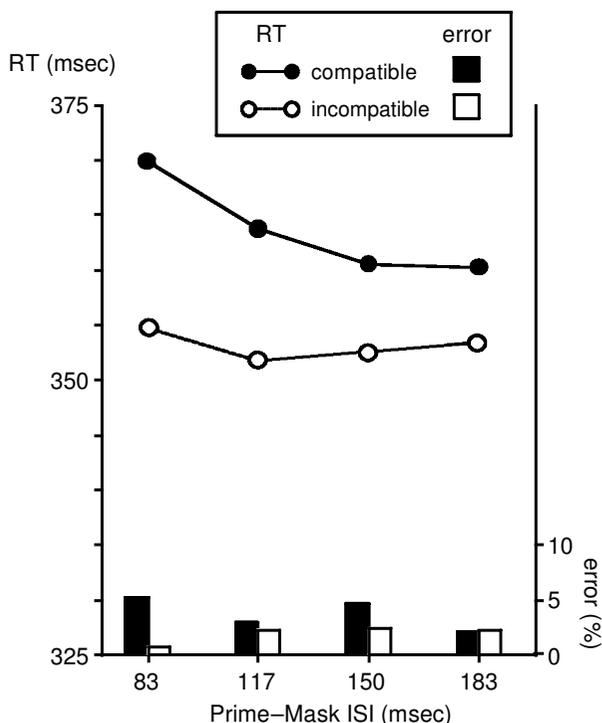


Figure 3. Experiment 2: Reaction times (RTs, line graphs) and error rates (bar graphs) in compatible trials (black) and incompatible trials (white) for the four prime–mask interstimulus interval (ISI) conditions.

both conditions, 10 different degradation fields were constructed prior to the experiment by a random generator. In the zero degradation condition, an empty frame, subtending the same visual angle as the degradation fields, was presented. This experiment was run in a different experimental chamber than were the other experiments reported here: Viewing distance was approximately 115 cm, rather than 100 cm, and the visual angle of the stimuli was correspondingly reduced ($1^\circ \times 0.35^\circ$ for primes/targets, $1.2^\circ \times 0.6^\circ$ for the mask).

Procedure. The experimental setup was similar to that in the previous experiments. Experimental blocks consisted of 80 trials, constructed as shown in Figure 4. In the medium and maximum degradation conditions, degradation fields were continuously present throughout each block. To maximize the impact of degradation on the perceptual salience of the primes, a dynamic degradation procedure was employed. Each prime was presented foveally for 17 msec embedded in a degradation field. This was immediately followed by a mask embedded in a new degradation field (117 msec). Next, a third degradation field was presented for 67 msec. Then, with a fourth degradation field, the target was presented for 117 msec, appearing approximately 2° above or below fixation (just outside the degradation field). Both target positions were equiprobable and randomized. A fifth degradation field was presented during the ITI, lasting 1,120 msec. In the zero degradation condition, a thin black frame was continuously present, instead of the degradation fields, to indicate the central area outside which targets were presented.

Degradation conditions (zero, medium, and maximum) were blocked. For each of the three conditions, 4 experimental blocks were run, resulting in a total of 12 experimental blocks, with 160 trials per condition. Order of blocks was completely randomized for each participant. At the beginning of the experiment, a practice block was

run, consisting of 20 trials and employing the medium degradation field.

At the end of the experiment, three staircase blocks of 60 trials each were run, one for each degradation condition. Order of presentation was randomized for each participant. In these blocks, degradation fields (or black frames in the zero degradation block), primes (i.e., arrow stimuli), and masks were presented as in the experimental blocks. Prime duration was varied, starting with a duration of 133 msec and going down to a minimum duration of 17 msec. In all other respects, the staircase procedure was identical to the one used in Experiment 1.

Data analysis. Repeated measures ANOVAs were performed on RTs in correct trials and on error rates in the experimental blocks for the factors of degradation (zero, medium, maximum) and compatibility (compatible, incompatible). For the staircase data, a repeated measures ANOVA was performed on the mean stimulus duration at correct–incorrect turns (see Experiment 1) for the degradation factor. Where appropriate, Greenhouse–Geisser adjustments to the degrees of freedom were performed.

