On the locus of priming and inverse priming effects

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Visual stimuli that are made invisible by a following mask can affect overt motor responses and nonmotor processing. Previous studies have compared the effects of primes that were perceptually similar to the subsequent stimulus with those of primes that were perceptually similar to an alternative stimulus. The present study examined the effect of congruent primes that are perceptually dissimilar to the target (or the cue) but are nonetheless associated with the same response (or the same task) as the later stimulus. Positive and inverse priming effects (negative compatibility effects) were studied in a target priming paradigm (Experiments 1 and 2) and in a cue priming paradigm (Experiments 3 and 4). The results showed stronger priming effects with similar primes than with dissimilar congruent primes. However, the effects of perceptually dissimilar congruent primes differed from those of dissimilar incongruent primes. These findings suggest that a substantial part of both positive target and cue priming effects is produced at levels of processing that are not affected by perceptual similarity. The version of inverse priming effects examined in this study, however, seems to arise from perceptual processing that is affected by the similarity between a prime and the stimulus that follows the mask.

A wealth of experimental evidence has demonstrated that the response to visual stimuli can be influenced by prior presentation of a visual prime stimulus, despite the prime being made invisible by masking (see, e.g., Klotz & Neumann, 1999; Mattler, 2003; Neumann & Klotz, 1994; Schmidt, 2000, 2002; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003, 2004; Wolff, 1989). Priming effects of masked stimuli typically consist of fast and accurate responses when the prime is perceptually similar to the following target stimulus (congruent condition) and responses that are slow and prone to error when the prime is perceptually similar to an alternative target stimulus (incongruent condition). In addition to these typical *positive priming effects*, however, recent findings from several research groups have demonstrated an *inverse priming effect* in which fast and accurate responses occur on incongruent trials but slow and erroneous responses occur on congruent trials (e.g., Eimer & Schlaghecken, 1998, 2002; Klapp & Hinkley, 2002; Mattler, 2005; Vorberg, 1998, 2000). The present study focused on the role of perceptual interactions between the visual stimuli in priming effects by varying the similarity between the prime and the target (or cue) stimulus. In the following section, I will introduce the paradigms that have been used to study the priming effects of masked stimuli and present the arguments that have been put forward for localizing such effects.

Target Priming Paradigm

Metacounter masking has been used in recent studies that applied a target priming paradigm to dissociate awareness of the prime stimuli and their effects on motor responses (Klotz & Neumann, 1999; Mattler, 2003, 2005; Neumann & Klotz, 1994; Schmidt, 2000, 2002; Vorberg et al., 2003, 2004; Wolff, 1989). In metacounter masking, the visibility of the briefly flashed prime is reduced by a subsequent spatially flanking masking stimulus that follows after a certain stimulus onset asynchrony (SOA; Breitmeyer, 1984). For instance, in Neumann and Klotz's study, participants responded with one hand to the overall black outline of a square-shaped target stimulus and with the other hand to a diamond-shaped target stimulus. Square- and diamond-shaped primes were made as small replicas of the target stimuli. Prime and target stimuli were constructed as frames with an inner opening. The inner contour of the target matched the outer contour of the combination of both prime stimuli. In other words, each prime fit into the inner contour of each target stimulus, so each target stimulus could mask both primes via metacounter masking. With this paradigm, Neumann and Klotz showed target priming effects in conditions in which participants could not recognize the effective stimuli. Further dissociations between priming effects and prime recognition performance were shown by the different time courses of priming effects and prime recognition performance (Mattler, 2003; Vorberg et al., 2003).

Such priming effects of masked stimuli have been located at levels of motor processing (see, e.g., Leuthold & Kopp, 1998; Vorberg et al., 2003). Evidence for a motor location was provided by electrophysiological studies that used event-related lateralized readiness potentials (LRPs)

I thank Dirk Vorberg for stimulating discussions, and Susan Meißner, Nico Brunzeck, and Jan-Ole Schumann for collecting the data. Correspondence concerning this article should be addressed to U. Mattler, Department of Experimental Psychology, Georg-Elias-Müller Institut für Psychologie, Georg-August-Universität Göttingen, Göttingerstr. 14, D-37073 Göttingen, Germany (e-mail: uwe.mattler@psych.uni-goettingen.de).

measured over the motor cortex. These measures showed that incongruent primes were processed all the way up to the motor system and that they activated the motor responses associated with them (Dehaene et al., 1998; Leuthold & Kopp, 1998). Behavioral evidence for this view was provided by the high rate of incorrect responses on incongruent trials, which suggested that primes can fully activate their motor responses (see, e.g., Vorberg et al., 2003).

Cue Priming Paradigm

A variant of the target priming paradigm has been used to demonstrate cue priming effects (Mattler, 2003, 2005, in press). In a cue priming paradigm that used stimuli similar to those of Neumann and Klotz (1994), the stimulus that followed the prime was not associated with a specific motor response, but served instead as a cue that provided obligatory information for the processing of a subsequent target stimulus. For instance, in a selective attention task, the cue indicated the stimulus modality of the subsequent target stimulus (visual vs. auditory); in a task cuing experiment, the cue provided information about the dimension (instrument vs. pitch) on which the subsequent sound had to be classified. Although cues were not associated with specific motor responses in the cue priming paradigm, observed priming effects were comparable to those found with target priming (Mattler, 2003, 2005).

The locus of cue priming effects has been contrasted with that of target priming effects. Because primes in the cue priming paradigm are not directly associated with specific motor responses, their effects on performance measures cannot be reduced to effects in the motor system. Instead, it has been argued that cue priming effects have to be located either at central levels of decision making or at subsequent levels that are influenced by central processing. For instance, from the finding that primes can activate overt motor responses in target priming tasks, it could plausibly be concluded that primes can also activate internal responses in cue priming tasks. Along this line, it has been suggested that cue priming effects should be regarded as the result of priming of mental operations (Mattler, 2003).

However, the similarity of the priming effects in target and cue priming could also result from a simple feature that both paradigms have in common. For instance, in the target priming paradigm, the prime is perceptually similar either to the subsequent target stimulus or to an alternative target stimulus (e.g., Neumann & Klotz, 1994; Vorberg et al., 2003). Thus, priming effects could result from facilitated perceptual processing of congruent target stimuli and from delayed perceptual processing of incongruent target stimuli. The same is true for the cue priming paradigm, in which the prime is similar to either the ensuing or the alternative cue (e.g., Mattler, 2003). The present study addressed this issue by comparing the effects of primes that are perceptually similar to the following target (cue) stimulus and of primes that are perceptually dissimilar but nonetheless congruent with the target (cue) stimulus.

Inverse Priming Paradigm

Another variant of the target priming paradigm has been used to study inverse target priming effects. In Eimer and Schlaghecken's (1998) study, the prime was followed by a separate mask before the subsequent target stimulus was presented. This minor change to the target priming paradigm inverted the priming effect, creating faster responses on incongruent than on congruent trials (Eimer, 1999; Eimer & Schlaghecken, 1998; Klapp & Hinkley, 2002; Schlaghecken & Eimer, 2000, 2002; Vorberg, 1998, 2000). Eimer and Schlaghecken (1998) used pattern masking, but inverse priming effects have also been demonstrated with an inverse priming paradigm that used metacontrast masking (see, e.g., Lingnau & Vorberg, 2005; Mattler, 2005, in press; Vorberg, 1998, 2000), and a comparable cue priming paradigm was used recently to demonstrate inverse cue priming effects (Mattler, in press). Research with this paradigm showed that inverse priming effects depend greatly on the presence of a separate mask and a sufficient SOA (about 150 msec) between the presentation of the mask and the following target stimulus (Eimer, 1999; Lingnau & Vorberg, 2005; Mattler, 2005, in press; Vorberg, 1998, 2000).

