



## Response facilitation and inhibition in subliminal priming

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### Abstract

The research reviewed in this article has investigated with behavioural, electrophysiological, and functional imaging methods how subliminally presented masked prime stimuli affect response-related processes. An initial response activation triggered by these primes was found to be followed by an inhibition of this response tendency, provided that the initial activation was strong enough to exceed an ‘inhibition threshold’. This biphasic pattern is assumed to reflect the presence of self-inhibitory circuits in motor control. In contrast to endogenous response inhibition, observed when response-relevant signals are consciously perceived, this exogenous mode of response inhibition appears to be mediated by corticostriate rather than by prefrontal mechanisms. Overall, results demonstrate that inhibitory mechanisms are involved in the control of response processes, even when motor activations are triggered by stimuli that are not accessible to conscious awareness.

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### 1. Introduction

Traditional models of perceptuo-motor interactions typically assume that perception and response processes constitute discrete stages, which are activated in a strictly successive order (e.g. Sternberg, 1969; Sanders, 1980). In contrast, models assuming an ‘asynchronous’ (e.g. Miller, 1982, 1988) or ‘continuous’ (e.g. Coles et al., 1985; Eriksen and Schultz, 1979) flow of information from sensory to motor systems hold that response processes can be activated by sensory information before perceptual analysis is completed. Evidence for this has been found in behavioural and electrophysiological experiments (e.g. Coles et al., 1985; Eriksen et al., 1985; Eriksen and Schultz, 1979; Smid et al., 1990), which have demonstrated

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effects of sensory information on response processes prior to the termination of stimulus analysis. More recently, it has been shown that even stimuli presented near or below the threshold of conscious awareness can trigger response activation processes (Dehaene et al., 1999; Klotz and Wolff, 1995; Neumann and Klotz, 1994). This ‘subliminal activation’ of motor responses has been interpreted as reflecting direct perceptuo-motor links (Neumann, 1990), which allow perceptual information to affect the motor system without necessarily being consciously perceived.

A continuous transmission of information from perception to action will frequently be beneficial, since it allows organisms to respond quickly and flexibly to rapid changes in its environment. However, it could be argued that this benefit might often come at a substantial cost. If stimuli that have not yet been fully analysed, or are even inaccessible to conscious perception, have the potential to activate motor responses, these response tendencies could interfere with ongoing performance, or even cause inappropriate behaviour. The present article reviews recent experimental evidence suggesting that—contrary to common belief—inhibitory processes can be activated in situations where response tendencies are triggered by subliminal stimuli, and that these processes might act to prevent such maladaptive consequences of a continuous flow of information between perception and action.

Many behavioural and electrophysiological studies have shown that response inhibition plays a crucial role in motor control (e.g. De Jong et al., 1990; De Jong et al., 1995; Eimer, 1993; Falkenstein et al., 1999; Jodo & Kayama, 1992; Kok, 1986; Naito and Matsamura, 1994). These studies have employed stop-signal or go/nogo tasks, where participants have to refrain from responding when presented with a specific signal. Here, response inhibition is initiated once the stop signal or nogo stimulus has been recognised. This *endogenous* inhibition is voluntary, optional, and is presumably mediated by executive mechanisms in prefrontal cortex (Band and van Boxtel, 1999). Since endogenous inhibition depends on the conscious detection of task-relevant signals, it is not available when stimuli are presented subliminally. Because of this fact, it has often been argued that inhibitory control processes are generally restricted to above-threshold stimulation conditions. Evidence for this hypothesis has been obtained in studies investigating negative priming (e.g. Allport et al., 1985; see also Neill et al., 1995), voluntary and involuntary shifts of spatial attention (McCormick, 1997), the disambiguation of polysemous words (Marcel, 1980), and the Stroop effect (Merikle et al., 1995). In all of these studies, it has been shown that endogenous inhibition—operating when stimuli are presented supraliminally—is absent when stimuli are presented subliminally. Evidence for automatic activation processes, in contrast, was still obtained with subliminal stimuli. From this it has been concluded that subliminally presented stimuli trigger only passive activation, and that for active inhibition to occur, stimuli have to be presented supraliminally.

The present article will review a number of recent studies which have challenged this view that inhibitory control is restricted to conditions where stimuli are accessible to conscious awareness. These experiments have shown that inhibitory processes are active even when response tendencies are triggered by subliminal stimuli. Unlike endogenous inhibitory control, this form of inhibition appears to be reflexive, does not depend on the conscious recognition of task-relevant signals, and will be referred to as *exogenous* inhibition. The present article surveys recent findings from behavioural, electrophysiological, and functional imaging studies, which have investigated exogenous inhibitory processes in motor

control. Section 2 describes the experimental procedures used to study response activation and inhibition triggered by subliminal stimuli, and discusses the time course and the possible neural basis of these processes. In Section 3, recent evidence is reviewed which suggests that a threshold mechanism is involved in the exogenous inhibition of response processes. Finally, Section 4 summarises the main findings and draws some general conclusions with respect to the functional principles involved in exogenous inhibitory motor control.

## 2. Response activation and inhibition processes triggered by subliminal prime stimuli

To investigate the impact of subliminal stimuli on response processes, we have used a ‘masked prime’ paradigm where briefly presented prime stimuli were immediately masked and then followed by imperative stimuli requiring a choice response. The critical manipulation concerned the relationship between masked prime and target stimuli. On any given trial, the prime was either mapped to the same response as the target (compatible trial), to the opposite response (incompatible trial), or not mapped to any response at all (neutral trial). In a typical experiment (e.g. Eimer and Schlaghecken, 1998), prime stimuli were presented for 16 ms, immediately followed by a mask (100 ms duration), and then by a target (100 ms duration), 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 inward- or outward-pointing arrows (‘<>’ or ‘><’) served as neutral primes. The mask was created by superimposing left-pointing and right-pointing double arrows upon one another, and all stimuli were presented at fixation.

Under these task conditions, the behavioural data revealed a surprising pattern of results: Instead of observing superior performance on compatible trials, where primes and targets were identical, and performance costs on incompatible trials, where they were mapped to opposite response, the reverse was found. Relative to neutral trials, reaction times (RTs) were faster and error rates lower in incompatible trials, whereas slower RTs and higher error rates were found in compatible trials. In other words, there were performance costs on compatible trials, and performance benefits on incompatible trials. This ‘negative compatibility effect’ has now been replicated many times, both in our lab (e.g. Eimer, 1999; Schlaghecken and Eimer, 2000, 2001, 2002) and in other labs (e.g. Klapp and Hinkley, 2002; Michel, 2000; Vorberg, 2000), and thus represents a robust, albeit surprising, effect of subliminal priming.