Results and Discussion

Identification performance in the staircase blocks decreased with increasing degradation, since mean stimulus duration at correct–incorrect turns increased from 36 to 41 to 49 msec [$F(2,26) = 5.81, p < .010, \epsilon = .936$], for the zero, medium, and maximum degradation blocks, respectively. This result confirms that increasing the density of the degradation field resulted in a reduction of the primes' perceptual salience. In addition, it also confirms that the

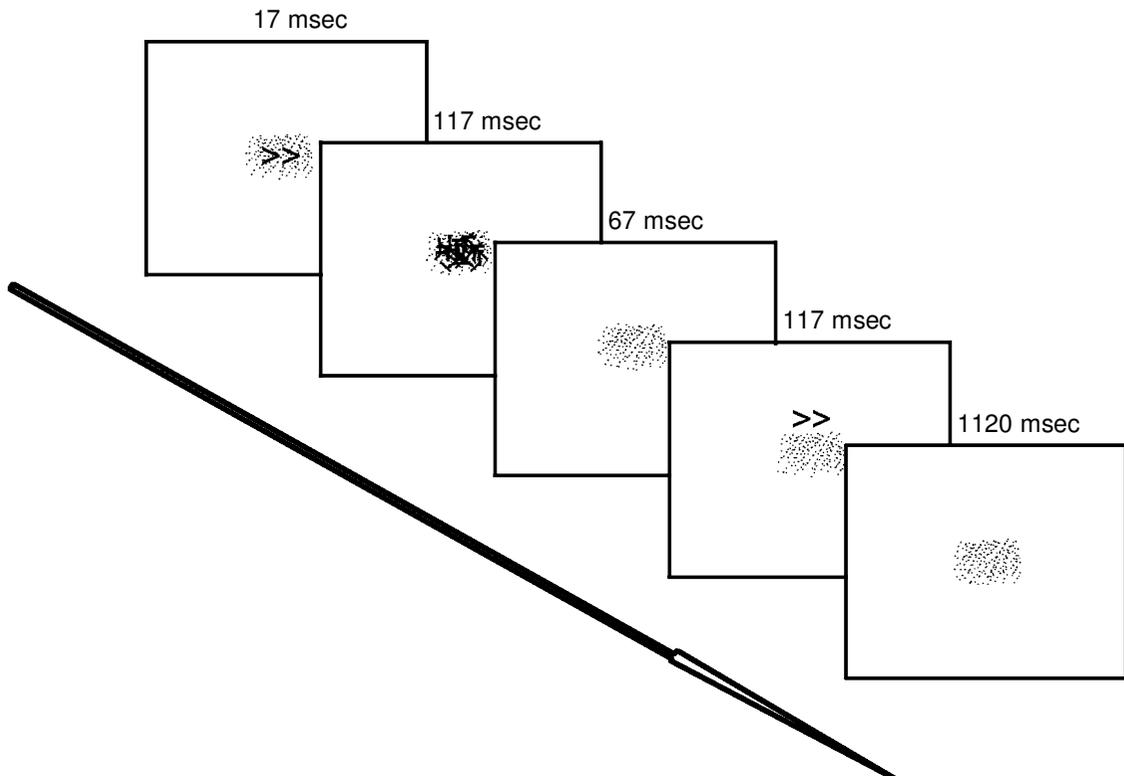


Figure 4. Schematic representation of the stimulus material and trial structure in Experiment 3.

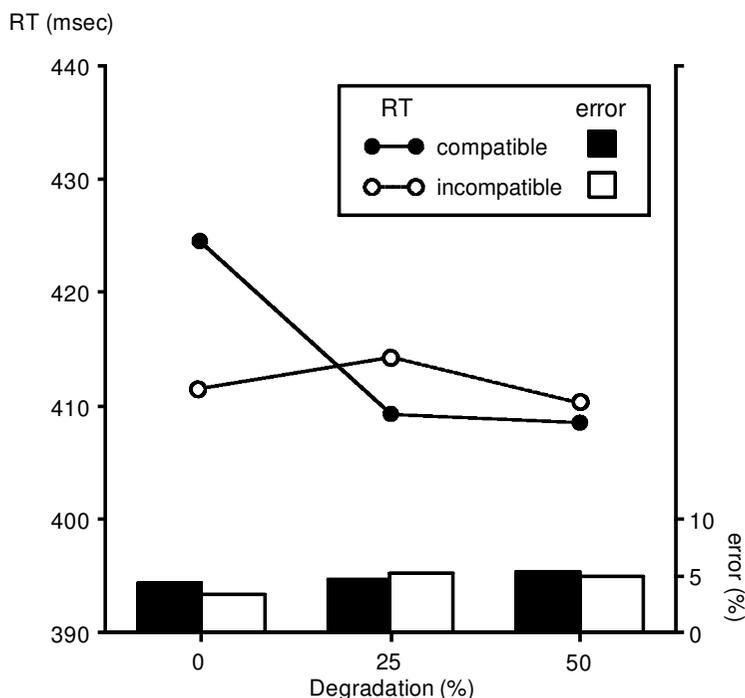


Figure 5. Experiment 3. Reaction times (RTs, line graphs) and error rates (bar graphs) in compatible trials (black) and incompatible trials (white) for the three degradation conditions.

prime duration employed in the experimental blocks (17 msec) was below identification threshold.