Initially, a motor account of inverse priming effects was suggested, on the basis of findings from electrophysiological studies (Eimer, 1999; Eimer & Schlaghecken, 1998; Verleger, Jaskowski, Aydemir, van der Lubbe, & Groen, 2004). Measures of LRPs suggested two phases of priming effects: early activation of the motor response associated with the prime, which is then reversed through a dominant activation of the opposite motor response. Schlaghecken and Eimer (2002) proposed a detailed motor account of inverse priming effects that assumes that inverse priming effects result from a competition between excitatory and inhibitory units in the motor system.

Behavioral findings have also been interpreted as evidence for response-related accounts of inverse priming effects. For instance, in Experiment 2 of Klapp and Hinkley (2002), participants responded with one response to either a downward-pointing arrow or a tone with low pitch, and with another response with the same hand to an upward-pointing arrow or a tone with high pitch. Responses were made by moving the index finger from a central home position to the appropriate switch. Arrow and tone target trials occurred unpredictably. Before target presentation in both types of trials, an arrow pointing either upward or downward was presented as a prime. The mask consisted of superimposed up and down arrows. The results showed priming effects of arrows to both arrow and tone targets. The authors interpreted this cross-modal priming effect as evidence that located inverse priming at the level of stimulus-response selection rather than at perceptual levels of processing.

Note that the cross-modal priming effects of Klapp and Hinkley (2002) have to be distinguished from cue priming effects. Cue priming effects result from primes that are not associated with any specific motor response. In the cue priming paradigm, the prime is associated with nonmotor

operations required to process the target stimulus (see, e.g., Mattler, 2003, 2005). In contrast, Klapp and Hinkley's Experiment 2 used arrow primes and mapped both arrow targets and auditory targets to two specific motor responses. Their experiment thus used an inverse target priming paradigm in which arrow primes were associated with specific motor responses and affected responses to either arrow or auditory targets.

In contrast to this pure motor account of inverse priming effects, recent findings from two research groups have suggested that inverse target priming effects can arise from perceptual interactions between visual stimuli (Lleras & Enns, 2004; Verleger et al., 2004). Both groups examined the effect in the inverse priming paradigm of a separate mask, which most often shares task-relevant stimulus features with the target stimuli. In Verleger et al.'s experiments, inverse target priming effects were absent when arrow primes were masked by a checkerboard mask rather than an arrow-pattern mask. These findings were interpreted in terms of an *active mask hypothesis*; according to this hypothesis, the priming effect is inverted when the mask contains structured patterns that are similar to the primes and that interact with processes evoked by the primes.

More specifically, Lleras and Enns (2004) applied the *object substitution theory* (Enns & Di Lollo, 1997) to account for their finding that inverse priming effects arise from interactions between the prime and the separate mask. According to this theory, the prime and the mask are interpreted as different instantiations of a single object, whose object-level features have to be updated as changes in the stimulus are detected. Because the prime and the mask share common features, most of the object updating will involve updating features that are present in the mask but absent from the prime. Therefore, after the presentation of the mask, object updating provides an advantage in future processing for those stimulus alternatives that differ from the prime, whereas stimuli that are perceptually similar to the prime have a disadvantage in future processing. Inverse priming effects thus arise from two effects: impaired processing of the target stimulus that is perceptually similar to the prime and facilitated processing of the dissimilar target stimulus. Lleras and Enns's findings also suggest that object updating includes updates of any links that have been established between an object representation and its associated motor responses. Thus, inverse priming effects arise from perceptual interactions of visual stimuli as accounted for by object updating, which has the consequence that associated motor responses are also updated (Neumann, 1990).

Overview

The present study compared the effects of primes that are perceptually similar to the target (or cue) with the effects of dissimilar primes, either congruent or incongruent. Experiments 1 and 2 examined positive and inverse priming in a target priming paradigm. Experiment 3 used a cue priming paradigm and examined positive and inverse cue priming. Experiment 4 extended the findings from the cue priming paradigm in Experiment 3 by com-

paring the time courses of cue priming effects with similar and dissimilar primes. The results of all four experiments showed that priming effects are modulated by the perceptual similarity between primes and targets. However, significant target and cue priming effects were found with dissimilar primes, whereas the inverse priming effects in the present study seemed to depend on the perceptual similarity between the primes and the stimulus that followed the mask.

EXPERIMENT 1

Target Priming and Inverse Target Priming

Experiment 1 was designed to examine the effects of perceptual similarity in target priming and inverse target priming. In contrast to previous experiments on target priming, Experiment 1 distinguished between perceptually similar, perceptually dissimilar congruent, and perceptually dissimilar incongruent prime trials. To this end, two stimuli were used as the target stimuli for a left-hand response and two for a right-hand response. This setup allowed us to combine primes and targets with similar shapes, as well as primes and targets with dissimilar shapes but the same instructed response association. In target priming conditions, the following pattern of results was expected: If target priming effects arise entirely from perceptual interactions between the prime and target stimuli, it was reasoned that similar primes would facilitate response times (RTs), whereas dissimilar congruent primes trials would prolong RTs to the same degree as incongruent primes. On the other hand, if dissimilar congruent primes facilitate RTs relative to incongruent prime trials, target priming effects cannot be reduced entirely to the perceptual interactions between the prime and the subsequent stimuli. Along this line of reasoning, a similar pattern of results was expected in inverse priming conditions: If inverse target priming effects result from a perceptual interaction of prime, mask, and target stimuli, RTs should not differ between dissimilar congruent and incongruent prime trials; otherwise, inverse priming effects cannot be entirely located at perceptual levels.

Method

Participants. Nine students from the University of Magdeburg (8 women and 1 man) from 20 to 25 years of age ($M = 22.7$ years) participated in the experiment. All but 1 reported being right-handed, and all had normal or corrected-to-normal vision. Each participant took part in four 1-h sessions; 8 of the participants received course credit for participation, and 1 received €12.