Before this effect can be interpreted as evidence for the exogenous inhibitory control of response tendencies triggered by subliminal stimuli, several issues need to be addressed. First, the question arises whether the masked prime stimuli were genuinely subliminal, or whether the masking procedures used in these studies have been insufficient to completely prevent conscious awareness of the primes. We have employed forced choice present/absent tasks (Eimer and Schlaghecken, 1998, Exp. 2 & 3), forced choice prime identification tasks (Eimer and Schlaghecken, 1998, Exp. 1; Schlaghecken and Eimer, 1997), and staircase procedures (Eimer and Schlaghecken, 2002), to test for prime visibility. In all these experiments, results demonstrated that the masked primes could not be consciously detected or discriminated. Furthermore, results in Eimer and Schlaghecken (2002) confirmed a close

link between direction of priming effects and prime visibility: negative compatibility effects were restricted to primes that could not be consciously identified, while suprathreshold primes resulted in positive compatibility effects (performance benefits on compatible trials, and costs on incompatible trials). A corresponding result has been obtained by Klapp and Hinkley (2002), demonstrating that unmasked, visible primes elicit positive compatibility effects. Taken together, these findings virtually rule out the possibility that residual prime visibility can account for negative compatibility effects.

A second question is whether negative compatibility effects reflect response-related processes, or whether these effects originate at perceptual or central semantic levels. Phenomena like ‘repetition blindness’ (Hochhaus and Johnston, 1996; Kanwisher, 1987) demonstrate a bias of the perceptual system against the repeated processing of identical stimuli. Thus, the negative compatibility effect might reflect impaired target processing on compatible trials, where the target is a repetition of the prime. To investigate this issue, we conducted experiments where a subset of compatible and incompatible trials contained targets which were physically dissimilar to the masked primes, and appeared in different locations (Eimer, 1999, Exp. 1; Schlaghecken and Eimer, 2000, Exp. 2). Negative compatibility effects were still elicited under these conditions, thus ruling out an explanation of these effects in terms of a perceptual bias. The possibility that they are due to semantic processes at a central level (e.g. abstract ‘left’ and ‘right’ codes that represent response side independent of response modality) was ruled out by the absence of any transfer of negative compatibility effects across response modalities (hand versus foot responses; see Eimer et al., 2002, for details).

If negative compatibility effects do not originate at perceptual or central processing stages, the one remaining option is that they are generated within the motor system. The most direct evidence for the influence of masked primes on motor processes comes from experiments studying subliminal priming with the lateralized readiness potential (LRP). This electrophysiological measure 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 et al., 1988; De Jong et al., 1988; Coles, 1989; Eimer, 1998; Eimer and Coles, 2003; Gratton et al., 1988). LRP waveforms obtained by Eimer and Schlaghecken (1998); Exp. 1a) for compatible, neutral, and incompatible trials (measured from the onset of the prime stimulus, with target onset after 116 ms indicated by ‘T’) are shown in Fig. 1a (upper left panel). Downward-going (positive) amplitude values represent activation of the correct response (i.e. the response mapped to the target stimulus on any given trial), while upward-going deflections represent an opposite response activation tendency. As can be seen from Fig. 1a, an initial activation of the response assigned to the prime was elicited about 200 ms after prime onset, reflected in a partial activation of the correct response in compatible trials and partial incorrect response activation in incompatible trials (indicated by ‘A’ in Fig. 1a). No such early response activation was present in neutral trials. However, this initial effect reversed polarity around 300 ms after prime onset (‘I’ in Fig. 1a), resulting in an activation of the correct response on incompatible trials, and in the opposite response activation tendency on compatible trials.

We have interpreted this LRP pattern as a sequence of response activation followed by inhibition (Eimer and Schlaghecken, 1998). Initially, the response assigned to the prime is activated (‘A’ in Fig. 1a), presumably due to a continuous flow of information between sen-