In the experimental blocks, no main effect of degradation or compatibility was obtained for RTs (both F s < 2.0, both p s > .19). However, a highly significant interaction between these factors [$F(2,26) = 39.77$, $p < .001$, $\epsilon = .944$] was found; in line with the threshold hypothesis, an RT advantage for incompatible trials obtained in the zero degradation condition turned into RT advantages for compatible trials with medium and maximum degradation (see Figure 5). Subsequent paired t tests confirmed the existence of a significant negative compatibility effect with zero degradation [$t(13) = 7.43$, $p < .001$], as well as a significant positive compatibility effect with medium degradation [$t(13) = 2.69$, $p < .018$]. These results thus provide evidence for the idea that less salient foveal primes trigger response activations that are not strong enough to be subject to active inhibition. The numerical tendency for a positive compatibility effect in the maximum degradation condition was not significant ($t < 0.9$, n.s.). This might be taken as evidence that in this condition, the primes' perceptual strength was too low to trigger any significant motor activation.

For error rates, there was a main effect of degradation, as error rates increased slightly with increasing degradation [$F(2,26) = 5.49$, $p < .011$]. Although error rates tended to show the same pattern of results as RTs (i.e., more errors on compatible trials in the zero degradation condition, and more errors on incompatible trials when

primes were degraded), no other effects reached significance.

Although these results are entirely in line with the prediction derived from the inhibition threshold hypothesis, there is an alternative explanation that might account for the present pattern of results. Since degradation reduced perceptual salience, sensory processing may have been delayed for degraded primes, relative to undegraded primes. This may have resulted in a corresponding delay of response activations triggered by these primes. If this was the case, activation of the target-related response may have coincided with the initial prime-related activation, rather than with the subsequent inhibition when primes were degraded. This would result in positive compatibility effects (see Eimer, 1999; Schlaghecken & Eimer, 1997, 2000), but these effects would then be entirely inconclusive with respect to the presence or absence of response inhibition. Therefore, the present results need to be replicated under conditions in which this possibility is eliminated. This was done in Experiment 4.

EXPERIMENT 4

To rule out the explanation that the results of Experiment 3 were due to a *delayed* sensory-motor processing of degraded primes (rather than to a *reduced* motor activation triggered by these primes), these results need to be replicated under conditions in which the *relative* timing of prime- and target-related motor activations is sim-

ilar across degradation conditions. To achieve this, target stimuli in Experiment 4 were presented within degradation fields, rather than above or below these fields, as in Experiment 3. Under these conditions, RTs to the targets should increase with increasing degradation. This delay of target-related response activation should compensate for any delay in prime-related activation caused by the primes' reduced perceptual salience. If positive compatibility effects were still to be observed with degraded primes, this could be interpreted unequivocally as evidence for the absence of response inhibition.

Method

Participants. Ten paid volunteers (5 male), 19–30 years of age (mean age, 24.5 years), participated in the experiment. All the participants but 1 were right-handed, and all had normal or corrected-to-normal vision.

Stimuli and Apparatus. The stimulus and apparatus were identical to those in Experiment 3, except that no frame was presented in the zero degradation condition and all the stimuli were presented at fixation.

Procedure. The procedure was similar to that in Experiment 3, with the following exceptions: The targets were presented foveally (i.e., within the degradation fields), viewing distance was 100 cm, and no staircase blocks were run.

Data analysis. The data analysis was identical to that in Experiment 3.

Results and Discussion

As was intended, mean RTs increased with increasing degradation from 351 to 378 to 406 msec [$F(2,18) =$

45.49, $p < .001$, $\epsilon = .805$]. There was no overall RT difference between compatible trials and incompatible trials [$F(1,9) < 0.3$, $p > .60$]. However, a highly significant interaction of compatibility and degradation [$F(2,18) = 39.07$, $p < .001$, $\epsilon = .822$] was present, since a reliable negative compatibility effect obtained with undegraded primes [$t(9) = 5.43$, $p < .001$] gave way to positive compatibility effects with medium and maximum degradation [both $t_s(9) > 2.5$, both $p_s < .033$]. Inspection of Figure 6 suggests that this effect increased with increasing degradation. A subsequent t test, comparing effect sizes in the medium- and the high-degradation condition, confirmed that this difference was significant [$t(9) = 2.48$, $p < .035$].⁴

Overall error rate was 4.1%, and there were no main effects of degradation or compatibility on error rates (both $F_s < 0.6$, both $p_s > .55$). The interaction between these factors was significant [$F(2,18) = 6.67$, $p < .015$, $\epsilon = .723$]. As can be seen from Figure 6, error rates tended to be higher on compatible than on incompatible trials in the zero degradation condition, whereas this tendency was reversed in the medium and maximum degradation condition. However, subsequent paired t tests showed that differences in error rates were reliable only in the maximum degradation condition [$t(9) = 3.22$, $p < .01$; all other $t_s(9) < 2.0$, $p_s > .08$].