Stimuli. Prime and target stimuli consisted of modified square stimuli with an arrow-like black outline (Figure 1). Four arrows were created from the square stimuli by incorporating a small arrowhead in one of the square's sides. In this way, each prime and each target stimulus consisted of the same number of pixels. Primes were constructed as small replicas of each target, with the restriction that the outer contour of primes fitted exactly within the inner window of each target. Primes subtended a visual angle of about 1.0° in height and width, with an increase in the direction of the arrowhead to about 1.2° . The height and width of the outer contour of targets subtended about 1.6° of visual angle, about 2° in the direction of the arrowhead. Separate masks consisted of a combination of all four

Figure 1. Examples of the visual stimuli used in the experiments of this study. (A) Two stimuli were mapped to left-hand responses and two to right-hand responses in Experiments 1 and 2. In the other experiments, these stimuli were used as cues for either a timbre or a pitch task. (B) On one third of all trials, primes were (respectively) similar, congruent, or incongruent to the target stimulus. The mask resulted from the superposition of all four target alternatives. In half of the trials of Experiment 1, the mask preceded the target stimulus with a mask–target stimulus onset asynchrony (MT-SOA) of 153 msec, and in the other half the mask was absent (0-msec MT-SOA). Note that one prime–target pair was presented on each trial and that each target stimulus was presented with equal frequency. Also note that the last stimulus served as the target in Experiments 1 and 2 but as a cue in Experiments 3 and 4; therefore, it was the interval between the mask and the cue (MC-SOA) that was varied in the latter experiments.

variants of the target stimulus (Figure 1). All stimuli were presented in black on white on a computer monitor, at a refresh rate of 60 Hz. The stimuli were positioned at the fixation cross in the center of the monitor. Right- and left-pointing arrows were associated with a right-hand response, up- and down-pointing arrows were associated with a left-hand response. With this setup, it was possible to combine primes and targets in three ways: those with perceptually similar shapes, with perceptually dissimilar shapes but congruent response associations, and with perceptually dissimilar shapes and incongruent response associations (Figure 1). The primes were similar, congruent, or incongruent to the following target on one third of the trials, and congruency varied randomly between trials. Prime duration was 17 msec and target duration 102 msec. The duration of the mask was 102 msec. The temporal interval between the mask and the target (MT-SOA) was either 0 or 153 msec. With the 153-msec MT-SOA, the mask followed the prime after 102 msec; at the 0-msec MT-SOA the mask was absent, so instead the target followed the prime after 102 msec (see Figure 2). In the case of an error, the

German word *Fehler* (“error”) was presented for 1 sec and followed by a pause of 2 sec.

Task. When the black outline of an arrow pointed up or down, the participants had to respond with the left hand, and when the outline pointed left or right, they had to respond with the right hand.

Procedure. The participants were tested individually in single sessions on separate days. They were instructed to focus on the fixation stimulus, to ignore the mask, and to respond as quickly as possible to the target without making errors. The stimulus sequence is given in Figure 2. Trials started with the fixation cross, followed by the prime and then the mask, both of which were positioned around the fixation cross. The interval between fixation and the prime was 650 msec. Responses were given by pressing the appropriate response button with the left or right index finger. The computer monitored for a response within 2 sec after target onset. In case of a wrong response, visual feedback was given after this period, followed by a rest of 2 sec. The warning signal for the next trial appeared after a random interval with a mean of 1,500 msec.

Figure 2. Schematic diagram of stimulus events in Experiments 1 and 2. In the choice reaction time (RT) task, the participant responded to the target stimulus presented after the mask. Priming effects were assessed via the effects of prime-target congruency on RTs. Note that the mask was absent in the 0-msec MT-SOA condition of Experiment 1 but present in some conditions of Experiment 2. Nonetheless, the 0-msec MT-SOA conditions in both experiments resulted in positive target priming effects. When the mask was followed by the target after an MT-SOA of 153 msec, inverse target priming effects were found. In the prime recognition task of Experiment 2, participants reported the prime.

Summary feedback (mean RT, percentage correct) was given at the end of each session.

Design. The effect of primes on RTs was determined by comparing the mean RTs of similar, congruent, and incongruent trials. A practice session was followed by three sessions of the choice RT task. In this way, the choice RT task was studied with 288 replications of each of the 6 conditions resulting from the combination of MT-SOA (0 vs. 153 msec) and congruency (similar, congruent, and incongruent). All combinations were presented in random order. The dependent variables were RT and error rate, and the independent variables were MT-SOA and congruency.

Statistical analysis. The first block per session was considered a warm-up and was excluded from data analysis. Choice RTs were summarized by trimmed means, determined for correct trials per subject and condition, excluding posterror trials. RTs and error rates for the choice RT task were analyzed through a two-way repeated measures ANOVA. Error rates were analyzed through a similar ANOVA on arcsine transformed mean proportions correct. All reported p values are based on Greenhouse-Geisser corrected

degrees of freedom, but for the sake of readability the stated degrees of freedom are uncorrected. This statistical analysis remained identical across all experiments.

Results

RTs. The MT-SOA of 153 msec prolonged response times (575 msec) relative to trials with the 0-msec MT-SOA (547 msec) [$F(1,8) = 19.7$, $MS_e = 558$, $p = .002$]. RT was significantly modulated by the interaction of congruency and MT-SOA [$F(2,16) = 97.2$, $MS_e = 91.4$, $p < .001$]. Figure 3A shows the priming effects for conditions with 0-msec MT-SOA, with fast responses on similar-prime trials (517 msec), prolonged responses on incongruent-prime trials (574 msec), and intermediate RTs on congruent-prime trials (550 msec). The effect of congruency was significant in conditions with the 0-msec MT-SOA [$F(2,16) = 32.3$, $MS_e = 227$, $p < .001$]. Scheffé tests confirmed the reliability of the 33-msec difference between similar and congruent trials and of the 24-msec difference between congruent and incongruent trials ($ps < .05$).

With a 153-msec MT-SOA, the inverse priming effect occurred (Figure 3A). On trials with similar primes, RTs were prolonged (594 msec) relative to those with consistent (568 msec) or inconsistent (564 msec) primes [$F(2,16) = 6.6$, $MS_e = 363$, $p = .01$]. The reliability of the 26-msec difference between similar and consistent trials was confirmed by a Scheffé test ($p < .05$), but the 4-msec difference between consistent and inconsistent trials was not significant.

Errors. Errors occurred on 1.6% of the trials. The interaction of congruency and MT-SOA reached significance on arcsine transformed error rates [$F(2,16) = 4.9$, $MS_e = 0.009$, $p = .023$]. Figure 3B shows the mean error rates as a function of congruency and MT-SOA.

Discussion

Experiment 1 replicated previous findings of priming and inverse priming effects in a target priming paradigm. With a 0-msec MT-SOA, RTs were facilitated by perceptually similar primes in comparison with dissimilar congruent primes, although incongruent primes prolonged RTs relative to congruent primes. This finding suggests that priming effects, which have been previously reported to be the difference between perceptually similar and incongruent primes, actually consist of two parts. One part of the priming effect results from facilitated perceptual processing of target stimuli when the prime and the target are perceptually similar, but another part does not result from facilitated perceptual processing, because dissimilar congruent primes facilitated responses relative to incongruent primes. This second part of target priming effects seems to be located at later levels of processing that are not affected by perceptual similarity.

These findings resemble a similar pattern of results from the flanker compatibility task (B. A. Eriksen & Eriksen, 1974). In the flanker task, a central target stimulus is flanked by stimuli that are associated either with the same response as the target (compatible flanker) or with another response (incompatible flanker). RTs are facilitated by

Figure 3. Mean RTs and error rates in Experiment 1 for target priming and inverse target priming, as a function of prime–target congruency and MT-SOA. (A) Effects of perceptually similar, dissimilar congruent, and dissimilar incongruent primes on mean choice RTs. (B) Effects of these primes on choice error rates.

identical flanker stimuli in comparison with perceptually dissimilar compatible flankers, but incompatible flankers lead to RTs that are further prolonged (see, e.g., C. W. Eriksen & Schultz, 1979; Grice & Gwynne, 1985).

