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Facilitatory and inhibitory effects of masked prime stimuli on motor activation and behavioural performance

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Abstract

Three experiments investigated the impact of information provided by masked stimuli on motor activation. Masked primes were presented prior to target stimuli and these primes were identical to the target on compatible trials, identical to the target mapped to the opposite response on incompatible trials and task-irrelevant on neutral trials. A previous study [Eimer, M., & Schlaghecken, F. (1998). Effects of masked stimuli on motor activation: Behavioural and electrophysiological evidence. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 1737–1747] found performance costs for compatible trials and benefits for incompatible trials. Experiment 1 showed that these effects are not due to 'perceptual repetition blindness'. Experiments 2 and 3 obtained evidence for an initial response facilitation triggered by the primes that was followed by inhibition. With short intervals between prime presentation and response execution, performance benefits were found for compatible trials and these turned into costs at longer intervals. It is argued that an early response facilitation mediated by direct perceptuo-motor links is subsequently inhibited by a central mechanism operating to prevent behaviour from being controlled by irrelevant information.

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1. Introduction

Our environment presents an immense amount of potentially important information, while our actions are controlled by a small subset of external objects and events. Attentional mechanisms are essential to establish appropriate links between perception and action. Attention gates perceptuo-motor interactions by selecting objects and events in order to link them to specific responses in a way that serves an organisms' current interests and objectives in a given context (Neumann, 1987). Inhibitory mechanisms are likely to play an important role in this process. Houghton and Tipper (1994) have described a functional model of attentional selectivity and its role in gating the access of perceptual information to response processes. In this model, parameters of motor responses are activated in a competitive way by sensory information that is transmitted to response systems in a cascade fashion. Facilitatory and inhibitory attentional mechanisms bias this competition in favour of currently relevant information to ensure that responses are controlled by target objects instead of distractors. The specific role of inhibition in this selective control of perception-action links is reflected in the phenomenon of negative priming. Responses to objects that had to be ignored in a previous trial are slowed relative to responses to novel stimuli, presumably due to the inhibition of previously unattended information (Tipper, 1985).

In the Houghton and Tipper (1994) model, attention operates on object representations prior to their contact with the response system and adequate response activation depends upon a successful attentional foregrounding of target information. However, motor processes can be affected by sensory information before attentional processes can intervene. Direct links between perceptual and response-related stages can allow unattended information to determine response parameters. For example, the location of a target affects performance even when it is irrelevant for response selection, with RT benefits when stimulus and response locations correspond and RT costs when they are incompatible (Simon effect: Simon, 1969). Electrophysiological studies have shown that task-irrelevant spatial features activate spatially corresponding responses even when these responses are inappropriate (De Jong, Liang & Lauber, 1994; Eimer, 1995). In noise-compatibility tasks, irrelevant items can activate their corresponding responses, as reflected in performance (Eriksen & Eriksen, 1974) and electrophysiological indicators of motor activation (Gratton, Coles & Donchin, 1992). These examples clearly demonstrate that perceptual information can affect response-related stages without intervention of attentional selectivity. Because attention is not always successful in preventing irrelevant information from affecting motor stages, inhibitory mechanisms may not only be involved in making perceptual information available to response processes, but also more directly in motor control. Response tendencies triggered by task-irrelevant information may have to be actively inhibited to prevent them from resulting in overt behaviour.

Motor inhibition is not restricted to situations where unwanted response tendencies result from imperfect attentional selectivity, but will generally be involved when such tendencies, regardless of their origin, are rendered inappropriate because they conflict with current task sets, or with sudden changes in the environment. The latter situation

has been studied with the stop-signal paradigm (see Logan, 1994, for a review) where participants perform a speeded RT task and are occasionally interrupted by a stop signal indicating that the response on that trial has to be withheld. Performance in this task has been modelled as a race between independent response activation and inhibition processes that compete to control response execution. As predicted by the race model, the rate of successfully inhibited responses increases as the interval between the task stimulus and the stop signal is reduced. The assumption that activation and inhibition are independent processes is supported by several findings. First, the time required to process the stop signal is not affected by the complexity of the primary task (Logan & Cowan, 1984). Second, event-related brain potentials (ERPs) related to motor activation were virtually identical in trials without a stop signal and in trials where a response was executed despite the presence of a stop signal, indicating that central response activation is not affected by the processing of the stop signal (De Jong, Coles, Logan & Gratton, 1990; De Jong, Coles & Logan, 1995).

An important question with respect to motor inhibition concerns the level at which inhibitory control becomes effective. The inhibition of inappropriate motor tendencies may be brought about by central or peripheral mechanisms (De Jong et al., 1995). Central inhibition operates on response activation processes in motor cortex in order to prevent the transmission of central motor commands to peripheral motor structures, whereas peripheral inhibition temporarily shuts down the execution of any motor commands. Evidence for peripheral inhibition comes from the observation that cortical motor activation as reflected in event-related brain potentials often exceeds the level normally associated with movement onset even when overt responses are completely inhibited (De Jong et al., 1990). Because peripheral inhibition acts by suppressing all response tendencies non-selectively, it may not be appropriate under conditions where only specific responses have to be inhibited. De Jong et al., 1995 provided evidence for the idea that peripheral inhibition is primarily responsible for motor inhibition in the standard stop-signal task, where all response tendencies can be aborted in stop signal trials, whereas central inhibition is more important in a 'stop-change' task, where the stop signal not only requires participants to inhibit an already activated response, but also to execute an alternative response.

In the present research, motor activation and inhibition processes were investigated in an experimental situation that was considerably different from the stop-signal paradigm. Response tendencies were induced by briefly presented and subsequently masked stimuli (primes) that were immediately followed by response-relevant target stimuli. The response assigned to a target could be identical to or different from the response associated with the prime. There were several reasons for adopting this new procedure. In contrast to the stop-signal task, participants were required to execute a response on all trials. Following De Jong et al., 1995, it was assumed that any inhibition of response tendencies activated by the primes would primarily be accomplished by central mechanisms, since non-selective peripheral inhibition would interfere with the execution of responses to the target stimuli. Second, response activation and inhibition processes induced by the primes were expected to be directly reflected in overt performance to the targets. In contrast to the stop-signal paradigm, where the time course of response activation and

inhibition is inferred on the basis of a mathematical race model and thus critically depends on the validity of the assumptions made in this model, this new approach may thus allow a more direct access to these processes. As will be shown below, the time course of motor activation and inhibition can be investigated systematically by examining effects of primes on responses to targets for different RT bins (Experiment 2) and different prime-target SOAs (Experiment 3). Third, the present approach may allow to study response activation and inhibition in the absence of corresponding explicit intentions. In contrast to the stop-signal paradigm, participants were neither instructed to prepare a response to the prime, nor to abort it prior to responding to the target. In fact, the masking procedure was employed to prevent any conscious perception of the prime stimulus.