These results confirm and extend the evidence obtained in Experiment 3 that reducing the perceptual strength of foveal primes eliminates the inhibition of the response tendencies elicited by these primes. Specifically, the fact that

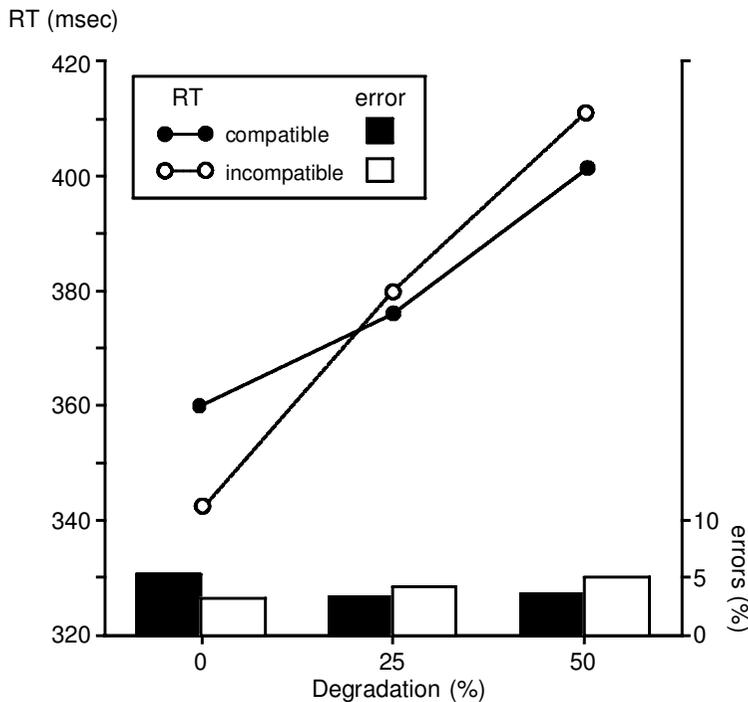


Figure 6. Experiment 4: Reaction times (RTs, line graphs) and error rates (bar graphs) in compatible trials (black) and incompatible trials (white) for the three degradation conditions.

positive compatibility effects were obtained with degraded primes despite the corresponding delay in overall response latencies rules out the idea that the effect obtained in the medium degradation condition of Experiment 3 was due to a temporal overlap of prime-related and target-related response activation. Taken together, the pattern of results obtained in Experiments 3 and 4 thus strongly supports the predictions derived from the inhibition threshold hypothesis: Whereas undegraded foveal primes trigger a response activation that is sufficiently strong to give rise to inhibition, degraded primes result in response activation below the inhibition threshold.

GENERAL DISCUSSION

Successfully masked prime stimuli that are potential targets are able to trigger response activation processes (Dehaene et al., 1999; Neumann & Klotz, 1994; Schwarz & Mecklinger, 1995), thereby influencing overt responses to the subsequent targets. This has been attributed to motor activations via direct perceptuomotor links: Once a stimulus–response mapping has been established, activation of the respective motor response might be mediated by pathways that bypass stimulus recognition processing stages (Neumann, 1990; Neumann & Klotz, 1994).

Under certain conditions, such response activation is later subject to inhibition (Eimer, 1999; Eimer & Schlaghecken, 1998; Schlaghecken & Eimer, 1997, 2000, 2001), a finding that seems to be at odds with the idea that inhibitory control is restricted to conditions of above-threshold stimulation (e.g., Allport et al., 1985; Marcel, 1980; McCormick, 1997; Merikle et al., 1995). However, previous experiments have found initial evidence that the presence or absence of response inhibition and the perceptual strength of masked primes are in fact closely linked (Schlaghecken & Eimer, 1997, 2000). Effects attributable to response inhibition were obtained with foveally presented primes, whereas peripheral primes elicited only response facilitation. According to the inhibition threshold account, this central–peripheral asymmetry is due to differences in the strength of sensory traces elicited by peripheral and foveal stimuli. Stronger sensory traces produce stronger motor activations, which are more likely to reach a hypothetical inhibition threshold than is motor activation in response to weak stimulation.