Inverse priming effects were found in conditions with a 153-msec MT-SOA. In trials with perceptually similar primes, RTs were prolonged relative to those in perceptually dissimilar trials, irrespective of prime–target congruency. This finding is evidence for the view that the perceptual interaction of prime, mask, and target stimuli is the source of inverse priming effects, because perceptual similarity determined the effect to a greater extent than did the congruency of the primes. Note that the nonsignificant RT difference between congruent and incongruent conditions was counteracted by a difference in the opposite direction for error rates, which signifies a speed–accuracy trade-off. Therefore, these behavioral findings together suggest that the inverse target priming effect arises from

perceptual levels of processing that are affected by the similarity between prime and target stimuli.

On first sight, this conclusion of Experiment 1 stands in contrast to the Experiment 2 results of Klapp and Hinkley (2002). As mentioned above, these authors found inverse priming effects when arrow primes preceded an arrow-pattern mask and the mask was followed on some trials by an arrow target and on others by an auditory target. The finding that arrow primes elicit inverse priming effects on responses to auditory targets shows that inverse priming effects do not depend on the perceptual similarity between prime and target. The same conclusion emerges from Klapp and Hinkley's Experiment 5, in which the prime and mask stimuli were not followed by a target in some trials. In this experiment, the participants showed a tendency to select a response that was opposite the one associated with the prime.

Lleras and Enns (2004), however, located the source of these inverse priming effects at perceptual levels of processing involved in the updating of object representations, which also include the updating of the motor responses associated with those representations. For instance, in Klapp and Hinkley's (2002) Experiment 2, the mask included both of the prime stimulus alternatives (an up and a down arrow). Therefore, object updating would have led to an updated representation of the object sharing features with the mask that did not correspond to the prime. Thus, an up-pointing prime arrow followed by the double arrow mask would have led to updates of the object representation for the down-pointing arrow and of the associated response. This updating would have facilitated motor responses to a low-pitched tone (a stimulus incongruent to the prime) but competed with activation of the response to a high-pitched tone (congruent to the prime). In this way, the perceptual interaction between prime and mask would lead to inverse priming effects via the support of associated motor responses.

EXPERIMENT 2

Inverse Target Priming: The Role of the Mask and MT-SOA

A shortcoming of Experiment 1 is the confound of SOA and the presence of the separate mask, because the mask was absent with short MT-SOA but present with long MT-SOA. Therefore, it is not clear from this experiment whether the inverse priming effects were due to the timing of events or to whether the mask was present or not. Previous reports of otherwise unpublished data have suggested that inverse priming depends on both a sufficiently long MT-SOA and the presence of a separate mask (Vorberg, 1998, 2000). Experiment 2 was designed to disentangle this confound. The presence of the separate mask was orthogonally combined with MT-SOAs of 0 and 153 msec. Thus, Experiment 2 consisted of the conditions of Experiment 1 and two additional conditions: a mask with the 0-msec MT-SOA and no mask with the 153-msec MT-SOA. In addition, Experiment 2 examined the effectiveness of masking by measuring prime

visibility with a forced choice prime discrimination task, as previous studies have done (e.g., Klapp & Hinkley, 2002; Lleras & Enns, 2004, 2005).

Method

Participants. Twelve new students from the University of Magdeburg (9 women and 3 men) from 19 to 25 years of age ($M = 21.8$ years) participated in the experiment. All but 1 reported being right-handed, and all had normal or corrected-to-normal vision. Each participant took part in three 1-h sessions and received €12 for participation.

Stimuli. Prime and mask stimuli were the same as those used in Experiment 1 (Figure 1). However, targets were constructed as large replicas of the four target stimuli of Experiment 1, with the restriction that the outer contour of the mask fitted exactly into the inner window of each target. Targets subtended visual angles of about 2.1° in height and width, or about 2.4° in the direction of the arrowhead. With these large target stimuli, it was possible to present the mask and the target stimuli together in the 0-msec MT-SOA condition. Therefore, the presence of the mask could be orthogonally combined with the 0- and 153-msec MT-SOAs.

Tasks. Two tasks were employed. (1) In a choice RT task, the participants had to respond as in Experiment 1, with a left-hand response to black outline arrows pointing up or down and a right-hand response to those pointing left or right. (2) The entire third session was used to measure prime recognition performance. In this session, the participants were informed of the presence of the primes and were asked to respond without speed stress to the black outline arrows presented as primes. The S-R mapping was the same as in the choice RT task. Note that the trials in this prime recognition session were identical to those in the choice RT sessions, except that the participants had an increased amount of time to respond and the feedback was given according to the new mapping.

Procedure. Experiment 2 differed from Experiment 1 in the following ways. At the beginning of the final session, the direct prime recognition task, the prime and all subsequent stimuli were shown to the participants with long stimulus durations and long interstimulus intervals. This slow demonstration of the stimuli ensured that the participants understood the task and recognized the perceptual interaction between the prime, the mask, and the following target. They were instructed to identify the primes as accurately as possible and were given ample time. In this session, the computer monitored for a response within 6 sec after the onset of the target. As in the choice RT task, visual feedback was provided on error trials, and summary feedback (mean RT, percentage correct) was given at the end of the session.

Design. A practice session was followed by one session with the choice RT task and a session with the prime recognition task. In this way, the choice RT task was studied with 72 replications of each of the 12 conditions resulting from the combination of mask (present or absent), MT-SOA (0 or 153 msec), and congruency (similar, congruent, or incongruent). The same number of trials was applied in the prime recognition task, resulting in 216 trials for each combination of mask and MT-SOA. All combinations were presented in random order. The dependent variables were RT and error rates, and the independent variables were mask, MT-SOA, and congruency.

Results

RTs. The main effect of congruency was significant [$F(2,22) = 31.6$, $MS_e = 926$, $p < .001$], with means of 512, 530, and 561 msec for similar, congruent, and incongruent trials, respectively. The MT-SOA of 153 msec prolonged response times (543 msec) relative to trials with the 0-msec MT-SOA (526 msec) [$F(1,11) = 9.4$, $MS_e = 1,152$, $p = .011$], and the presence of the mask (540 msec) increased RTs relative to trials with no mask (529 msec)

[$F(1,11) = 11.1$, $MS_e = 404$, $p = .007$]. The effect of congruency was modulated by MT-SOA [$F(2,22) = 6.5$, $MS_e = 412$, $p = .007$] and by the presence of the mask [$F(2,22) = 104.0$, $MS_e = 149$, $p < .001$]. Moreover, the MT-SOA $\times$ mask interaction was significant [$F(1,11) = 26.8$, $MS_e = 446$, $p < .001$].