This new approach was first employed in experiments where masked prime stimuli were followed by targets requiring a left-hand or right-hand response (Eimer & Schlaghecken, 1998). The primes were identical to the subsequent target in compatible trials, identical to the other target in incompatible trials and task-irrelevant in neutral trials. It was assumed that the primes would activate their corresponding responses, but due to the intervention of the mask, this activation would not be sufficient to elicit an overt response. However, these initial response tendencies should be differentially reflected in behavioural performance in the three prime-target compatibility conditions. Prime stimuli were presented for 16 ms and then immediately followed by a mask and a target which required a left-hand or right-hand response. Left-pointing and right-pointing double arrows ('≪' and '≫'), mapped to left-hand and right-hand responses, served as primes and targets and '< >' or '> <' served as neutral primes. Masks and targets were presented for 100 ms. The mask was created by superimposing left-pointing and right-pointing arrows upon one another and all stimuli were presented at fixation.

Performance costs were found when primes and targets were identical and benefits when they were mapped to opposite responses. RTs were fastest and error rates were low in incompatible trials, whereas slow RTs and high error rates were found in compatible trials (Fig. 1, top). Eimer and Schlaghecken (1998) also recorded the Lateralized Readiness Potential (LRP), which provides a continuous index of left-hand and right-hand response activation. The LRP is computed on the basis of the event-related brain potentials obtained above motor cortex areas that control right and left hand movements (for details, see Coles, Gratton & Donchin, 1988; De Jong, Wierda, Mulder & Mulder, 1988; Coles, 1989; Eimer, 1998). LRP waveforms for compatible, neutral and incompatible trials (measured from the onset of the prime stimulus) are shown in Fig. 1 (bottom). As expected, an initial activation of the response assigned to the prime was found, reflected in a partial activation of the correct response in compatible trials and partial incorrect response activation in incompatible trials (Fig. 1, bottom, black arrow). No response activation was present in neutral trials within this time interval. This initial effect reversed polarity around 300 ms after prime onset (Fig. 1, bottom, white arrow). Eimer and Schlaghecken (1998) interpreted this LRP pattern as a sequence of response activation followed by inhibition. Initially, the response assigned to the prime is partially activated, presumably mediated by perceptuo-motor links that allow

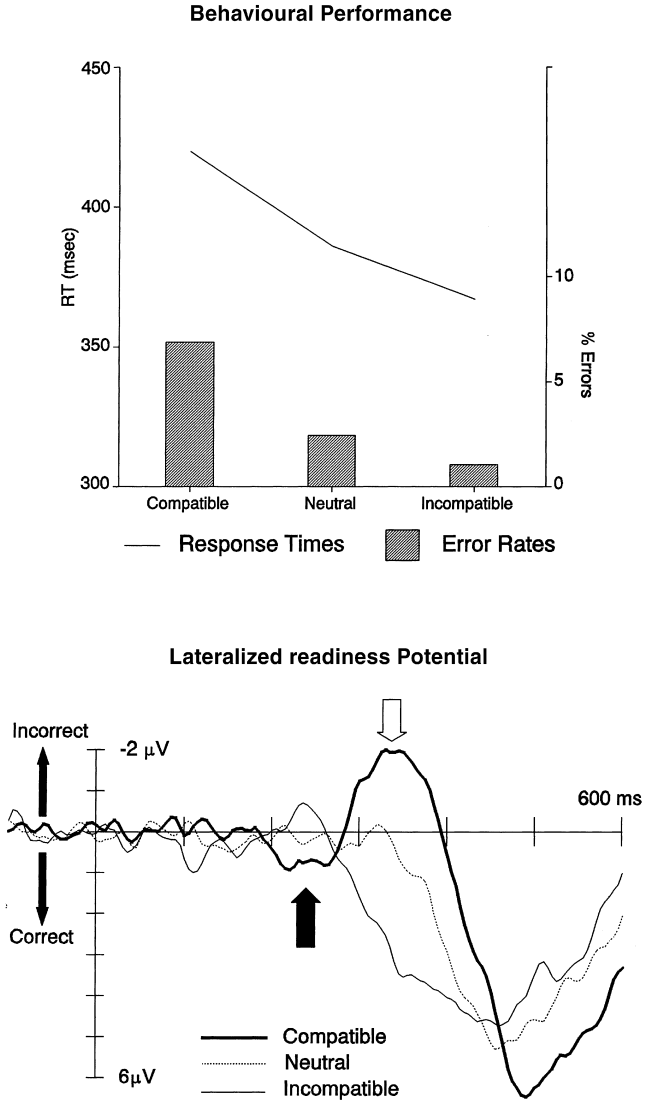

Fig. 1. Behavioural performance (upper panel) and lateralized readiness potentials (lower panel) measured in an experiment (Eimer & Schlaghecken, 1998), Experiment 1(a) where left-pointing or right-pointing target arrows were preceded by compatible, neutral, or incompatible masked primes (see text for details). Upper panel: response times (line graph) and error rates (bar graphs) obtained in compatible, neutral, and incompatible trials. Lower panel: LRP waveforms obtained in compatible, neutral, and incompatible trials in the time interval between prime onset and 600 ms after prime onset. Downward-going (positive) deflections indicate activation of the correct response (the response assigned to the target), upward-going (negative) deflections indicate activation of the incorrect response. The black arrow indicates the time interval where the initial response activation was observed, the white arrow indicates the subsequent reversal of this effect (see text for details).

information derived from the prime to affect response-related processing. The reversal of these effects was interpreted as subsequent inhibition of the initial activation and this inhibitory phase was assumed to be responsible for the cost-benefit pattern in behavioural performance. Further behavioural evidence for response inhibition was found in blocks where only a single fixed overt response had to be performed (Eimer & Schlaghecken, 1998, Experiment 3) . Left-pointing and right-pointing arrows (Go stimuli), mapped to left-hand and right-hand responses, were presented in separate blocks. On half of the trials, a Nogo stimulus ('< >') was delivered. Both Go and Nogo stimuli were preceded by masked Go and Nogo primes. Responses to the Go stimulus were delayed in trials where the Go prime was presented and the rate of False Alarms to a Nogo stimulus was much smaller when it was preceded by a Go prime than when the Nogo prime was presented (3.3% vs 10.6%). Both findings suggest that the response assigned to the Go prime was actively inhibited even when there is no competing response alternative.