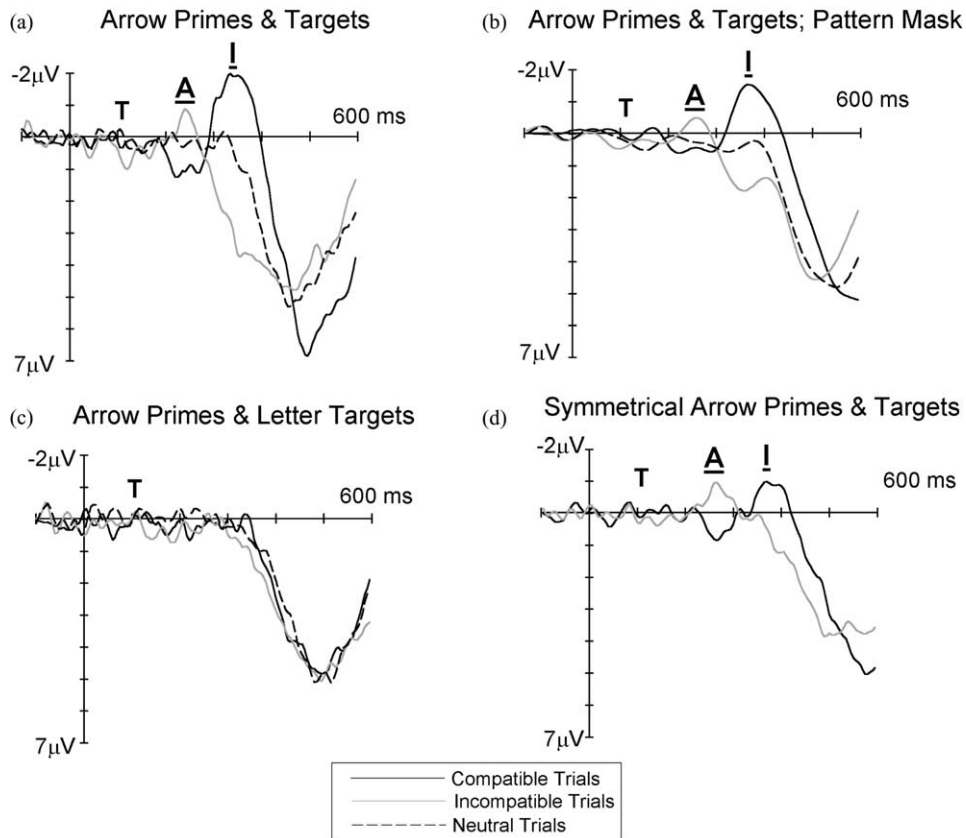


Fig. 1. LRP waveforms measured in compatible, incompatible, and neutral trials, displayed relative to the onset of the masked primes. 'T' indicates the onset of the target stimulus. Downward-going (positive) deflections indicate activation of the correct response, upward-going (negative) deflections reflect a relative activation of the opposite response. 'A' indicates the initial response activation triggered by the masked primes, 'I' marks the subsequent inhibition of this response activation. (a) LRP waveforms obtained when masked arrow primes were followed by arrow targets. Data from Eimer and Schlaghecken (1998); Exp. 1). (b) LRP waveforms obtained when arrow primes were followed by a pattern mask and arrow targets. Unpublished data. (c) LRP waveforms obtained when masked arrow primes were followed by letter targets. Data from Eimer and Schlaghecken (1998); Exp. 1). LRP waveforms obtained in an experiment where all primes and targets were symmetrical, and no neutral trial condition was included. Data from Eimer and Schlaghecken (1998); Exp. 2). See text for full details.

sory and motor stages which allow sensory information to rapidly affect response processes. For compatible trials, this initial primed response tendency is reflected in a partial early activation of the correct response (that is, the response assigned to the subsequent target). For incompatible trials, primed response activation gives rise to a partial early activation of the incorrect response. The subsequent reversal of these early effects ('I' in Fig. 1a) was interpreted as subsequent inhibition of the initial activation. On compatible trials, this inhibition is reflected by an upward-going (incorrect) response activation, while on incompatible trials, it results in a downward-going (correct) LRP modulation, which partially overlaps with

the subsequent activation of the correct response triggered after the identification of the target stimulus.

Given this pattern of primed response activation followed by inhibition revealed by the LRP waveforms, we explained the observed behavioural negative compatibility effects by assuming that in these experiments, the response to the target stimulus is selected during the second, inhibitory phase between 300 and 400 ms after prime onset (that is, between 200 and 300 ms after target onset). In this time interval, the response mapped to the prime is inhibited, and this inhibition is reflected in faster responses on incompatible as compared to compatible trials.

In this context, it is important to note that as a consequence of the way it is derived, the LRP reflects the relative, rather than the absolute activation level of left-hand and right-hand response tendencies (see Coles, 1989; Eimer, 1998; Eimer and Coles, 2003, for further details). Thus, the upward-going deflection observed for compatible trials in the 300–400 ms interval following prime onset indicates that activation level of the primed response was reduced (inhibited) relative to the activation of the opposite response, but not necessarily that the incorrect response was selectively activated during this interval.

Additional follow-up LRP experiments were conducted to rule out alternative interpretations of this pattern of LRP results. First, it is possible that these effects may at least in part be an artefact of the specific masking procedure used in the Eimer and Schlaghecken (1998) study, where masks consisted of superimposed left and right double arrows. However, behavioural negative compatibility effects have also been obtained with other types of masks, such as letter masks (Klapp and Hinkley, 2002), random pattern masks (Eimer and Schlaghecken, 2002; Schlaghecken and Eimer, 2002), and when using a metacontrast masking procedure (Eimer, 1999), thus demonstrating that these effects do not depend on specific physical properties of the masking stimulus. This is also illustrated in Fig. 1b, which shows the LRP results from a recent, yet unpublished experiment, where arrow primes were followed by pattern masks, which consisted of a dense array of overlapping lines of different length and orientation. Fig. 1b clearly shows that both early response activation ('A') as well as subsequent inhibition ('I') were elicited when primes were followed by such pattern masks, and this was also reflected behaviourally in negative compatibility effects.

Finally, one could argue that because left and right arrow stimuli were used as primes and targets, the observed LRP effects do not reflect specific stimulus-response mappings as implemented via experimental instructions, but are due to an automatic activation of a left or right response triggered by left-pointing and right-pointing arrows. To investigate this, we ran an experiment where primes were again left-pointing and right-pointing arrows, but targets were now letter stimuli ('L' and 'R') which were mapped to left and right responses (Eimer and Schlaghecken, 1998, Exp. 1b). Under these conditions, where no response was assigned to the arrow primes, no behavioural priming effects were observed, and there were no differences between LRP waveforms obtained in compatible, incompatible, and neutral trials (Fig. 1c). In another study (Eimer and Schlaghecken, 1998, Exp. 2), we recorded LRPs under conditions where both primes and targets were symmetrical ('<' and '>'). Here, a negative compatibility effect was observed behaviourally, and LRP waveforms (shown in Fig. 1d) again showed the biphasic pattern of an initial response activation ('A') followed by inhibition ('I').

In the experiments discussed so far, behavioural negative compatibility effects were interpreted as evidence for the inhibition of a response tendency initially triggered by the masked primes. This sequence of ‘response activation followed by inhibition’ was inferred from the specific sequence of LRP modulations as shown in Fig. 1. Given these LRP results, it should be possible to obtain direct behavioural evidence for the presence of an initial response activation process by manipulating the timing of prime and target presentation. Under conditions where it is possible to select the response to target stimuli already during the early response activation phase (‘A’ in Fig. 1), performance benefits should be observed for compatible trials, and performance costs for incompatible trials.

We investigated these predictions by systematically manipulating the stimulus onset asynchrony (SOA) between masked primes and targets (Schlaghecken and Eimer, 2000). Two groups of participants were tested with either short mask-target SOAs (between 0 and 96 ms), or long SOAs (between 96 and 192 ms). In the 0 ms SOA condition, mask and targets were presented simultaneously, and mask-target SOA was increased in steps of 32 ms for the other SOA conditions. Masked arrow primes were presented at fixation, arrow targets were presented bilaterally to the left and right of fixation, and mask-target SOA was varied between blocks. When SOAs are short, response selection can already take place during the initial response activation phase, and this should result in positive compatibility effects. When SOAs are longer, responses have to be selected during the subsequent inhibitory phase, and this should be reflected in negative compatibility effects, as observed in the experiments described above.