Most importantly, the congruency $\times$ MT-SOA $\times$ mask interaction was also significant [$F(2,22) = 58.3$, $MS_e = 169$, $p < .001$]. Figure 4A shows the priming effects on RTs for each combination of MT-SOA and mask. Visual inspection of the figure shows that inverse priming effects occurred only in the condition with a 153-msec MT-SOA when the mask present. In all other conditions, positive priming effects were found. This finding was corroborated by further statistical analyses. The inverse priming effect in the condition with the 153-msec MT-SOA and a mask present was significant [$F(2,22) = 8.6$, $MS_e = 371$, $p = .003$]. Scheffé tests confirmed the reliability of the 26-msec difference between similar and congruent trials ($p < .05$), but not the 4-msec difference between congruent and incongruent trials. All positive priming effects in the three other conditions were significant [$F(2,16) > 21.3$, $p < .001$, in all cases]. Scheffé tests confirmed the reliability in each case of the difference between similar and congruent trials, as well as the difference between congruent and incongruent trials ($p < .05$). A comparison of the positive priming effects in the condition with a 0-msec SOA showed that the presence of the mask had only a marginal effect [$F(2,22) = 3.1$, $MS_e = 105$, $p = .07$]. However, without the mask, positive priming effects were significantly larger with the 153-msec rather than the 0-msec MT-SOA [$F(2,22) = 4.0$, $MS_e = 316$, $p = .04$].

Errors. Errors occurred on 2.4% of the trials. The main effect of congruency was significant [$F(2,22) = 5.0$, $MS_e = 0.022$, $p = .02$], with means of 2.5%, 1.6%, and 3.1% errors on similar, congruent, and incongruent trials, respectively. The congruency $\times$ mask interaction reached significance [$F(2,22) = 9.5$, $MS_e = 0.020$, $p = .001$]. Figure 4B shows the mean error rates as a function of congruency for each condition of MT-SOA and mask.

Prime recognition. Prime recognition performance was analyzed with an ANOVA on arcsine-transformed mean proportions correct, determined separately for each participant and target, and then averaged across congruency for each level of MT-SOA and mask. Overall, prime recognition responses were correct in 82.8% of the trials. Prime recognition performance was worse when the mask was present (76.9%) than when it was absent (88.7%) [$F(1,11) = 84.8$, $MS_e = 0.016$, $p < .001$]. The interaction of mask and MT-SOA was significant [$F(1,11) = 113.9$, $MS_e = 0.019$, $p < .001$]. The worst prime recognition performance was observed with the mask and a 153-msec MT-SOA (69.2%), and prime recognition performance was significantly increased in the conditions with a 0-msec MT-SOA, both with [84.6%; $F(1,11) = 31.3$, $MS_e = 0.028$, $p < .001$] and without [81.6%; $F(1,11) = 14.9$, $MS_e = 0.003$, $p = .003$] a mask. When the latter condition was compared with the 153-msec MT-SOA condition without a mask, the increase in prime recognition

Figure 4. Mean RTs and error rates in Experiment 2 for target priming and inverse target priming, as a function of presence/absence of the mask, MT-SOA, and prime-target congruency. (A) Effects of perceptually similar, dissimilar congruent, and dissimilar incongruent primes on mean choice RTs. (B) Effects of these primes on choice error rates.

accuracy was significant [95.7%; $F(1,11) = 79.7$, $MS_e = 0.017$, $p < .001$].

To assess whether prime recognition performance modulated the inverse priming effect, the 6 participants with poor prime recognition performance in the condition with a mask and a 153-msec MT-SOA (59.7% correct responses) were compared with the 6 best participants in this condition (78.7% correct). In both groups, prime recognition performance differed significantly from the chance level of 50% [for the poor group, $t(5) = 3.1$, $p = .03$, two-tailed, 95% confidence interval (95% CI) 51.5%–67.9%; for the good group, $t(5) = 9.6$, $p < .001$, 95% CI 71%–86.4%], and prime recognition performance differed significantly between groups [$t(10) = 4.4$, $p = .001$, two-tailed]. Despite this difference in prime visibility, however, inverse priming effects did not differ between groups [$F(2,20) =$

1.8, $p = .19$, and $F(2,20) < 1$, $p = .98$, for the group $\times$ congruency interactions for RTs and arcsine-transformed choice error rates, respectively; see Figure 5].

Discussion

Findings from Experiment 2 replicated and extended those of Experiment 1 by showing that two conditions are necessary to produce inverse target priming effects: the presence of the separate mask, and a sufficiently long MT-SOA. This conclusion is consistent with those of previous studies with arrow stimuli (Vorberg, 1998, 2000). Replicating the results of Experiment 1, the inverse target priming effect depended on the similarity between prime and target stimuli, although positive target priming effects were at least partly independent from stimulus similarity. Comparing priming effects with 0- and 153-msec MT-

Figure 5. Inverse target priming effects as a function of prime–target congruency and prime recognition performance in Experiment 2. Priming effects are shown for the subgroups of participants with good and poor prime recognition performance in the condition with a mask and a 153-msec MT-SOA.

SOAs in conditions without a mask (which led to effective prime–target SOAs of 102 and 255 msec, respectively) replicated previous findings that positive target priming effects increase with increasing prime–target SOAs (e.g., Mattler, 2003, 2005; Vorberg et al., 2003, 2004). In those conditions that Experiments 1 and 2 shared, positive and inverse target priming effects were surprisingly similar (compare Figures 3 and 4). Interestingly, the priming effects with the 0-msec MT-SOA did not differ significantly in conditions with and without the mask.

Analyses of prime recognition performance showed that participants can discriminate between primes in conditions without a masking stimulus. In contrast, with a 0-msec MT-SOA, prime recognition performance was greatly reduced even when the mask was absent. This finding becomes reasonable when one considers that the

target stimuli act as metacontrast masks because the outer outline of the primes fitted into the inner window of the target stimuli (Figure 1). An account in terms of metacontrast masking is further supported by the fact that substantial masking was found with the 0-msec MT-SOA in Experiment 2, despite a 102-msec SOA between the prime and masking stimuli (see also Experiment 3). Whereas normal backward masking shows reduced masking effects under such conditions, metacontrast masking can lead to substantial masking effects in this temporal range (Breitmeyer, 1984; Francis, 1997; Mattler, 2003, 2005; Vorberg et al., 2003).

Across participants, inverse priming effects did not depend on the extent to which participants could recognize the primes. This finding replicates those of a previous study (Mattler, in press) and suggests that the visibility of the prime is not a critical factor for this version of inverse target priming. Therefore, this version of inverse priming might have in common with positive priming that both are independent from visual awareness of the prime (Mattler, 2003; Vorberg et al., 2003).

Experiment 2 disentangled the confounding that was present in Experiment 1 by varying SOA and mask (present vs. not present) in a factorial design. Nonetheless, the two following experiments on cue priming used the same stimuli as Experiment 1 and a similar design. This seemed to be justified, despite the disadvantage of the confounding, for two reasons. First, because of the lower number of conditions, the design of Experiment 1 is more efficient than that of Experiment 2. Second, the similarity between the findings of Experiments 1 and 2 makes it unlikely that the confounding of MT-SOA and the presence of the mask had any serious effects. Despite its replication in Experiment 2, the defective Experiment 1 was not excluded from this study in order to allow a comparison of results with the following cue priming experiments, which used as cues the same small targets and other visual stimuli used for target priming in Experiment 1.

EXPERIMENT 3 Cue Priming and Inverse Cue Priming

A number of experiments have shown that cue priming effects follow the same laws as target priming effects (Mattler, 2003, 2005). Most recently, a study showed that even inverse priming effects can be obtained with cue priming (Mattler, in press). A major inconvenience for the interpretation of cue priming effects that are similar to target priming effects has derived from the obvious commonality between the designs used to study each of these effects. As mentioned above, the common findings in both kinds of studies could be due to the perceptual similarity between the stimuli used as prime, mask, and either target or cue. According to this view, target and cue priming effects result from primes facilitating the processing of a perceptually similar subsequent stimulus, whereas incongruent primes hinder perceptual processing of a following stimulus that is perceptually dissimilar to the prime.