Effects of masked stimuli on choice RT have previously been reported by Neumann and Klotz, 1994 and Klotz and Wolff, 1995 in experiments where participants had to respond to a target which also served as mask for a preceding prime. In contrast to Eimer and Schlaghecken (1998), facilitatory effects were obtained when primes and targets were identical. This apparent contradiction will be considered in the General Discussion. In the Neumann and Klotz (1994) study, signal detection analyses showed that the primes could not be consciously discriminated. Eimer and Schlaghecken (1998) also determined whether the primes were consciously perceived by instructing participants to identify them in forced choice discrimination blocks. Identification performance was at chance level, indicating that the masking procedure prevented the conscious perception of the primes.

In summary, Eimer and Schlaghecken (1998) found initial evidence for a facilitation-followed-by-inhibition pattern in motor activation. The three experiments reported below were conducted to provide further and more direct evidence in favour of this idea and to demonstrate that the masked prime paradigm can provide a useful tool for studying the time course of these processes. Experiment 1 tested the idea that the effects observed before are primarily perceptual in nature, reflecting reduced visual sensitivity to immediate stimulus repetitions ('perceptual repetition blindness'). In Experiments 2 and 3, the time course of motor facilitation and inhibition was studied directly by investigating the impact of response priming separately for different RT bins and different prime-target SOAs. In the general discussion, the functional role and possible mechanisms of response facilitation and inhibition will be considered.

2. Experiment 1

Eimer and Schlaghecken (1998) obtained performance costs in trials where primes and targets were physically identical. Instead of attributing this to an inhibition of motor activation, one may argue that the priming procedure affected perception of the target stimuli differentially in compatible and incompatible trials. The presenta-

tion of two identical stimuli in rapid succession can have negative effects on the perceptual analysis of the second stimulus. Hochhaus and Johnston, 1996 found that the detectability of masked words was reduced when they were identical to a word presented immediately before, possibly reflecting perceptual inhibition caused by the first presentation of the word. This effect was termed 'perceptual repetition blindness' and was regarded as a special case of the repetition blindness effect (a reduced accuracy in reporting the identity of stimuli that have been presented shortly before) reported by Kanwisher (1987, 1991). To test whether the performance costs observed for compatible trials are at least partially due to 'repetition blindness', responses to centrally presented arrow targets were compared to responses to laterally presented targets that were physically dissimilar to the preceding primes. In both cases, arrows were used as masked primes. If the effects observed before reflected perceptual costs arising when a prime stimulus immediately reappears as target, they should be restricted to trials with arrow targets. If the impact of the masked primes was independent of perceptual repetition blindness, responses to lateral targets and centrally presented arrow targets should be similarly affected by prime-target compatibility.

2.1. Method

Participants. Twelve paid volunteers (eight female), aged 20–38 years, participated in the experiment. All participants were right-handed and had normal or corrected-to-normal vision.

Stimuli and Procedure. Participants were seated in a dimly lit, electrically shielded and sound attenuated chamber, with response buttons under their left- and right-hands. A computer screen was placed 110 cm in front of the participant's eyes and positioned so that the screen centre was in the centre of the participant's horizontal straight-ahead line of sight. All stimuli were presented in black in front of a white background. Left-pointing double arrows, right-pointing double arrows, or neutral stimuli ('< >') were presented as primes for 16 ms and were immediately followed by a mask consisting of superimposed left-pointing and right-pointing double arrows that was presented for 100 ms. Immediately after mask offset, target stimuli were presented for 100 ms. In 50% of all trials, centrally presented left-pointing and right-pointing double arrows were presented as targets. In the remaining trials, '+' signs (covering a visual angle of about $0.3° \times 0.3°$) were presented as targets on the left or right side of the screen with a horizontal eccentricity of 2.6° from the screen centre. All other stimuli (primes, masks, arrow targets) were delivered at fixation and covered a visual angle of approximately $0.8° \times 0.35°$. The interval between target offset and the onset of the next prime stimulus was 1 s. Participants were instructed to respond with a left-hand button press to left-pointing arrows and to the '+' sign when it was presented on the left side. Right-hand responses were required to right-pointing arrows and to the ''+' when it appeared on the right side. All combinations of prime-target compatibility (compatible, neutral, incompatible), target type (central arrow, peripheral '+' sign) and response side (left, right) were presented in random sequence and with equal probability in six experimental blocks, each consisting of 84 trials.

Data Analysis. Repeated measures ANOVAs were conducted on RTs and error rates obtained in the experimental blocks for the factors target type (central vs peripheral), prime-target compatibility (compatible vs neutral vs incompatible) and response side (left vs right). Greenhouse–Geisser adjustments to the degrees of freedom were performed when appropriate and p-values associated with the corrected degrees of freedom are reported.

2.2. Results and discussion

Effects of prime-target compatibility on RTs and error rates for centrally presented arrows and lateral targets are shown in Fig. 2. For RT, a prime-target compatibility effect was obtained ($F(2,22) = 37.66$; $p < 0.001$; Greenhouse–Geisser $\varepsilon = 0.626$) without interaction between compatibility and target type ($F < 0.3$). RTs for compatible, neutral and incompatible trials were 433, 405 and 396 ms, for central arrow targets and 437, 412 and 401 ms, for lateral targets. Additional comparisons using paired t-tests revealed that for both target types, significant RT costs for compatible trials and significant RT benefits for incompatible trials relative to neutral trials were present (all $t(11) > 2.82$; all $p < 0$ .017). More errors were observed in compatible than in neutral trials and only few errors were made in incompatible trials (Fig. 2, bar graphs). This was reflected in a main effect of prime-target compatibility ($F(2,22) = 44.75$; $p < 0$ .001; Greenhouse–Geisser $\varepsilon = 0.663$). A compatibility x target type interaction was found ($F(2,22) = 6.95$; $p < 0.008$; Greenhouse–Geisser $\varepsilon = 0.821$), presumably reflecting the fact that error rates in compatible trials were about twice as large for central targets than for lateral targets (see Fig. 2). However, prime-target compatibility affected error rates significantly in the arrow target condition ($F(2,22) = 28.34$; $p <$ 0.001; Greenhouse–Geisser $\varepsilon = 0.595$) as well as in the lateral target condition ($F(2,22) = 13.75$; $p < 0.001$; Greenhouse–Geisser $\varepsilon = 0.901$).