Fig. 2 (upper panel) shows RTs for compatible and incompatible trials obtained for each mask-target SOA. Results fully confirmed the predictions derived from the activation-followed-by-inhibition account. A positive compatibility effect (faster responses for compatible trials) was obtained for short SOAs (0 and 32 ms). In contrast, a negative compatibility effect was elicited when mask-target SOA was 96 ms, and this effect remained to be present up to the longest SOA of 192 ms. This pattern of effects was also present in error rates, with more errors on incompatible trials with short SOA, and higher error rates on compatible trials for SOAs of 96 ms and above. Analogous results have also been obtained by Eimer (1999), Exp. 3) using a metacontrast masking procedure, thus demonstrating that the time course of response activation and inhibition as initially revealed by LRP measures (Fig. 1) is directly reflected in priming effects on behavioural performance.

These observations show that performance is not affected by prime-related response inhibition when the interval separating the masked prime and the target is sufficiently short (see Section 4 for a more detailed discussion). This opens up the possibility of isolating the brain processes activated during the early facilitatory phase of subliminal priming with functional imaging measures. We have recently used event-related functional magnetic resonance imaging (fMRI) to localise brain areas selectively activated during the response activation triggered by masked primes (this unpublished data has been obtained in the context of an experiment investigating fMRI BOLD responses of prime-related inhibition, Aron et al., 2003). In this experiment, mask-target SOA was either 0 or 150 ms, and compatible, neutral, and incompatible trials were delivered. The behavioural results obtained in the scanner confirmed previous findings, with positive compatibility effects for the 0 ms SOA condition, and negative compatibility effects for the 150 ms SOA condition. Analyses aimed at identifying brain areas activated during the early response activation phase were restricted

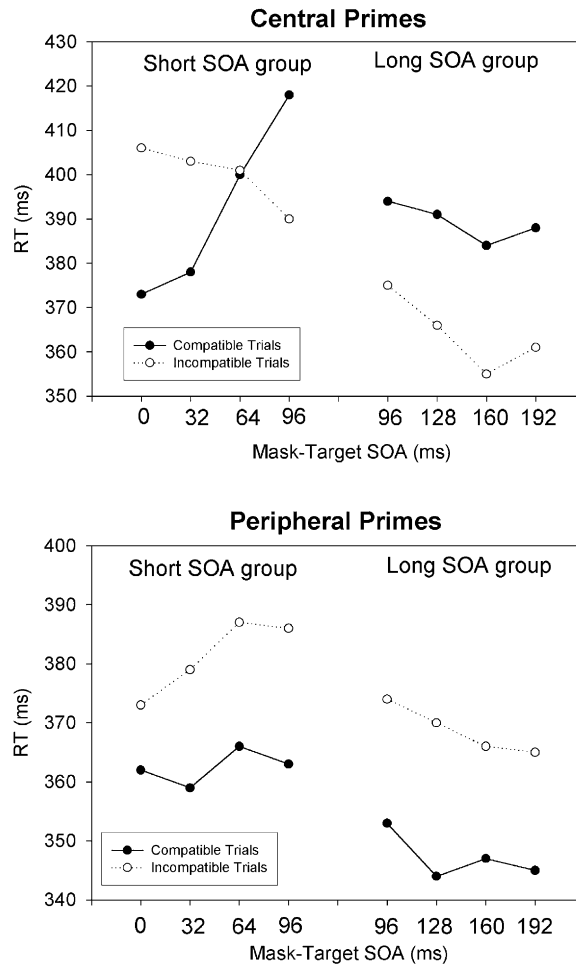


Fig. 2. Mean reaction times (RTs) observed in compatible and incompatible trials for different mask-target SOAs. Top panel: Results obtained for central masked primes. Bottom panel: Results obtained for peripheral masked primes. Data from Schlaghecken and Eimer (2000), Exp. 1).

to the 0 ms SOA condition, where the initial activation was assumed to be unaffected by subsequent prime-related inhibition. Fig. 3 shows prime-related activation in response to left and right masked primes, respectively, obtained by comparing compatible trials with neutral trials requiring the same response (thus holding activations due to response selection and activation constant). Fig. 3 (left) shows voxels which showed a significant increase in activation during compatible trials where a left-pointing arrow prime was followed by a left-pointing arrow target (requiring a left-hand response), relative to neutral trials where a neutral prime was followed by a left arrow target. Fig. 3 (right) shows the results of the analogous contrast involving compatible/right response and neutral/right response trials. Significant activations were observed in the hand area of contralateral primary motor cortex



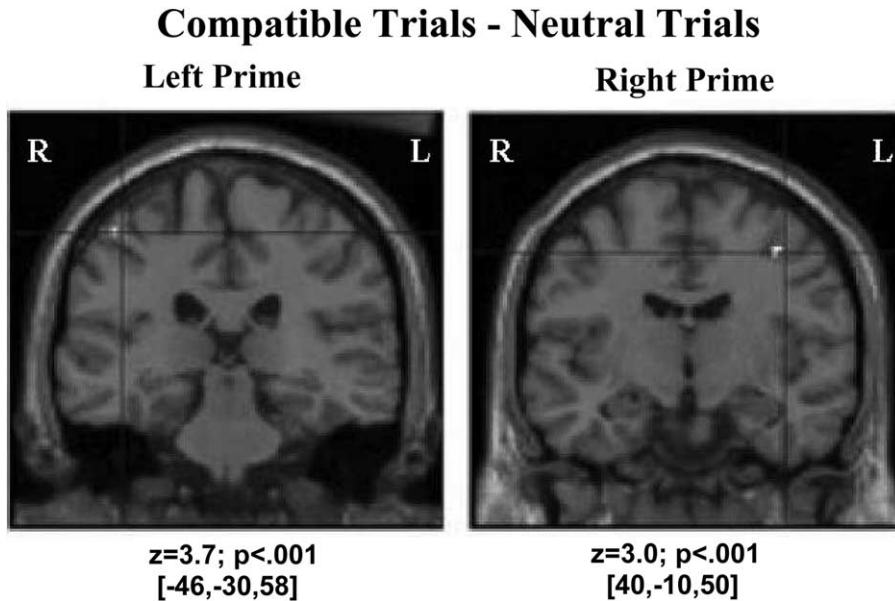


Fig. 3. Results of fMRI contrast analyses investigating brain areas selectively activated during primed response activation. Coronal MRI slices through motor cortex are shown, along with normalized Z scores, *P*-values, and peak voxel Talairach coordinates. In both cases, the focus is hand area of motor cortex. Left panel: right motor cortex activation to left arrow primes. Right panel: Left motor cortex activation to right arrow primes. See text for further details.

for both contrasts. Primes mapped to a left response activated the right motor cortex, and primes mapped to a right-hand response activated the left motor cortex. The same pattern of results was also obtained for contrasts where incompatible and neutral trials were compared (not shown in Fig. 3).