This plausible interpretation of cue priming effects has been confronted with various arguments in previous articles (Mattler, 2003, 2005, in press), but the issue nonetheless has not yet been addressed in a straight empirical test. Therefore, Experiment 3 was set up to test the role of perceptual similarity in cue priming and inverse cue priming.

Method

Participants. Ten new students from the University of Magdeburg (10 women) from 20 to 27 years of age ($M = 21.6$ years) participated in the experiment. All reported being right-handed and having normal or corrected-to-normal vision. Each participant took part in five 1-h sessions and received course credit for participation.

Stimuli. Experiment 3 differed from Experiment 1 in that the target stimulus that had been used in Experiment 1 was not the imperative stimulus for the response in Experiment 3. Instead, the participants had to use this stimulus as a cue for the categorization of a following sound stimulus. The same visual stimuli were used as in

Experiment 1 (see Figure 1) but the meaning of the stimuli changed. Stimuli with right- and left-pointing arrows were used to cue a timbre discrimination task, and stimuli with up- and down-pointing arrows were used to cue a pitch discrimination task. As in Experiment 1, this setup allowed three types of prime–cue congruency, with perceptually similar, dissimilar congruent, and dissimilar incongruent primes. The SOA between the mask and the cue (MC-SOA) was either 0 or 153 msec. A MIDI sound was presented over headphones 119 msec after the cue, either the sound of a piano or of a marimba with high or low pitch (which differed by seven tones). No visual stimulus accompanied the presentation of the sounds. Except for the target stimulus, the sequence of stimuli and the procedure were identical to those of Experiment 1 (see Figure 6). When an error occurred, feedback was given as in Experiment 1.

Tasks. Two tasks were employed. (1) In a choice RT task, the participants indicated either the pitch (low vs. high) or the timbre (piano vs. marimba) of the sound by pressing the left or right alt key on the keyboard with their left or right index finger. The task in effect was indicated by the shape of the cue: Up- and down-pointing arrows indicated the pitch task, whereas left- and right-pointing arrows indicated the timbre task. (2) The entire fifth session was used to measure prime recognition performance. As in Experiment 2, the participants were informed of the presence of the primes and were asked to respond to the overall outline of the prime arrows in the same way as in Experiment 2.

Procedure. Experiment 3 differed in the following points from the two previous experiments. In the choice RT sessions, the participants were instructed to focus on the fixation stimulus, to use the arrow as a cue indicating the task to be performed on the sound stimulus, and to respond as quickly as possible to the sounds, without making errors. They were instructed to process the cue prior to the target stimulus. The timing of visual stimulation was identical to that in Experiment 1 (compare Figures 2 and 6). Note, however, that the cue could not be used for any motor preparation in Experiment 3. The stimulation was identical in all sessions, but the procedure of the final session, the direct prime recognition task, was the same as that of Experiment 2.

Design. A practice session was followed by three sessions with the choice RT task and one with the prime recognition task. The choice RT task was studied with 288 replications of each of the six conditions resulting from the combination of MC-SOA (0 vs. 153 msec) and congruency (similar, congruent, and incongruent). The prime recognition task resulted in 96 replications of each of the six conditions. All combinations were presented in random order. The dependent variables were RT and error rates in the choice RT task and percent correct in the prime recognition task. The independent variables were MC-SOA and congruency.

Results

RTs. The effects of MC-SOA and congruency were significant [$F(1,9) = 17.6$, $MS_e = 1,341$, $p < .005$, and $F(2,18) = 4.6$, $MS_e = 299$, $p < .05$, respectively]. The interaction of MC-SOA and congruency was also significant [$F(2,18) = 29.4$, $MS_e = 219$, $p < .001$]. Figure 7A shows mean RTs as a function of MC-SOA and congruency. With the 0-msec MC-SOA, the effect of congruency was significant [$F(2,18) = 35.9$, $MS_e = 166$, $p < .001$]. Scheffé tests revealed that responses were faster on similar prime trials (651 msec) than on congruent prime trials (672 msec), which in turn were faster than incongruent prime trials (700 msec, $p < .05$). In conditions with the 153-msec MC-SOA, an inverse priming effect was found, as revealed by the significant effect of congruency [$F(2,18) = 5.3$, $MS_e = 351$, $p < .05$]. Scheffé tests showed that RTs were

Figure 6. Schematic diagram of stimulus events in Experiments 3 and 4. In the choice response time (RT) task, participants used the stimulus that followed the prime or the separate mask as a cue. The imperative stimulus was a sound presented via headphones after the cue. Priming effects were assessed via the effects of prime–cue congruency on RTs. In the prime recognition task of Experiment 3, participants reported the prime.

Figure 7. Mean RTs and error rates in Experiment 3 for cue priming and inverse cue priming, as a function of prime–target congruency and MC-SOA. (A) Effects of perceptually similar, dissimilar congruent, and dissimilar incongruent primes on mean choice RTs. (B) Effects of these primes on choice error rates.

prolonged on trials with similar primes (729 msec) relative to trials with congruent (704 msec) and incongruent (707 msec) primes, which did not differ.

Errors. Errors occurred on 3.1% of the trials. Analysis of arcsine-transformed error rates revealed a significant main effect of consistency on error rates [$F(2,18) = 4.5$, $MS_e = 0.006$, $p < .05$]. This main effect of consistency was modulated by MC-SOA [$F(2,18) = 4.8$, $MS_e = 0.003$, $p < .05$]. Separate analyses for conditions with 0- and 153-msec MC-SOAs revealed that error rates were not affected by consistency on trials with a 0-msec MC-SOA [$F(2,18) = 1.5$, $p = .24$], whereas consistency did affect error rates on trials with a 153-msec MC-SOA [$F(2,18) = 6.0$, $MS_e = 0.006$, $p < .05$]. Figure 7B shows that error rates increased on trials in which the prime and the cue were similar (4.6%) in comparison with the trials

with congruent (2.6%) and incongruent (2.9%) primes, which did not differ.

Prime recognition. Prime recognition performance was analyzed with an ANOVA on arcsine-transformed mean proportions correct, determined separately for each participant and target and then averaged across congruency for conditions with 0- and 153-msec MC-SOAs. Overall, prime recognition responses were correct in 63.8% of the trials. The main effect of MC-SOA showed that the presence of the separate mask reduced prime recognition performance from 71.1% to 56.6% correct responses [$F(1,8) = 10.1$, $MS_e = 0.158$, $p < .05$].

The most interesting aspect of the analysis was the relation between participants' prime recognition performance and the effects of primes in the choice RT task. To assess this relation, the entire group of participants was divided into groups with good and poor individual prime recognition performance in the conditions with a 153-msec MC-SOA. The poor group's prime recognition performance (50.9% correct responses) did not differ significantly from the chance level of 50% [$t(4) = 0.6$, $p = .61$, two-tailed, 95% CI 46.2%–55.6%]. In the good group, however, the prime recognition performance of 63.4% correct responses was above chance [$t(4) = 3.3$, $p = .03$, two-tailed, 95% CI 51.9%–74.9%]. Despite this significant difference in prime visibility [$t(8) = 2.8$, $p = .02$, two-tailed], the inverse priming effect did not differ between groups [$F(2,16) = 2.1$, $p = .18$, and $F(2,16) = 2.6$, $p = .12$, for the group $\times$ congruency interactions on RTs and choice error rates, respectively]. Figure 8 shows the inverse priming effects on RTs and choice error rates for the groups with good and poor prime visibility.