The aim of the present study was to test this inhibition threshold idea directly. If the presence or absence of response inhibition in masked priming was linked to the perceptual strength of the prime stimuli, it should be possible to elicit response inhibition (resulting in negative compatibility effects) with peripheral primes by increasing their perceptual strength. Correspondingly, it should be possible to eliminate response inhibition triggered by foveal primes (and thus to obtain positive compatibility effects) by decreasing their perceptual strength. These predictions were tested in four experiments. In Experiments 1 and 2, the perceptual salience of peripheral

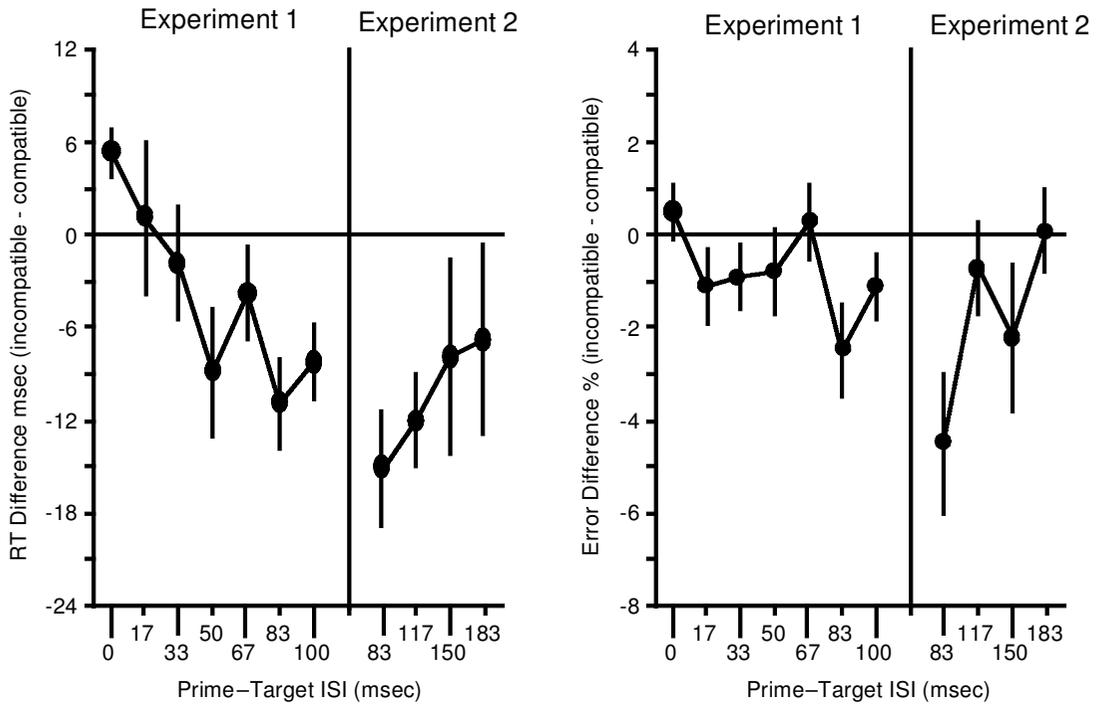
primes was increased by increasing the ISI between prime and mask, whereas in Experiment 3 and 4, the perceptual salience of foveal primes was decreased by embedding them in a random-dot degradation field.

The results were entirely in line with the predictions derived from the inhibition threshold hypothesis (see Figure 7 for a summary of the results). Positive compatibility effects were obtained when primes were perceptually weak (i.e., when presented peripherally and immediately followed by a mask, or when presented foveally embedded in a degradation field). Negative compatibility effects were found when primes were perceptually strong (i.e., for undegraded foveal primes, or for peripheral primes with a long prime–mask ISI).⁵ The fact that positive as well as negative compatibility effects can be obtained in response both to foveal and to peripheral primes demonstrates that the central–peripheral asymmetry observed in previous studies does not reflect fundamental functional differences between foveal and peripheral visuomotor pathways.

The present results thus provide empirical evidence for the existence of an inhibition threshold in motor control. A response tendency triggered by a masked prime will be inhibited only when primes are of sufficient perceptual salience, whereas no such response inhibition processes will be triggered when the perceptual traces elicited by the primes are weak. From a functional perspective, it seems reasonable to assume that this relationship may reflect a general principle in motor control. Weak response tendencies produced by perceptually weak stimuli are less likely to affect overt behavior than are stronger motor activations, which might eventually result in overt behavior even without conscious perception of the triggering stimulus (see, e.g., Fehrer & Raab, 1962). Thus, the inhibition of strong response tendencies triggered by near-threshold stimuli may be as relevant as the inhibitory control of response tendencies triggered by above-threshold events.