The observation that the masked primes selectively activated the hand area of contralateral motor cortex not only provides strong evidence that unperceived stimuli can have substantial effects on primary motor cortex. It also points to the likely neural basis of the initial response activation phase previously observed with LRP measures ('A' in Fig. 1). These converging findings illustrate that despite their respective limitations in terms of spatial and temporal resolution, electrophysiological and functional imaging measures can be combined successfully to investigate both the time course as well as the neural basis of short-latency transient motor processes.

The main aim of our recent fMRI study (Aron et al., 2003) was to identify neural correlates of prime-related response inhibition. To this purpose, we identified those areas that showed significant BOLD responses in compatible *and* incompatible trials for the 150 ms SOA condition (relative to the corresponding neutral trials), but did *not* show similar effects in the 0 ms SOA condition. These contrasts were based on the assumption that prime-related response inhibition is present with longer, but not with short mask-target SOAs, and always follows the initial prime activation, regardless of prime-target compatibility (see Fig. 2,

top). Prime-related response inhibition was found to be associated with significant changes in blood oxygen levels in the posterior parietal cortex (near the midline) and in several subcortical areas, most notably the dorsomedial thalamus, pulvinar, and head of caudate. Interestingly, no inhibition-related activation modulation of prefrontal areas was observed, which is in marked contrast to other functional imaging studies investigating the neural basis of endogenous inhibition in stop-signal or go/nogo tasks (e.g. Konishi et al., 1998; Menon et al., 2001).

In summary, the findings discussed in this section have demonstrated that inhibitory control processes can be observed with masked prime stimuli that are inaccessible to conscious awareness, and that the prime-related inhibition follows an initial response activation triggered by masked primes. Unlike endogenous inhibition observed under conditions where response-relevant signals are presented supraliminally (such as in stop-signal and go/nogo tasks), this exogenous response inhibition appears to be a direct consequence of the initial response activation triggered by subliminal primes, and seems to be mediated by corticostriate rather than prefrontal mechanisms.

A biphasic pattern of facilitation followed by inhibition is a characteristic feature of self-inhibitory control circuits, where the activation of a unit directly causes its subsequent inhibition (e.g. Arbuthnott, 1995; Houghton and Tipper, 1996). If prime-related response inhibition is mediated by self-inhibitory mechanisms in motor control, inhibition should be an immediate, automatic, and unavoidable consequence of any primed response activation. However, the evidence to be discussed in the next section demonstrates that even when the time interval separating primes and targets is sufficiently long, there are conditions where masked primes result in response activation without subsequent inhibition. These findings have led to the suggestion that a threshold mechanism may be involved in the exogenous inhibitory control of response processes.

### **3. The central-peripheral asymmetry: evidence for a threshold mechanism in the exogenous inhibitory control of responses**

In the experiments discussed in Section 2, masked primes were always presented at fixation. Under these conditions, positive compatibility effects were observed when prime-target SOAs were short, and these turned into negative compatibility effects when this interval was increased, thus reflecting a sequence of effects characteristic of self-inhibitory control circuits. However, a very different pattern of results emerged when masked primes were moved from fixation to peripheral locations. Schlaghecken and Eimer (2000) presented masked prime stimuli in the periphery of the visual field ( $2.8^\circ$  above or below fixation), while subsequent targets were delivered close to fixation, and varied mask-target SOA between 0 and 192 ms. Fig. 2 (bottom panel) shows RTs obtained in compatible and incompatible trials under these conditions. In marked contrast to the pattern of results obtained in the same experiment with centrally presented primes (Fig. 2, upper panel), there was no indication of any negative compatibility effect with peripheral primes. RTs were faster for compatible relative to incompatible trials when mask-target SOAs were short (as was also observed with central primes), and this positive compatibility effect remained present throughout the range of mask-target SOAs included in this experiment.

This striking difference in the impact of centrally and peripherally presented masked primes on behavioural performance is also reflected in distinctive modulations of LRP waveforms. Fig. 4 shows unpublished LRP results observed with central masked primes (left panels) or peripheral masked primes (right panels) for mask-target SOAs between 0 and 96 ms. When masked primes were presented centrally and SOAs were short (0 and 32 ms), LRPs revealed a partial activation of the response assigned to the prime ('A'), without a trace of any subsequent response inhibition. In contrast, with longer SOAs (64 and 96 ms), both response activation and subsequent inhibition processes ('I') began to become visible in the LRP waveforms. With peripherally presented masked primes (Fig. 4, right), LRPs only reflected the presence of the initial response activation phase ('A'), which became more pronounced with longer SOAs. In contrast to the central prime condition, there was no evidence for any inhibition of the primed response when SOAs were increased.

This pattern of behavioural and electrophysiological results suggests that while both central and peripheral masked primes initially activate their corresponding response, this response activation is inhibited when primes are presented centrally with sufficiently long mask-target SOAs (96–192 ms), but not in the case of peripherally presented primes, even when SOAs are equally long (although the possibility remains that response inhibition may be elicited with peripheral primes when even longer SOAs are used). It should be noted that this 'central-peripheral asymmetry' in the impact of masked primes is not restricted to situations where primes and targets are mapped to left-hand and right-hand responses, but can also be found for other response modalities, such as saccadic eye movements and vocal responses (Eimer and Schlaghecken, 2001).

One possible explanation for this asymmetry is that the current focus of spatial attention determines whether primed response tendencies are or are not subject to inhibition. When attention is directed to the expected location of target stimuli, which are delivered close to fixation, centrally presented primes are situated within the attentional focus, while peripheral primes are located at unattended positions. However, this possibility was ruled out in an experiment (Schlaghecken and Eimer, 2000, Experiment 3) where both masked primes and targets were presented either 3.2° above or below fixation, and peripheral cues were presented at one of these locations at the beginning of each trial to summon attention to this location. If the central-peripheral asymmetry was determined by the current locus of attention, negative compatibility effects analogous to the results observed previously with central primes should be found when masked primes are presented at cued (attended) peripheral locations, while positive compatibility effects should be present for masked primes at uncued locations. Results did not provide any support for this assumption. Although RTs were significantly faster and error rates lower in response to target stimuli at cued location, demonstrating that the cues were effective in attracting attention, prime-target compatibility effects were entirely unaffected by spatial cueing. A positive compatibility effect was obtained when masked primes were delivered at cued/attended locations, and this positive effect was even numerically larger than the effect observed with masked primes at uncued locations.