Discussion

Experiment 3 replicated previous findings in terms of both cue priming and inverse cue priming effects (Mattler, 2003, 2005, in press). Comparing the findings of Experiment 3 to those of Experiments 1 and 2 revealed a number of similarities between target priming and cue priming (see Figures 3, 4, and 7). First, with a 0-msec MC-SOA, responses were facilitated by perceptually similar primes to a greater extent than by perceptually dissimilar congruent primes. This finding suggests that part of the cue priming effect is due to facilitated perceptual processing of the cue in trials in which it is preceded by a perceptually similar prime. Second, significant cue priming effects were found when congruent and incongruent primes were compared. This finding suggests that part of the cue priming effect is located at levels of processing that are not affected by perceptual similarity. Note, however, that cue priming effects cannot result from response priming as the effects from the target priming paradigm do, because in the cue priming paradigm prime stimuli are not associated with any specific motor response. Instead, the findings suggest that cue priming effects occur either at more central levels of processing or at later levels of nonmotor processing that are affected by central levels of processing.

Figure 8. Inverse cue priming as a function of prime-target congruency and prime recognition performance in Experiment 3. The priming effects are shown for the subgroups of participants with good and poor prime recognition performance in the condition with a mask and a 153-msec MC-SOA.

Third, an inverse cue priming effect was found with the 153-msec MC-SOA. This finding replicates the finding of a recent study that examined the time course of inverse priming effects in target and cue priming (Mattler, in press). Interestingly, inverse priming effects consisted of an increase in RT on trials with similar primes relative to congruent and incongruent trials, which did not differ. Thus, Experiment 3 underscores the conclusion of Experiments 1 and 2 that these inverse priming effects arise from perceptual processing of the stimulus sequence prime-mask-target.

Finally, inverse cue priming effects did not depend on the extent to which participants could recognize the primes. This finding replicates Experiment 2 in a cue priming paradigm, and it also replicates findings from a previous study (Mattler, in press). Note that prime visibility in the condition with no mask and a 0-msec MC-SOA reached only

71.1%, whereas it reached 81.6% with a 0-msec MT-SOA in Experiment 2. This difference most likely results because metacontrast masking was more efficient in Experiment 3, which used smaller target stimuli that fitted more closely around the outer outline of the prime stimuli (Breitmeyer, 1984; Francis, 1997). Overall, the picture emerges that visual awareness of the prime is not a crucial determinant for such inverse priming effects.

EXPERIMENT 4 The Time Course of Cue Priming

The temporal onset asynchrony between the prime, mask, and target (cue) stimuli is an important factor for positive target and cue priming effects (see, e.g., Mattler, 2003; Vorberg et al., 2003), as well as for inverse target and cue priming effects (see, e.g., Eimer, 1999; Mattler, in press; Lingnau & Vorberg, 2005). Therefore, the effects found in the prior experiments of this study might be restricted to the particular temporal intervals used, and might not be found with other intervals between the mask and the ensuing stimulus. To address this potential limitation of the findings from the three previous experiments, Experiment 4 replicated Experiment 3 but varied the SOA between the mask and the cue with more steps between 0-msec and 153-msec MC-SOAs.¹

Method

Participants. Twelve new students from the University of Magdeburg (7 women and 5 men) from 18 to 32 years of age ($M = 22.8$ years) participated in the experiment. All but 2 reported being right-handed, and all had normal or corrected-to-normal vision. Each participant took part in three 1-h sessions. Six participants received course credit for participation, and the other 6 received €16.

Task, Stimuli, Procedure, and Design. Experiment 4 differed from Experiment 3 in that MC-SOA was varied randomly between trials to values of 0, 51, 102, and 153 msec. After a practice session, the participants finished two experimental sessions of 128 trials in each of the 12 conditions resulting from the factorial combination of MC-SOA and congruency. The prime recognition session was omitted in Experiment 4.

Results

RTs. There was a main effect of congruency [$F(2,22) = 8.8$, $MS_e = 806$, $p = .006$], with means of 773, 767, and 790 msec on similar, congruent, and incongruent trials, respectively. The interaction of congruency and MC-SOA was significant [$F(6,66) = 3.6$, $MS_e = 614$, $p = .012$]. Figure 9A shows the time course of mean RTs for each congruency condition. In conditions with the 0-msec MC-SOA, the congruency effect was significant [$F(2,22) = 5.5$, $MS_e = 535$, $p = .017$]. Separate analyses of the time course of the effect of each type of prime-cue congruency revealed a significant effect of MC-SOA in trials with perceptually similar primes [$F(3,33) = 5.8$, $MS_e = 610$, $p = .007$] but no significant effect in either the congruent or incongruent prime trials [$F(3,33) < 1.2$, $p > .33$]. The comparison of the time courses of congruent and incongruent prime trials (excluding trials with similar primes) revealed a sig-

Figure 9. Performance measures as a function of the stimulus onset asynchrony between the separate mask and the cue (MC-SOA) in Experiment 4. (A) Effects of perceptually similar, dissimilar congruent, and dissimilar incongruent primes on mean choice RTs. (B) Effects of these primes on choice error rates.

nificant difference of 23 msec between the congruent and incongruent prime trials [$F(1,11) = 19.6$, $MS_e = 679$, $p = .001$], which was not significantly modulated by MC-SOA [$F(3,33) < 1$]. Comparing perceptually similar to congruent prime trials, however, revealed a significant interaction of congruency and MC-SOA [$F(3,33) = 5.2$, $MS_e = 714$, $p = .009$]. No other effect reached significance.

Errors. Across all trials, the error rate was 5.0%, and there was no significant effect of any independent variable (see Figure 9B).

Discussion

Experiment 4 provided two important findings. First, the comparison between congruent and incongruent trials showed a significant positive cue priming effect that did not depend on MC-SOA. This finding replicates one

result of Experiment 3 and provides further evidence for the view that positive cue priming effects do not depend on stimulus similarity.

Second, with an MC-SOA of 153 msec the effects of primes differed in Experiment 4 from those in Experiment 3, because the RT difference between perceptually similar and incongruent prime trials did not reach negative values in Experiment 4. In other words, there was no “inverse” priming effect in the literal sense. However, this finding resembles those of Lingnau and Vorberg (2005), who showed that target priming effects in conditions with separate masks do not always lead to an inversion, although the time course of priming effects shows that the RTs on congruent and incongruent trials come close to each other. When MT-SOA varies in the inverse target priming paradigm, RT decreases with increasing SOA on incongruent trials and increases on perceptually similar trials (Lingnau & Vorberg, 2005). In line with these findings, RT increased with MC-SOA on trials with perceptually similar primes in Experiment 4. Therefore, the priming effect—determined as the difference between incongruent and perceptually similar trials—decreased with MC-SOA and reached values near zero with a 153-msec MC-SOA.