The notion of an *inhibition threshold*, as employed to account for the results observed in the present research, requires some additional comment. In the experiments reported above, prime–target compatibility effects were found to gradually turn from positive to negative or vice versa. This pattern of results seems inconsistent with the simple idea that there is a fixed level of sensory strength above which there is response inhibition and below which only passive facilitation was elicited. One could argue that the gradual decrease or increase of compatibility effects simply reflects a constant proportional relationship between response facilitation and inhibition on each trial, although the fact that these effects reverse polarity requires some additional assumptions. Alternatively, increasing the perceptual salience of a prime may increase the likelihood that response inhibition will be elicited on any given trial and, thus, the overall percentage of trials on which response inhibition is present. Although clearly important, these distinctions are not crucial for the present line of argument. A threshold can be implemented mathematically as a sig-

Increasing the perceptual strength of peripheral primes:



Decreasing the perceptual strength of foveal primes:

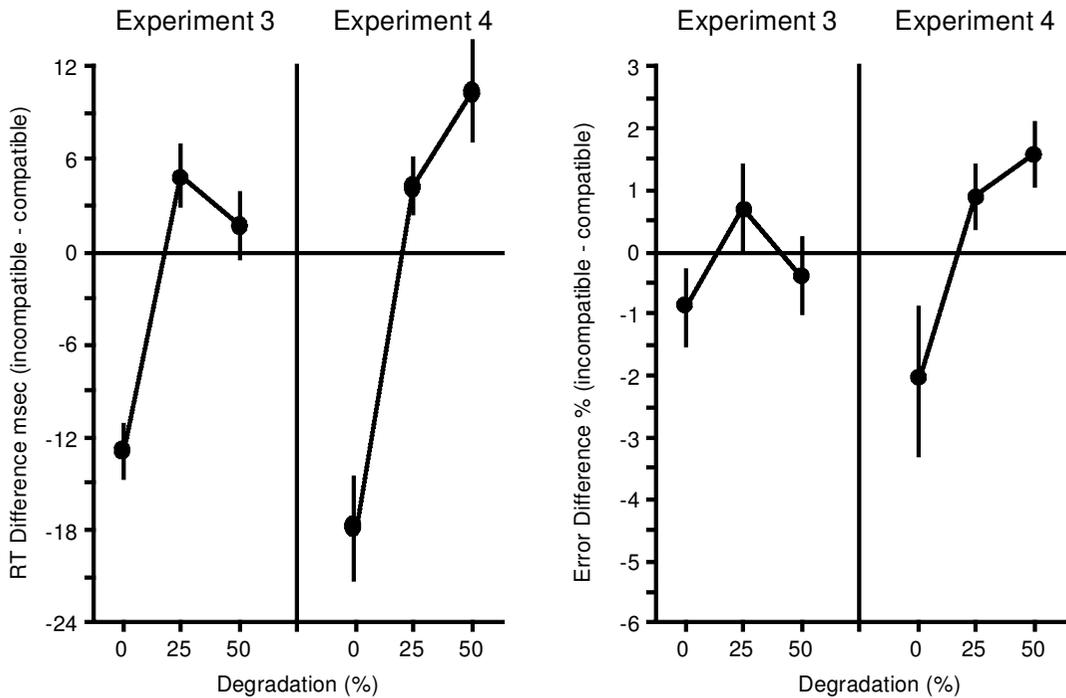


Figure 7. Summary of prime–target compatibility effects on reaction times (RTs, left panels) and error rates (right panels) obtained in the present study. Upper panel: Positive compatibility effects turning into negative effects with increasing strength of peripheral primes (Experiments 1 and 2). Lower panel: Negative compatibility effects turning into positive effects with decreasing strength of foveal primes (Experiments 3 and 4). Positive values indicate behavioral benefits on compatible trials; negative values indicate behavioral benefits on incompatible trials. Vertical lines indicate the standard error of the mean.

modal function, and the slope of this function might be anywhere between steep (approximating a fixed *all-or-nothing* threshold) and shallow (approximating proportional as well as probabilistic relationships). We use the concept of *inhibition thresholds* in this general sense, without any more specific assumptions about the slope of the threshold function or about the relationship between perceptual strength and response inhibition on individual trials.

In the following, we propose a simple functional model of early motor control to account for the complex pattern of effects obtained in the masked prime paradigm. In Figure 8, the elementary architecture of this model is depicted, consisting of an early sensory processing subsystem, a motor control subsystem, and a response execution stage. The motor control system consists of activation ($M+$) and inhibition ($M-$) components for each response alternative. Both components receive a common input from early perceptual processing stages as soon as there is any

sensory evidence for a particular response. It is assumed that input via these direct visuomotor links is excitatory (enhancing the activation level) for $M+$, whereas it is inhibitory (reducing the activation level) for $M-$. Importantly, $M+$ and $M-$ are interconnected by an *asymmetric* activation/inhibition loop: Whereas $M+$ continually activates $M-$, $M-$ will inhibit $M+$ only if its activation level exceeds a criterion value (without specific assumption about the exact nature of this threshold function; see above). Overt response execution processes are initiated once activation in $M+$ exceeds a motor output threshold. Finally, response alternatives compete with one another via inhibitory links of $M+$ with $M+$.