Experiment 1 provided clear-cut evidence against the assumption that the effects observed before primarily reflect perceptual repetition blindness (Hochhaus & Johnston, 1996). Performance benefits for incompatible trials and costs for compatible trials were not only found for targets that were physically identical to the primes, but also for targets that were dissimilar and presented at a different location than the masked primes. The pattern of results observed by Eimer and Schlaghecken (1998) thus is not due to effects of the physical identity or spatial proximity of primes and targets on perceptual analysis. Having ruled out this possibility, Experiments 2 and 3 further explored the idea that the masked primes are responsible for a sequential facilitation and inhibition of response tendencies.

3. Experiment 2

In the previous experiments, targets were presented more than 100 ms after prime onset. It was argued that the identification of the target and the subsequent activation of the correct response take place when the response tendency initially

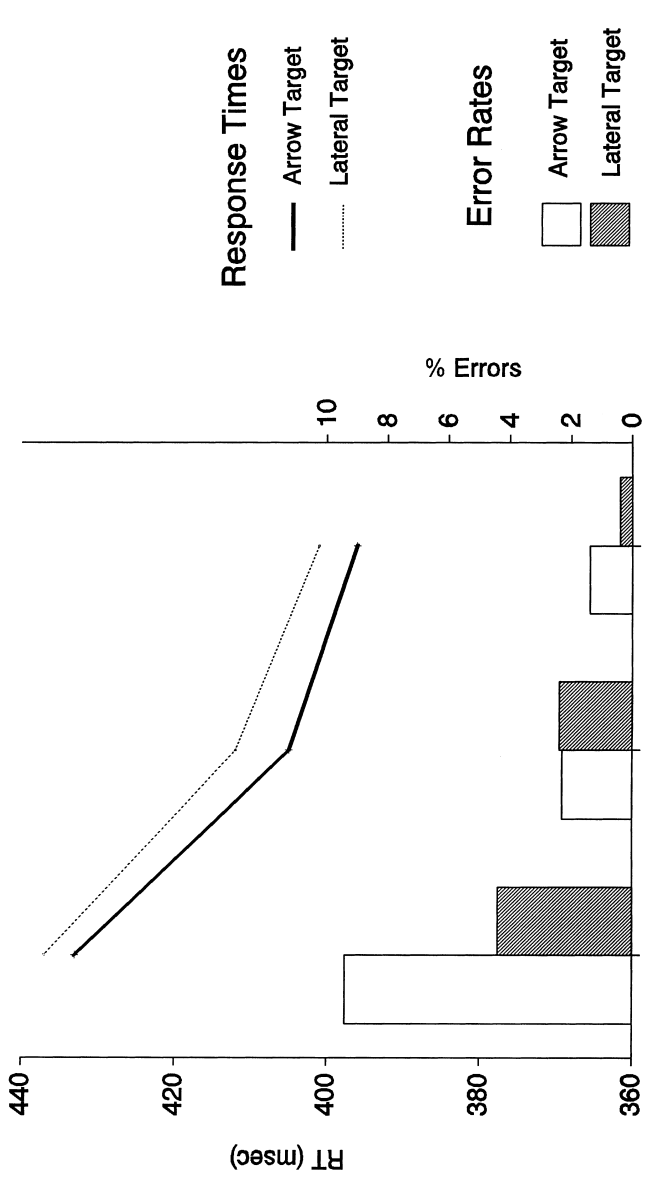

Fig. 2. Experiment 1: Response times (line graphs) and error rates (bar graphs) obtained in compatible, neutral, and incompatible trials in response to centrally presented arrow targets and to laterally presented "+" targets.

triggered by the prime was subject to inhibition and that the behavioural costs-benefit patterns result from this fact. However, this idea of a facilitation-followed-by-inhibition in motor activation is primarily based on LRP effects as shown in Fig. 1 (bottom) and thus needs independent verification by performance measures. If response inhibition is the result of an initial transient response facilitation, prime-target compatibility effects of opposite polarity (performance benefits for compatible trials and costs for incompatible trials) should be observed when the target can be identified and the corresponding response selected during the first, facilitatory phase. Generally, the direction of prime-target compatibility effects should critically depend upon the time interval between prime presentation and response execution. This interval can be varied by manipulating prime-target SOA and this was done in Experiment 3. Another possibility to study the dependence of prime-target compatibility effects on prime-response intervals is to analyse such effects separately for fast and slow responses. Performance advantages for compatible trials should be found for the fastest responses, while the opposite pattern should be observed for slower responses. To study the relationship between response speed and prime-target compatibility, individual RT distributions were divided into ten RT bins (deciles). RTs and error rates were analysed separately for compatible and incompatible trials within individual deciles. To ensure that the fastest responses would be executed when the prime-related response facilitation was still present, mask duration was reduced to 50 ms. [1] In addition, the lateralized readiness potential was recorded to confirm that motor activation patterns similar to those described by Eimer and Schlaghecken (1998) would still be elicited with shorter mask durations.

3.1. Methods

Participants. Nine paid volunteers participated in the experiment. One of them had to be excluded due to excessive eye blink activity, so that eight participants (four female), aged 23–37 years, remained in the sample. All participants were right-handed and had normal or corrected-to-normal vision.

Stimuli and procedure. Six experimental blocks, consisting of 80 trials each, were delivered. The trials were identical to the central presentation condition of Experiment 1, except that no neutral trials were included and mask duration was reduced to 50 ms. Compatible and incompatible trials and trials requiring a left-hand and right-hand response were presented in random order and with equal probability. After the experimental blocks, a forced choice performance block consisting of 40 trials was delivered where arrow primes (16 ms duration) were followed by a 50 ms mask and participants were instructed to signal the identity of the prime (left or right double arrow) with a left-hand or right-hand button press.

[1] A mask duration of 50 ms was chosen as a compromise between the conflicting aims of reducing the prime-response interval as much as possible, while keeping masking efficiency comparable to the previous experiments.