While the 'central-peripheral asymmetry' appears to be unrelated to spatial attention, it is strongly affected by variations in perceptual sensitivity. This was demonstrated in an experiment (Schlaghecken and Eimer, 2000, Exp. 4) where the eccentricity of masked primes was varied gradually between 0 and 3.3°. As masked primes were moved from the fovea into the periphery of the visual field, negative compatibility effects decreased gradually, and

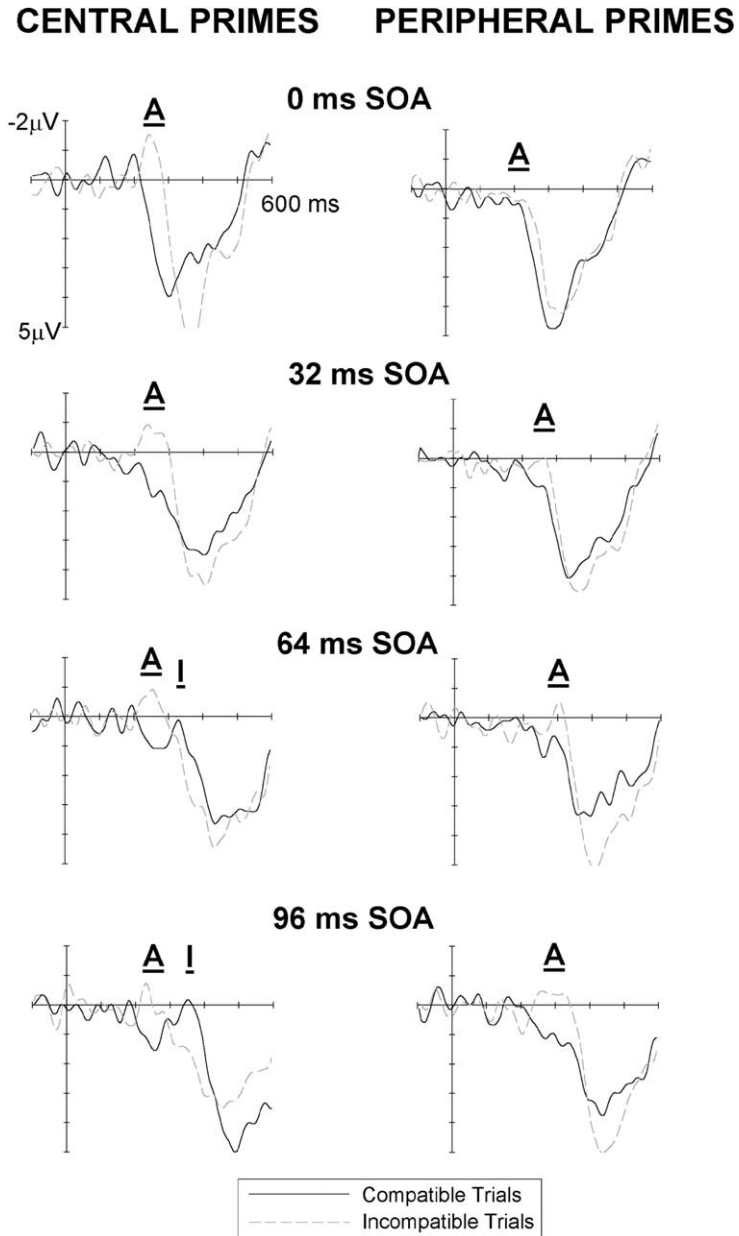


Fig. 4. LRP waveforms measured in compatible and incompatible trials, displayed relative to the onset of the masked primes. Downward-going (positive) deflections indicate activation of the correct response, upward-going (negative) deflections reflect a relative activation of the opposite response. 'A' indicates the initial response activation triggered by the masked primes, 'I' marks the subsequent inhibition of this response activation. Left panels: LRPs elicited for four different mask-target SOAs with central masked primes. Right panels: LRPs elicited for four different mask-target SOAs with peripheral masked primes. Unpublished data.

eventually turned into positive effects, parallel to the gradual decrease of perceptual sensitivity from the central to the peripheral retina (e.g. Lie, 1980). Most importantly, the transition from negative to positive compatibility effects occurred earlier when primes were displaced vertically than with horizontal displacements, parallel to the faster decrease of perceptual sensitivity along the vertical relative to the horizontal meridian (Rijsdijk et al., 1980).

This pattern of results seems to suggest that the ‘central-peripheral asymmetry’ is closely linked to retinal sensitivity, and thus to variations in the strength of sensory traces elicited by masked primes. As the strength of primed response activations is likely to be a function of the strength of the primes’ sensory representations, motor tendencies triggered by foveal primes will be stronger than motor tendencies elicited by peripheral primes. The absence of inhibition with peripheral primes, and the presence of inhibition with central primes might therefore reflect the existence of an ‘inhibition threshold’. It seems conceivable that only relatively strong prime-induced motor activations will be actively inhibited, while weak prime-induced motor activations, which are less likely to interfere with overt behaviour, only passively decay over time. When primes are presented foveally, they will be more likely to give rise to strong motor activations, and these are then subject to inhibition. In contrast, peripheral primes are more likely to produce weaker response activations, which remain below a hypothetical inhibition threshold, thus producing response facilitation without subsequent inhibition.

We have recently tested this ‘inhibition threshold’ account directly by manipulating the perceptual strength of both foveal and peripheral masked prime stimuli (Schlaghecken and Eimer, 2002). If positive compatibility effects observed with peripheral primes reflected the absence of inhibition due to below-threshold response activation, increasing the perceptual strength of peripheral primes should eventually result in negative compatibility effects (i.e. response inhibition). Analogously, if negative compatibility effects observed with foveal primes reflected the presence of inhibition following above-threshold response activation, decreasing the perceptual strength of foveal primes should eventually turn them into positive effects (i.e. no response inhibition).