Since any sensory evidence activating $M+$ simultaneously inhibits $M-$, the activation level of $M-$ will reach above-threshold values only if there is both strong excitatory influence from $M+$ and no or only weak inhibitory influence from the sensory system. If only one of these conditions is fulfilled, the activation level of $M-$ will re-

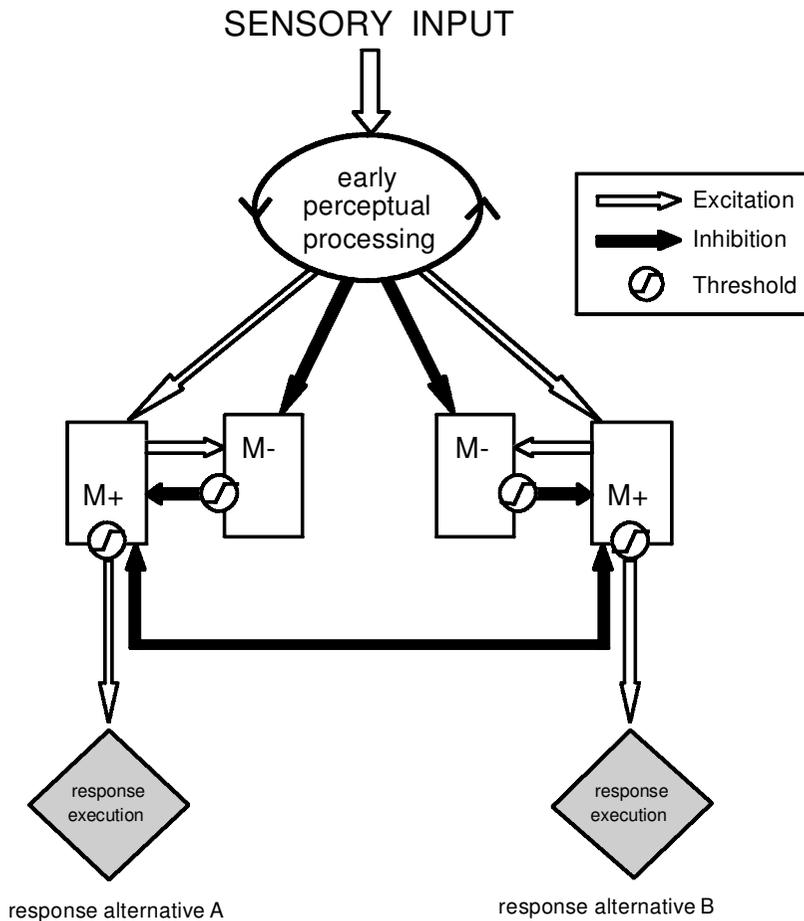


Figure 8. A threshold model of early inhibitory control of motor activation. White arrows indicate excitatory connections; black arrows indicate inhibitory connections. Circles with a “Z”-like sign symbolize an activation threshold that has to be crossed before activation from the respective component is transmitted to other components. See the text for details.

main below threshold. When perceptual input is weak, M+ activation is insufficient to produce above-threshold activation of M-. In this case, the initial activation of M+ will not be inhibited. This is the situation observed with perceptually weak prime stimuli, like primes presented in the periphery with a short prime-mask ISI or primes presented foveally embedded in a degradation field. Here, positive compatibility effects reflect response facilitation without subsequent inhibition.

However, increasing the strength of the perceptual input in itself is not sufficient to produce above-threshold activation of M-. As long as there is sufficiently strong input from the sensory system, any activation of M- via M+ will be counterbalanced by sensory inhibition. Consequently, the activation level of M- will not reach the inhibition threshold, owing to continuous sensory inhibition, and again, the initial activation of M+ will not be inhibited. This is the situation observed with unmasked irrelevant information, as in the Eriksen flanker effect, where distractor stimuli are assumed to selectively prime a corresponding motor response (e.g., Coles et al., 1985; Eriksen et al., 1985; Eriksen & Schultz, 1979; Smid et al., 1990). Note that the absence of response inhibition under these conditions is independent of the strength of sensory traces. Since the inhibitory perceptual input to M- is assumed to be of the same magnitude as the excitatory perceptual input to M+, any activation of M- via M+ will be counterbalanced by perceptual inhibition of equivalent strength. Consequently, behavioral benefits for the primed response are to be expected. The *magnitude* of these positive priming effects, however, should depend on the perceptual strength of the primes, since direct visuomotor links are supposed to lead to a strong activation of M+ in response to strong primes and to a weak activation of M+ in response to weak primes. This relationship may be reflected in the gradual decrease of Eriksen flanker effects with increasing retinal eccentricity of the flanking distractors (Goolkasian, 1997; Miller, 1991).