EEG recording and data analysis. EEG was recorded with Ag–AgCl electrodes from Fpz, 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 O2 and T6, respectively), according to the 10–20 system (Jasper, 1958). Only the data from C3′ and C4′ that were used to compute the lateralized readiness potential are reported. All electrodes were referenced to the right earlobe. Electrode impedance was kept below 5 kΩ. The amplifier bandpass was 0.1–40 Hz. EEG was sampled with a digitisation rate of 200 Hz and stored on disk. EEG was averaged off-line for epochs of 700 ms, starting 100 ms prior to prime onset and ending 600 ms after prime onset. Epochs with eyeblinks, eye movements, muscular artefacts, or incorrect responses were excluded from analysis. EEG was averaged separately for compatible and incompatible trials and for left and right responses. The lateralized readiness potential was computed for compatible and incompatible trials relative to a 100 ms baseline interval prior to prime onset. To obtain the LRP, C3′–C4′ difference potentials for right-hand response trials were subtracted from C3′–C4′ difference potentials for left-hand response trials. Positive deflections in the resulting LRP waveforms thus indicate the activation of the response assigned to the target stimulus in a given trial, whereas negative deflections indicate incorrect response activation. LRP mean amplitudes obtained for compatible and incompatible trials in the interval between prime onset and 450 ms after prime onset were compared within consecutive 50 ms time windows with repeated measures ANOVAs.

RTs and error rates were analysed with repeated measures ANOVAs for the factors prime-target compatibility and response side. An additional distributional analysis was conducted in the following way. First, an RT distribution was computed for each participant for compatible and for incompatible trials, including both correct and incorrect responses. Each distribution was then partitioned into ten RT bins, each containing 10% of all trials. Mean correct RTs and error percentages were computed for each bin and repeated measures ANOVAs were conducted on these data with decile and prime-target compatibility as factors. Compatible and incompatible RTs for individual deciles were compared using paired *t*-tests.

3.2. Results and discussion

Fig. 3 (top) shows the LRPs obtained for compatible and incompatible trials. Similar to the results reported by Eimer and Schlaghecken (1998), an initial activation of the response corresponding to the prime was followed by an opposite response activation tendency and a delayed onset of LRP activation related to the execution of the correct response in compatible trials. Effects of compatibility were obtained from 200 to 300 ms after prime onset ($F(1,7) = 8.25$ and 31.07; $p < 0.024$ and 0.001, in the 200–250 ms and 250–300 ms intervals, respectively). Within both intervals, paired *t*-tests showed that LRP mean amplitudes were significantly positive in compatible trials and negative in incompatible trials. Between 300 and 350 ms after prime onset, compatibility was only marginally significant ($F(1,7) = 4.46$; $p < 0.073$). While Fig. 3 (top) suggests a partial activation of the incorrect response in compatible trials, LRP amplitude did not differ significantly from zero within this

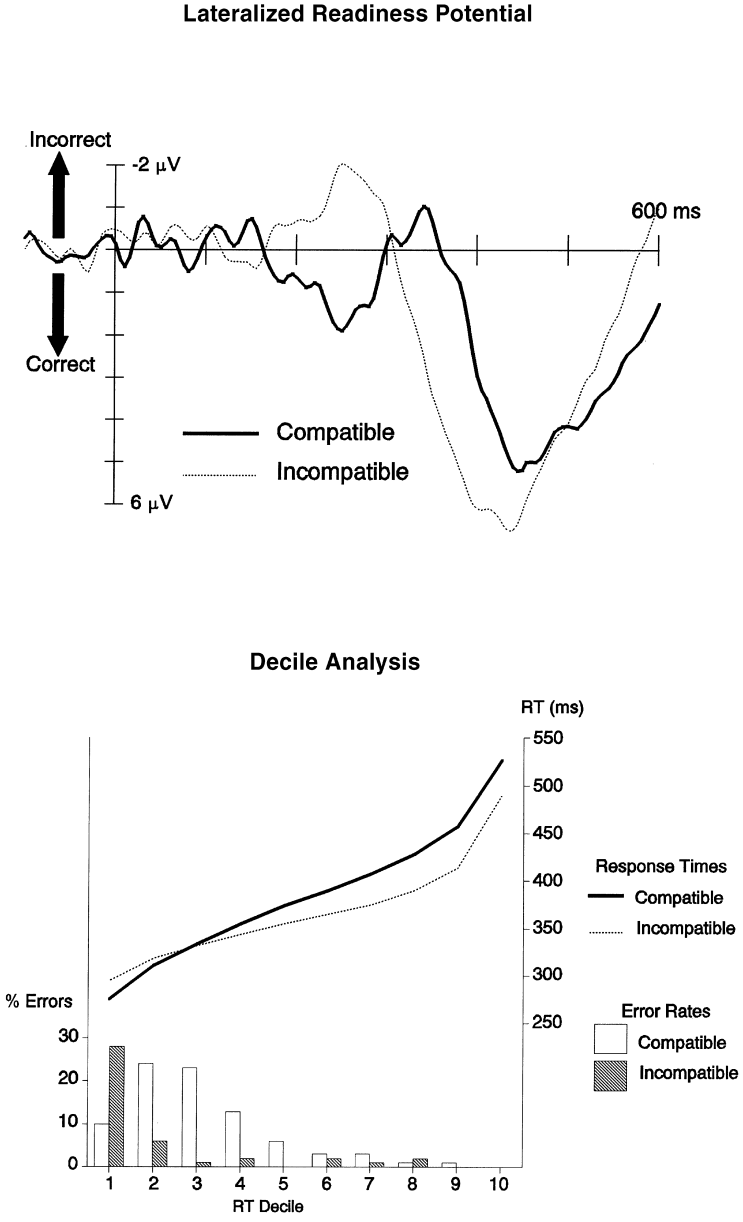

Fig. 3. Experiment 2. Upper panel: LRP waveforms obtained in compatible and incompatible trials in the time interval between prime onset and 600 ms after prime onset. Downward-going (positive) deflections indicate activation of the correct response (the response assigned to the target), whereas upward-going (negative) deflections indicate activation of the incorrect response. Lower panel: Response times and error rates in compatible and incompatible trials as a function of response speed. Mean RTs and error percentages are shown for the 1st to 10th decile of the individual RT distributions for compatible and incompatible trials.

time window. Between 350 and 400 ms after prime onset, correct response activation was significant for compatible and for incompatible trials, but an effect of compatibility ($F(1,7) = 8.53$; $p < 0.022$) reflected that this process was delayed in compatible trials.