The perceptual strength of peripheral primes was varied by gradually increasing the inter-stimulus interval (ISI) separating primes from the subsequently presented masks from 0 to 100 ms, while leaving mask-target SOA constant at 100 ms (Schlaghecken and Eimer, 2002, Exp. 1). Results for the 100 and 0 ms ISI conditions are shown in Fig. 5 (top panel). When the mask followed the peripheral prime immediately (0 ms ISI), a positive compatibility effect was obtained, thus replicating findings from previous studies. However, and more importantly, when the perceptual strength of the peripheral prime was increased by delaying mask presentation until 100 ms after prime offset, a significant negative compatibility effect was obtained, thus indicating the emergence of response inhibition with peripheral masked primes.

The perceptual strength of central primes was manipulated by superimposing these stimuli with random dot degradation fields under conditions where primes were immediately followed by masks, and mask-target SOA was 100 ms (Schlaghecken and Eimer, 2002, Exp. 3). Degradation decreases the central primes’ perceptual strength, and should therefore reduce their impact on the motor system. Results obtained when central primes were presented undegraded or degraded are shown in Fig. 5 (bottom panel). With undegraded masked primes, the usual negative compatibility effect was obtained. However, when central

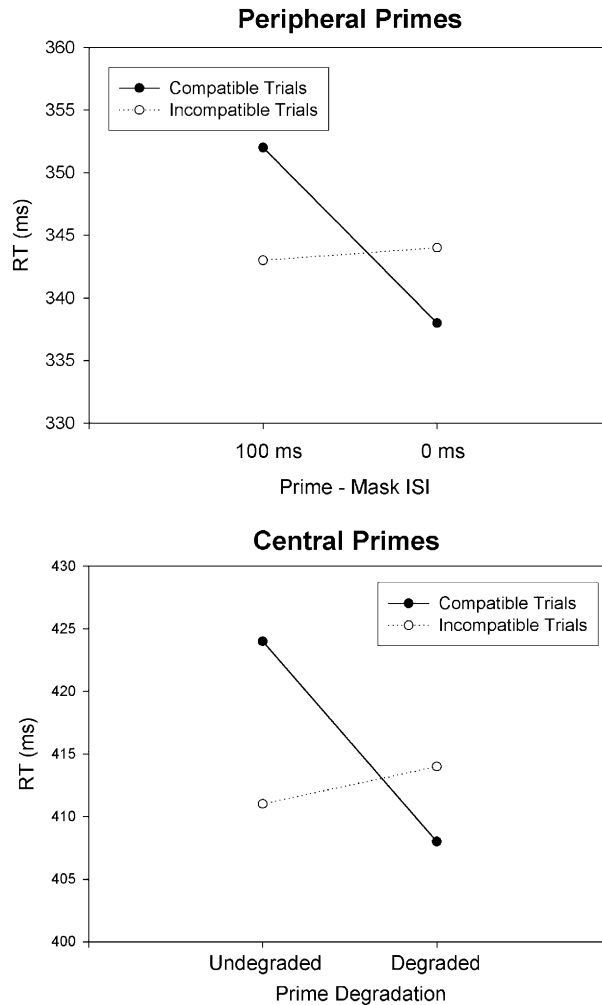


Fig. 5. Mean reaction times (RTs) observed in compatible and incompatible trials. Top panel: Results obtained for peripheral masked primes when prime-mask interval was either 100 or 0 ms. Bottom panel: Results obtained for undegraded and degraded central masked primes. Data from Schlaghecken and Eimer (2002).

primes were degraded, a significant positive compatibility effect was observed, indicating that when the primes' strength is reduced, response inhibition is eliminated.

The similarity of the results shown in Fig. 5 for peripheral and central primes demonstrates that regardless of prime eccentricity, negative compatibility effects (Fig. 5, left side) turn into positive effects (right side) when the primes' perceptual strength is reduced. It should be noted that this pattern of results appears quite counterintuitive, as performance benefits for one response alternative can be produced by decreasing the sensory evidence for this response. However, these results conform exactly to the predictions derived from the inhibition threshold hypothesis. The inhibition of response tendencies triggered by masked

stimuli is a function of the perceptual strength of these stimuli, with strong perceptual traces resulting in response activation followed by inhibition, and weaker perceptual traces producing response activation that remain below an inhibition threshold.

Viewed from a functional perspective, this relationship may reflect a general principle in inhibitory motor control. Weak response tendencies produced by perceptually weak stimuli are unlikely to influence ongoing behaviour, but stronger motor activations might affect overt performance even without conscious perception of the triggering stimulus. The presence of an inhibition threshold could ensure that response tendencies which are strong enough to potentially interfere with overt behaviour are subject to inhibition, while still allowing the continuous flow of information from sensation to have some impact on response-related processes.

#### 4. Summary and conclusions

The research reviewed in this article has demonstrated that inhibitory processes are involved in the control of response tendencies, even when response activations are triggered by stimuli that are not accessible to conscious awareness. Converging evidence from behavioural, electrophysiological, and functional imaging studies suggests that masked primes initially trigger their corresponding response, and that this response activation is then subject to inhibition, provided that the initial activation is strong enough to exceed an inhibition threshold. These findings challenge the view that all inhibitory processes are necessarily endogenous, and can only be elicited in response to suprathreshold stimulation. In addition to endogenous inhibitory control, which requires the conscious discrimination of task-relevant events, such as in go/nogo or stop signal tasks, there seems to be another, exogenous form of response inhibition, which is elicited reflexively, and even in the absence of conscious awareness of triggering stimuli. While endogenous inhibition is likely to be controlled by prefrontal cortex (c.f. Rubia et al., 2001; Konishi et al., 1998; Liddle et al., 2001), the exogenous inhibition of responses discussed here appears to be primarily mediated by corticostriate circuits, and may not involve any prefrontal control at all (Aron et al., 2003).

In line with this idea that endogenous and exogenous response inhibition processes are based on at least partially different neural substrates, a recent yet unpublished series of masked priming experiments has revealed atypically distributed amplitude modulations of the N2 component of the event-related brain potential. Enhanced N2 amplitudes are known to be elicited under response conflict conditions, and these effects are maximal at anterior electrodes with supraliminal stimuli (e.g. Kopp et al., 1996a, 1996b), presumably reflecting endogenous executive control mechanisms in prefrontal cortex (Band and van Boxtel, 1999). In the masked priming paradigm, larger N2 amplitudes can also be observed with response conflict (e.g. when a response is selected during the inhibitory phase of a compatible trial). However, this effect has a centro-parietal rather than an anterior maximum, thus supporting the assumption that the processes underlying the control of response tendencies triggered by subliminal information are different from those mediating endogenous executive control functions.