An above-threshold activation of M- will result only when a strong perceptual input is subsequently masked. Initially, strong activation of M+ will lead to strong excitatory input to the corresponding M- component, but this activation of M- is counterbalanced by perceptual inhibition. Once the masking stimulus removes the sensory evidence for a particular response, perceptual inhibition of M- terminates. As long as the activation level of M+ is still high, M- receives sufficient excitatory input to reach above-threshold activation, resulting in inhibition of M+. Moreover, the inhibited M+ component will no longer exert an inhibitory influence on the M+ component of the alternative response, which thus will become more active owing to disinhibition. Presenting the target during this stage will consequently result in behavioral costs for the correctly primed response and behavioral benefits for the incorrectly primed response.

This model has some similarities to the activation-followed-by-inhibition models proposed by Houghton and

Tipper (1994, 1996) and by Hagenzieker and colleagues (Hagenzieker & van der Heijden, 1990; Hagenzieker, van der Heijden, & Hagenaar, 1990). Similar to the former model, it includes a self-inhibition loop, where the presence of an activation tends to generate inhibitory feedback, and similar to the latter, it assumes that an activation threshold determines whether or not inhibition will occur. There are several differences between these models and the one proposed here: Houghton and Tipper (1994) link the presence or absence of inhibition to match/mismatch processes comparing the representation of the current stimulus with the stored description of a target, rather than to the perceptual strength of the sensory input. Hagenzieker and colleagues, although postulating a direct relationship between strength of sensory input and presence or absence of inhibition, assume that these processes occur within high-level "recognition units."

Overall, the present experiments provided conclusive and converging evidence for inhibitory processes in motor control, whose putative function is to inhibit response tendencies strong enough to result in inappropriate overt behavior. The results demonstrate that the inhibition of response tendencies triggered by masked stimuli is a function of the perceptual strength of these stimuli. Whereas strong perceptual traces give rise to response facilitation followed by inhibition, weaker perceptual traces will result in response activation processes that remain below a hypothetical threshold for response inhibition. These results may be regarded as particularly convincing because of their counterintuitive nature. What has been demonstrated is that selective advantages for one response alternative can be produced by decreasing the sensory evidence for this response (in the case of foveal primes) and by increasing the sensory evidence for the opposite response (in the case of peripheral primes). Although these results rule out the idea that the central-peripheral asymmetry in masked priming reflects fundamental differences between specialized foveal and peripheral visuomotor pathways, they do provide strong support for the inhibition threshold account. Further research is needed to obtain more detailed insights into the operation of inhibitory control processes involved in the regulation of direct perceptuomotor links.

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NOTES

1. In previous studies, arrow primes were masked by superimposed left- and right-pointing arrows, thus effectively "adding" the alternative

stimulus to the prime. This newly added stimulus might have favored activation of the opposite response either because it was perceptually more salient or because it resulted in the perception of an induced motion "away" from the direction of the prime. Although reliable prime–target compatibility effects have been obtained when masks were character strings that did not share visual features with the primes (Eimer & Schlaghecken, 1998), the influence of the masking procedure on these effects is not yet fully understood. Because of this, a scrambled pattern mask that did not bear any resemblance to prime and target stimuli was employed in the present study.

2. It might also be worth noting that the results cannot be explained in terms of eye movements to the prime location. First, since prime duration was only 17 msec in all conditions, the prime would have disappeared even before saccade onset. Second, on trials in which the participants accidentally fixated the location of the upcoming prime, they would have perceived an unmasked or insufficiently masked prime in the longer ISI conditions. This would clearly have resulted in positive rather than negative compatibility effects.

3. It should be noted that even with ISIs between 67 and 100 msec, only about 62% of all the masked stimuli were correctly identified in the staircase blocks.

4. The fact that a positive compatibility effect was found with maximum degradation in the present experiment, but not in Experiment 3, might be related to the difference in viewing distance and the corresponding difference in stimulus size. In Experiment 4, maximally degraded primes may have been sufficiently strong to trigger a motor activation because their visual angle was somewhat larger than that in Experiment 3.

5. Although the qualitative pattern of compatibility effects observed in the present study was in line with the results observed in previous experiments, the size of these effects was considerably smaller. This is most likely due to the new masking procedure. Effects observed previously might have been partially due to perceptual interactions between primes, masks, and targets. Since these were eliminated by the new procedure, the present results might provide a more objective estimate of the "true" size of prime–target compatibility effects.

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