RTs were faster in incompatible than in compatible trials (370 vs 392 ms), but this effect was only marginally significant ($F(1,7) = 4.29$; $p < 0.077$). More errors were observed in compatible as compared with incompatible trials (8.3% vs 4.1%), but this difference also failed to reach significance ($p > 0.1$). Fig. 3 (bottom) shows the results of the RT decile analysis. As predicted, the direction of prime-target compatibility effects on RTs was affected by response speed. Advantages for compatible trials were present for very fast responses and the opposite effect was visible for slower responses. This was reflected in a compatibility x decile interaction ($F(9,63) = 14.53$; $p < 0.001$; Greenhouse–Geisser $e = 0.172$). Additional paired t-tests were conducted for individual deciles. For the first decile, RTs were faster in compatible than in incompatible trials (276 vs 295 ms; $t(7) = 4.55$; $p < 0.003$) and this difference approached significance in the second decile ($t(7) = 2.08$; $p < 0.077$) No significant differences were obtained for the third to fifth decile and from the sixth decile onwards, RTs were reliably faster in incompatible than in compatible trials (see Fig. 3). This pattern of results was further tested by an additional simple regression analysis. The size and direction of the compatibility effect was computed by subtracting mean RT for incompatible trials from mean compatible RT for each participant and RT bin and a linear regression line was fitted through the resulting data points. Ar-square of 0.35 was obtained ($p < 0.001$) together with a positive slope of 6.8 and an intercept of -18.8 ms. Both regression parameters were significantly different from zero (both $p < 0.005$).

Conditional accuracy functions for compatible and incompatible trials for single latency bins are shown in Fig. 3. Errors were almost exclusively restricted to the first five latency bins. Within these bins, the accuracy of incompatible responses increased sharply from the first to the second and third RT bin and remained nearly perfect thereafter. Additional t-tests showed that error rates in incompatible trials were significantly larger for the first RT bin than in all subsequent bins. A different pattern emerged for compatible trials, where accuracy significantly decreased in the second and third RT bin relative to the first bin and reached asymptote considerably later than in incompatible trials. These differences were reflected by a compatibility x decile interaction ($F(4,28) = 5.47$; $p < 0.022$; $\varepsilon = 0.448$) in a repeated measures ANOVA conducted on the error rates obtained within the first five deciles.

In the Forced Choice blocks, participants identified the masked prime correctly on 47.2% of all trials. This performance was not significantly different from chance ($p > 0.25$), indicating that the reduction of mask duration did not critically affect masking efficiency.

The pattern of results obtained in Experiment 2 is in line with the idea that the masked prime stimuli trigger a transient response facilitation that is subject to inhibition. The LRP waveforms reflected the presence of an initial activation of the response assigned to the prime quite clearly. The overall compatibility effect of 22 ms failed to reach significance. This was not entirely unexpected, since it was predicted

that prime-target compatibility would affect RT differently for fast and slow responses. The 'facilitation-followed-by-inhibition' account was supported by the results of the RT distribution analyses. Initial facilitation was reflected in RT benefits for very fast compatible trials, resulting in a negative intercept of the linear regression function fitted through the net compatibility effects for each participant and RT bin. Subsequent inhibition was mirrored by the fact that RT benefits for fast compatible trials turned into benefits for incompatible trials as RTs became slower, reflected in a positive slope of the regression function. Additional evidence for this account comes from the conditional accuracy patterns for different RT bins. In incompatible trials, the majority of errors was found for very fast trials and error rates decreased sharply thereafter. In compatible trials, less errors were observed for very fast trials than for the second and third RT decile (see Fig. 3). This is exactly what a 'facilitation-followed-by-inhibition' hypothesis would predict, assuming that the initial facilitation of the response assigned to the prime is effective in the interval where the 10% fastest responses are prepared and executed and is then immediately replaced by inhibition.

In contrast to Eimer and Schlaghecken (1998), the incorrect LRP activation in compatible trials around 300 ms after prime onset was small and failed to reach significance. This is likely to be a result of the reduced mask duration, since an activation of the response required by the target will be under way within this interval in a considerable number of trials. The corresponding positive-going LRP deflections obtained in such trials are likely to attenuate the effects of response inhibition from trials with slower responses in the averaged LRP waveforms.

4. Experiment 3

The evidence for 'facilitation-followed-by-inhibition' obtained in Experiment 2 was based on RT latency distribution and conditional accuracy analyses and thus is still somewhat indirect. In Experiment 3, the interval between prime onset and response execution was manipulated directly by varying mask-target SOA. Primes were delivered either simultaneously with the masking stimulus, or 32, 64, 96 or 128 ms after mask onset. According to the facilitation-followed-by-inhibition account, the direction of compatibility effects should interact with mask-target SOA. Compatible trials should profit from short intervals between mask and target presentation, whereas advantages for incompatible trials should develop with increasing SOAs.

Because this SOA manipulation required masks and targets to be present simultaneously, they were delivered at non-overlapping locations. Primes, masks and targets were of different size, so that in spite of all being centred at fixation, their contours did not overlap (see Fig. 4, left). Square and diamond shapes, mapped to left-hand and right-hand responses, were employed as primes and targets. Similar stimuli were used in a metacontrast masking experiment by Klotz and Wolff, 1995. In contrast to the first two experiments, where left and right responses were assigned to left-pointing and right-pointing arrows or to stimuli presented on the left or right