In spite of these differences between exogenous and endogenous inhibitory control mechanisms, it seems reasonable to assume that both mechanisms contribute to motor control,

and both may be activated in parallel. Suppression of an incorrect motor tendency will be largely under voluntary, cognitive control (mediated by prefrontal structures) in situations like stop-signal and go-nogo tasks, where a particular stimulus—presented supraliminally and identified consciously—is assigned to a ‘withhold’ response. Suppression of an incorrect or premature response tendency will be largely under automatic, stimulus-driven control (mediated mainly by subcortical and perhaps parietal structures) in situations like the present masked prime task, where participants are not only unaware of the motor activation triggered by the prime, but are also unaware of the prime itself. However, in situations like the Eriksen flanker task—where response-irrelevant stimuli are presented supraliminally, but where the suppression of a motor tendency triggered by these stimuli is probably not an act of voluntary decision, both types of inhibition contribute to the control of incorrect response tendencies.

To conclude this review, we will now briefly discuss a possible functional implementation of exogenous inhibitory motor control (see Schlaghecken and Eimer, 2002, for a more detailed discussion). The simple model shown in Fig. 6 contains a perceptual processing system (bottom), a motor control system (middle), and a response execution system (top). Excitatory connections are indicated by solid lines, inhibitory connections by dashed lines, and activation thresholds are indicated by ‘Z’. The motor control system consists of activation units for each response alternative (RH and LH, for left-hand and right-hand responses, respectively), as well as inhibition units (R-inh. and L-inh.). All units within a given response channel (e.g. RH and R-inh.) receive input from perceptual processes whenever sensory evidence for this particular (right-hand) response is detected. This input is excitatory for the activation units, and inhibitory for inhibition units. Activation and inhibition units for each response alternative are interconnected, thus forming self-inhibitory loops. Response execution will start once activation in RH or LH (which are linked via inhibitory ‘competition’ connections) exceeds a response activation threshold (Z).

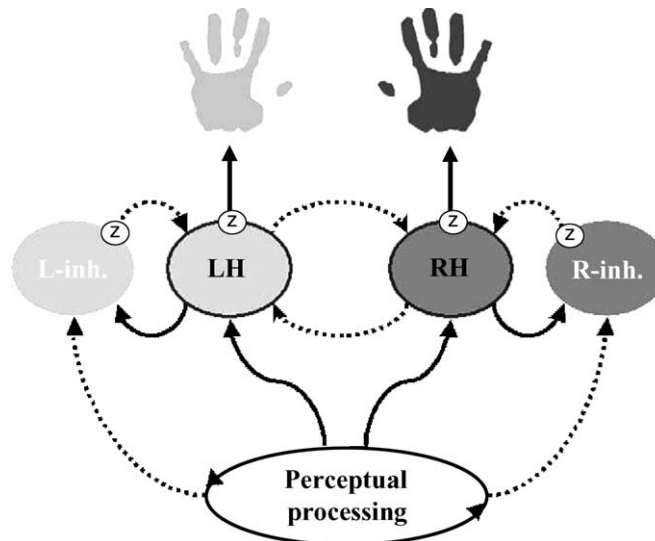


Fig. 6. Schematic illustration of a functional model of inhibitory motor control in subliminal priming. See text for details.



Because activation and inhibition units form self-inhibitory circuits, response activation will generate inhibitory feedback. Self-inhibition maintains overall stability, and can prevent specific response activation tendencies (which may be triggered frequently as a consequence of a continuous flow of information from sensory stages) from becoming dominant in the absence of unequivocal perceptual activation signals. Based on the results of the experiments discussed in Section 3, the important assumption has to be added that this self-inhibitory loop will only affect response processes when activation within this loop exceeds a certain criterion threshold ( $Z$ ).

Under standard experimental conditions, where response-relevant stimuli are presented supraliminally, self-inhibition will have no effect on performance. Here, the continuing presence of perceptual input favouring one response alternative increases activity within one activation unit, and decrease activation of the corresponding inhibition unit, thus eventually resulting in response execution. Although the self-inhibitory loop may still be active, response inhibition will be completely masked by facilitatory perceptual input. In the masked priming task, however, sensory evidence for a particular response alternative is only briefly available before it is removed by the mask, thus terminating any perceptual facilitation of the activation unit, and perceptual inhibition of the inhibition unit. Now, a sufficiently strong activity of the activation unit will trigger the self-inhibition loop, thus resulting in observable response inhibition.

It should be noted that the model illustrated in Fig. 6 is not entirely novel, but bears similarities to other activation-followed-by-inhibition models, such as proposed by Houghton and Tipper (1996) and by Hagenzieker and colleagues (Hagenzieker and van der Heijden, 1990; Hagenzieker et al., 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. However, it differs from both types of models in that it does not assume any high-level or 'cognitive' processes to guide response inhibition. Once a particular stimulus-response relationship has been established, the activation and inhibition processes within this response channel occur automatically, triggered exogenously by the perceptual properties of the masked prime. This does of course not imply that exogenous and endogenous inhibition are necessarily based on entirely different principles (see Houghton and Tipper, 1996, for a model of endogenous control that is very similar to our current account of exogenous inhibition), or that endogenous and exogenous inhibition always operate in an entirely separate, and independent fashion. The model presented here should be seen as one possible component of a more general model of motor control processes, representing those processes that operate at a very early, non-conscious stage of the perceptuo-motor interface. Future experimental research and modeling work needs to show how a model like this can be integrated with models of high-level motor control processes.

Most importantly, our model suggests that self-inhibition is a basic functional principle in early motor control. The presence of self-inhibition may have previously been overlooked because motor control tasks usually employed supraliminal stimuli. As outlined above, when task-relevant stimuli are presented supraliminally, there is no sudden removal of sensory evidence supporting a strongly pre-activated response. Hence, activation levels within the inhibition unit will not exceed threshold values, and no self-inhibition will be triggered. Thus, specific experimental circumstances (such as realised in the masked priming

paradigm) are required to ‘unmask’ the impact of self-inhibitory motor control circuits by eliminating the effects of facilitatory perceptual input on response processes.

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