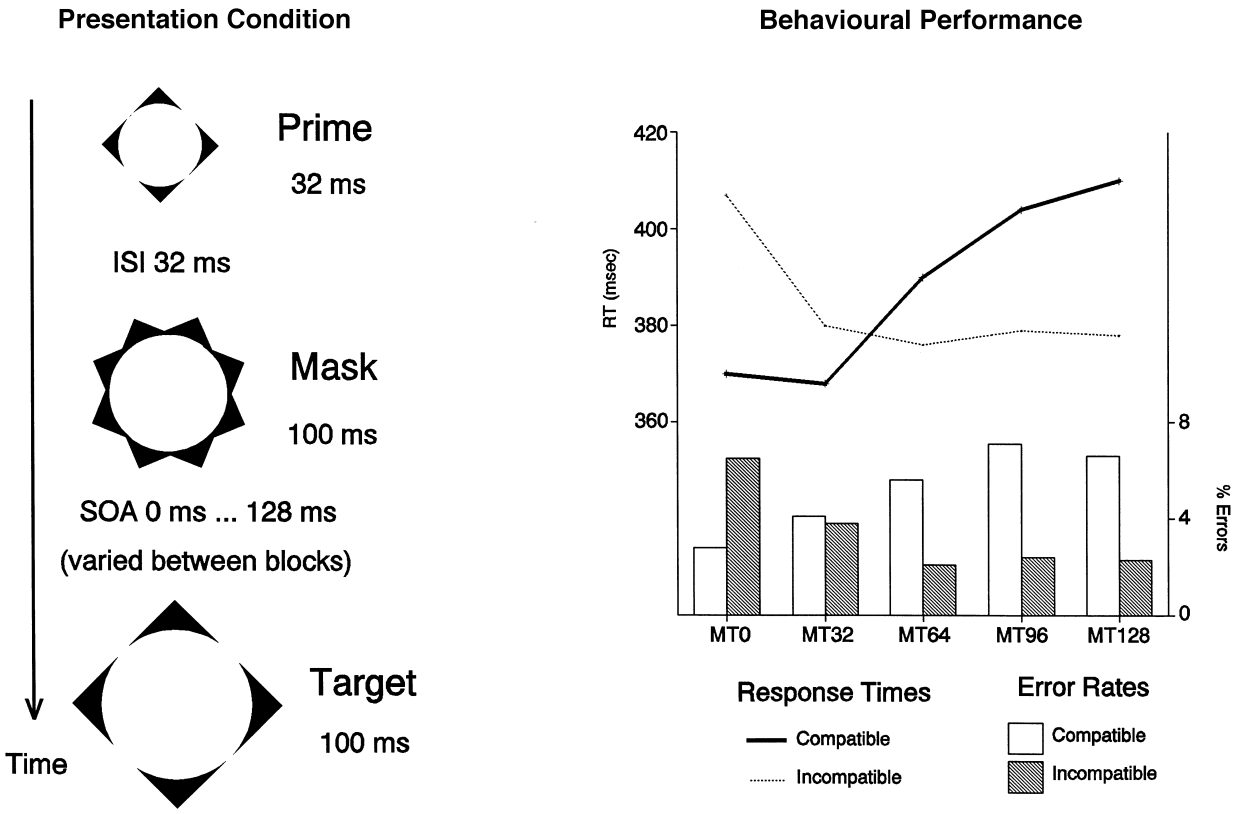

Fig. 4. Experiment 3. Left panel: Stimuli and presentation conditions in a compatible trial. Primes were presented for 32 ms, and were followed after an ISI of 32 ms by the mask (100 ms duration). Targets were presented for 100 ms either simultaneously with the mask or with an SOA of 32, 64, 96, or 128 ms. Mask-target SOA was varied between blocks. Right panel: response times (line graphs) and error rates (bar graphs) obtained in compatible and incompatible trials for the different mask-target SOAs.

side, the mapping between targets and responses was now entirely arbitrary. Another difference between this and the previous two experiments concerns the nature of the masking stimulus. In the first two experiments, the mask was created by superimposing both target stimuli. The presentation of the mask was in fact equivalent to adding the opposite target stimulus to the prime, which may have contributed to the activation of the opposite response. To control for this possibility, the mask employed in Experiment 3 was dissimilar from both targets, as it was created by superimposing and then rotating both target stimuli (Fig. 4, left). Previous experiments described in Eimer and Schlaghecken (1998) have already indicated that the identity of mask and target stimuli is not essential for prime-target compatibility effects to be produced. When masks were used that were physically distinct from primes and targets, behavioural effects were comparable to the effects obtained with arrow masks.

4.1. Method

Participants. Ten paid volunteers (seven female), aged 22–39 years, participated in the experiment. All were right-handed and had normal or corrected-to-normal vision.

Procedure. Square and diamond shapes were employed as primes and targets. The masking stimulus consisted of square and diamond shapes, superimposed upon another and rotated by 22.5° (Fig. 4, left). The outer diameters of primes, masks and targets were approximately 1°, 1.25° and 1.5°, respectively. Each trial began with a 32 ms presentation of a prime stimulus. After an ISI of 32 ms, the mask was presented for 100 ms. These temporal parameters were chosen because metacontrast masking is reported to be most effective with prime-mask SOAs between 30 and 80 ms (Lefton, 1973). Mask-target SOA was varied between blocks (0, 32, 64, 96 and 128 ms), termed MT0 to MT128, respectively. Each target was presented for 100 ms. Thus, in the MT0 condition, the mask and the target were presented simultaneously for 100 ms. The experiment consisted of 20 blocks (four blocks for each mask-target SOA) of 80 trials. The order in which these blocks were delivered was randomised. Compatible and incompatible trials and trials requiring a left-hand and right-hand response were presented in random order and with equal probability. Five participants responded with a left-hand response to square targets and with a right-hand response to diamond targets and these response assignments were reversed for the other five participants.

Following the experimental blocks, a forced choice block consisting of 80 trials was delivered where participants had to signal the identity of a prime stimulus with a left-hand or right-hand button press. A complete sequence of prime, mask and target was presented in each trial. Two mask-target SOAs (0 and 96 ms) were employed and these were delivered randomly and with equal probability.

Data analysis. Repeated measures ANOVAs were conducted on RTs and error rates for the factors prime-target compatibility (compatible vs incompatible), mask-target SOA (0, 32, 64, 96, 128 ms) and response side (left vs right). Separate analyses were conducted for single mask-target SOAs.

4.2. Results and discussion

Fig. 4 (right) shows RTs and error rates obtained in compatible and incompatible trials for the different mask-target SOAs. There was no main effect of prime-target compatibility on RT, but a significant compatibility x mask-target SOA interaction ($F(4,36) = 32.51$; $p < 0.001$; Greenhouse–Geisser $\varepsilon = 0.413$). Additional analyses conducted separately on RTs obtained for different mask-target SOAs found faster RTs for compatible as compared with incompatible trials in the MT0 condition ($F(1,9) = 47.26$; $p < 0.001$) and the opposite effect for the MT64, MT96 and MT128 conditions (all $F(1,9) > 5.85$; all $p < 0.039$). In the MT32 condition, prime-target compatibility failed to reach significance. A similar pattern was observed for the error rates. A mask-target SOA x compatibility interaction was found ($F(4,36) = 10.05$; $p < 0.001$; Greenhouse–Geisser $\varepsilon = 0.583$). In the MT0 condition, errors were more frequent in incompatible trials ($F(1,9) = 6.3$; $p < 0.033$). For the MT64, MT96 and MT128 conditions, more errors were observed in compatible trials (all $F(1,9) > 9.4$; all $p < 0.013$). In the forced choice block, participants correctly identified 61% of all primes, which was almost significantly better than chance performance ($p < 0.052$). [2]

The pattern of prime-target compatibility effects obtained for the different mask-target SOAs provides additional behavioural evidence in favour of a facilitation-followed-by-inhibition account. For short mask-target intervals, benefits were obtained for compatible trials, which turned into costs when these intervals became longer, presumably reflecting the inhibition of an initial response tendency. Experiment 3 further suggested that such effects are not limited to situations where spatially congruent stimulus-response pairings are used, but can be found for entirely arbitrary S-R mappings. It should however be acknowledged that no LRPs were recorded in this experiment, so there is yet no direct evidence to show that the pattern of effects observed here was primarily located at the response level. Perceptual conditions were considerably different in Experiment 3 than in the previous studies and these differences may have been responsible for the less-than-perfect efficiency of masking. Although the time course of the prime-target compatibility effects was very similar to the pattern observed before, the possibility remains that these effects were at least partially perceptual rather than motor.

5. General discussion

The experiments reported here confirmed and extended earlier findings (Eimer & Schlaghecken, 1998) regarding the effects of masked prime stimuli on behavioural

[2] This result was mainly due to two participants who identified the primes correctly on more than 80% of all trials. However, these participants showed the same interaction of compatibility with mask-target SOA as all other participants, with RT benefits for compatible trials of 54 ms and 34 ms in the MT0 and MT32 conditions, and costs of 9 ms, 21 ms, and 27 ms, in the MT64, MT96, and MT128 conditions.

performance and motor activation. Whereas previous research (Neumann & Klotz, 1994; Klotz & Wolff, 1995) found facilitatory effects in trials where primes and targets were identical and costs when they were mapped to opposite responses, this study demonstrated that the direction of such effects crucially depends on the time interval separating prime presentation and response execution. Performance benefits observed at short prime-target intervals when the prime was identical to the target turned into costs at longer intervals. This was interpreted as reflecting an initial response facilitation triggered by a prime stimulus that is later replaced by inhibition. The results reported by Neumann and Klotz, 1994 and Klotz and Wolff, 1995 are not at all incompatible with this account. In these studies, the masking stimulus served as target, resulting in short prime-response intervals, so that most responses were presumably executed during the initial facilitatory phase. In this respect, these studies are comparable to the MT0 condition of Experiment 3, where RTs were indeed faster in compatible trials.

Experiment 1 demonstrated that the performance costs in compatible trials are not caused by detrimental effects of the primes on the perceptual analysis of identical target stimuli, as suggested by the notion of 'perceptual repetition blindness'. Experiments 2 and 3 provided further evidence for a sequential pattern of facilitation followed by inhibition. The fact that the behavioural effects were mirrored in corresponding modulations of the lateralized readiness potential suggests that these effects are primarily located at response-related stages. The initial facilitation of the response assigned to the prime stimulus may reflect a direct link between perceptual analysis and motor processes, allowing sensory information obtained from the prime to partially activate a response prior to the intervention of controlled response selection processes. The subsequent inhibition may be achieved by a mechanism which detects and shuts down response tendencies caused by such a leakage of unattended information into the motor system. As lined out in the Introduction, it is likely that this type of inhibition primarily operates on central motor structures rather than peripherally. As the primes were always followed by response-relevant targets, a non-selective peripheral inhibition of motor commands would have interfered with the execution of the response required by the targets. The fact that prime-target compatibility was reflected in systematic LRP modulations also suggests that the locus of the inhibitory processes observed in the present experiments was primarily central.

An important aim of the present research was to investigate the time course of response activation and inhibition directly by analysing the impact of the primes on performance to the targets within different prime-response intervals. The LRP waveforms in Figs. 1 and 3 suggest that response facilitation started around 200 ms after prime onset and was replaced by inhibition about 100 ms later. Taking into account the transmission lag between central motor structures and peripheral motor effectors, one would expect behavioural facilitation turning into inhibition between 350 ms and 400 ms after prime onset. This estimate seems to correspond well with the pattern of results obtained in Experiments 2 and 3. It should be noted that in the standard stop-signal paradigm, stop-signal RT (the time needed for inhibition in response to the stop signal to become effective) is considerably faster, with estimates

ranging around 200 ms (Logan, 1994). A number of factors may be responsible for this difference, such as the presence or absence of explicit intentions with respect to response activation and inhibition, the presence or absence of a clearly defined stop signal, differences in the degree to which the initial response is activated and the possibility of fast peripheral inhibition in the stop-signal situation. Future studies will have to clarify the role of these factors for the time course of response activation and inhibition.

Central inhibitory motor control can be achieved through a self-inhibitory network described by Houghton and Tipper, 1994, where cognitive nodes representing object features are linked to excitatory and to inhibitory control units. Upon arrival of an object, specific feature nodes are activated, which will activate both excitatory and inhibitory control units, so that facilitatory and inhibitory impulses are fed back to the feature nodes. Importantly, the activity of these control units is modulated by processes sensitive to the relevance of stimulus features, so that for unattended features, the inhibitory feedback will exceed excitation. When an unattended object disappears, input from the inhibitory control unit will cause activity to drop below baseline (inhibitory rebound). When this object then reappears as target during this inhibitory rebound interval, negative priming is observed (cf., Houghton, Tipper, Weaver & Shore, 1996). Such self-inhibitory control processes may be of general importance to maintain a balanced stability within cognitive networks by preventing extreme and long-lasting activations which would otherwise result in maladaptive performance (cf., Arbuthnott, 1995). Self-inhibitory circuits in motor control could account for the facilitation-followed-by-inhibition pattern observed in the present study. An incoming interrupt signal may bias an opponent-process network in favour of inhibitory feedback. The performance benefits observed for incompatible relative to neutral trials may be explained by assuming that within such a network, inhibitory connections exist between alternative responses, resulting in lateral inhibition between competing response tendencies. [3] In such a system, an active inhibition of one response would result in a partial activation of the response alternative.

This type of inhibitory motor control would have to rely on a mechanism that detects irrelevant motor activation. This task may be accomplished by a sensory-motor 'confirmation loop' that continuously monitors whether the current state of motor activation is accounted for by incoming sensory information. In the masked prime situation, a masking stimulus arriving immediately after a prime would instantly wipe out the sensory information that previously triggered a partial response activation. The resulting lack of sensory evidence available to the confirmation loop would then cause an interrupt signal to be sent to opponent-process motor control circuits, resulting in response inhibition. Alternatively, one may assume that ongoing response tendencies are inhibited whenever the transmission of response-related information to the motor system is suddenly interrupted by a transient event. In this view, it is the onset of a new event, rather than its effect on currently active sensory

[3] Zorzi and Umiltà, 1995 presented a network model of the Simon effect that is partially based on this sort of lateral inhibition.

representations, that would trigger an inhibitory interrupt signal. No firm conclusions about these alternatives are possible at this moment. The functional relationship between masking, sensory transients and response inhibition has to await clarification from future studies.

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