Most importantly, priming effects were modulated by MC-SOA only in conditions in which the prime was perceptually similar to the cue. This result is consistent with the findings from the other experiments of this study, because it suggests that the phenomenon of inverse priming arises from processes that are modulated by the perceptual similarity of the prime and the stimulus that follows the mask. Thus, all four experiments of this study provide unequivocal support for the view that the source of these inverse priming effects is located at perceptual levels of processing.

Beyond this, however, it is interesting that congruency affected mean RTs in different ways in Experiments 3 and 4. In the directly comparable 153-msec MC-SOA condition, Experiment 3 revealed no RT difference between perceptually dissimilar congruent and incongruent trials, but Experiment 4 showed faster responses on congruent than on incongruent trials. Moreover, this difference between congruent and incongruent conditions did not depend on MC-SOA in Experiment 4, although RTs to perceptually similar prime–target combinations were significantly affected by MC-SOA. These findings show that inverse priming effects are sensitive to the differences between Experiments 3 and 4. One potentially crucial difference between experiments is the number of trials in which a mask was presented, which was increased in Experiment 4. A different sensitivity of inverse target priming effects was reported by Klapp and Hinkley (2002), who found larger inverse target priming effects in the second than in the first session. These findings together create a picture of inverse priming effects depending on various procedural variables, like the amount of practice and the frequency of trials in which a mask is presented. Further research is needed to identify the crucial variables and to determine how they modulate inverse priming effects.

GENERAL DISCUSSION

This study examined the role of perceptual similarity between the prime and the imperative stimulus in positive and inverse target priming and in positive and inverse cue priming. To this end, the effects of perceptually similar primes were compared with the effects of perceptually dissimilar congruent and incongruent primes. Positive target and cue priming effects were increased by similar primes, although significant priming effects were also found with perceptually dissimilar congruent primes in comparison with incongruent primes. In contrast, the inverse target and cue priming effects examined in this study were found to depend on the perceptual similarity between the prime and the following imperative stimulus.

The Locus of Target Priming

Experiments 1 and 2 examined the locus of target priming effects. The present findings strongly suggest that part of the positive target priming effect depends on the similarity between prime and target stimuli. In addition, however, performance differences between trials with perceptually dissimilar congruent and incongruent primes suggest that another part of the target priming effect is located at later levels of processing. On the one hand, findings are consistent with those of previous studies that suggested that the target priming effect is located at levels of the response system (e.g., Leuthold & Kopp, 1998; Vorberg et al., 2003). On the other hand, these findings extend previous views by pointing to a perceptual part of the target priming effect.

The Locus of Cue Priming

The results of Experiments 3 and 4 showed that, like target priming effects, positive cue priming effects also depend partially on the perceptual similarity between the prime and the subsequent cue. Most importantly, however, both experiments provided clear evidence that cue priming effects also arise in conditions in which primes and cues are perceptually dissimilar. These findings suggest that part of cue priming effects do not result from perceptual processing of similar stimuli, but instead from later levels of processing. In contrast to target priming, however, cue priming effects cannot be located at levels of the motor response system, because primes are not associated with specific motor responses. Therefore, it has been suggested previously that cue priming effects might be located at central levels of processing or at subsequent levels that are modulated by central processes (Mattler, 2003, 2005, *in press*).

Inverse Priming Effects and Prime Target Similarity

Each of the four experiments of this study provided evidence for the view that inverse priming effects arise primarily from perceptual interactions between stimuli. In the target priming paradigm of Experiments 1 and 2, RTs were prolonged in trials in which the target stimulus was

perceptually similar to the prime. In congruent and incongruent trials, in which the target was perceptually dissimilar to the prime, however, response times did not differ significantly. Experiment 3 showed a comparable pattern of results in a cue priming paradigm. The fact that perceptual similarity was crucial in the inverse target priming experiments as well as in the inverse cue priming experiment is consistent with the view that inverse priming effects arise from an interaction of the three stimuli at perceptual levels of processing. Additional evidence for a perceptual locus of inverse priming was provided by Experiment 4, which showed that the variation of MC-SOA did not affect the time course of RTs in congruent and incongruent trials but did in trials with perceptually similar primes.

On the one hand, similar findings have been reported in the literature. When arrow primes were combined with arrow targets in a series of trials, inverse priming effects have been found. However, these effects were absent in series of trials in which arrow primes were combined with dissimilar targets consisting of letters (Eimer & Schlaghecken, 1998, Experiment 1; Klapp & Haas, 2005, Experiments 2A and 2B) or of laterally presented response signals (Klapp & Haas, 2005, Experiment 3), although arrows were associated with the corresponding response by previous training. Unfortunately, these findings do not provide unequivocal support for the view that inverse priming effects depend on prime–target similarity. Instead, they might result from the requirement of having a currently activated S–R mapping that links features of the prime to motor responses, as has been proposed (for instance) in the direct parameter specification hypothesis (Klapp & Haas, 2005; Neumann, 1990; Neumann & Klotz, 1994). Inverse priming effects were also absent with dissimilar stimuli in Eimer, Schubö, and Schlaghecken's (2002) Experiment 1. In that experiment, arrow targets were replaced in half of the trials by a “+” sign that was presented to the left or right of fixation. Participants responded either to the direction of the arrow or to the position of the “+” sign. Inverse priming effects occurred with arrow targets but not with lateral targets. However, these findings are ambiguous because stimulus similarity was confounded with response modality (foot vs. hand response). A clear effect of stimulus similarity was found in Experiment 2 of Schlaghecken and Eimer (2000), in which arrow primes at fixation were followed by a central arrow presented as a target above or below fixation, or by a left or right lateralized “+” sign. Inverse priming effects in that study were larger on trials with arrow targets than with lateralized targets.

On the other hand, a number of studies have reported inverse priming effects when an arrow prime was followed by dissimilar nonarrow target stimuli. Arrow primes affected the response to letter targets in the training session of Klapp and Haas's (2005) Experiment 2B, when arrow and letter targets were presented in the same block of trials, and they affected the response to auditory targets in Experiment 2 of Klapp and Hinkley (2002), when arrow targets and auditory targets were combined. A similar effect was found in

Experiment 2 of Eimer (1999), in which an arrow target was combined with a "+" sign that was presented at a location to the left or right of fixation. Thus, in some situations inverse priming seems to occur independently of prime–target similarity, and in others it depends on such similarity. Therefore, the present findings might be related to one of two versions of inverse priming effects.

Two Versions of Inverse Priming Effects

Most recently, a distinction between two versions of inverse priming effects (negative compatibility effects, henceforth NCE) has been proposed by Klapp (2005). In marked contrast to the findings of Lleras and Enns (2004), Klapp demonstrated that inverse priming effects can arise when arrow primes are followed by an unrelated mask that does not share features of the prime. This finding was then replicated by Lleras and Enns (2005). On the basis of these results and the findings of Lleras and Enns (2004), Klapp proposed that there are two entirely different versions of inverse priming effects. On the one hand, there is an inverse priming effect that occurs when an irrelevant mask is used. This nonperceptual negative compatibility effect (NCE-NP) is observed only with low prime visibility, and it vanishes when prime visibility is increased. On the other hand, there is a perceptually generated negative compatibility effect (NCE-P) that arises from the interaction between the prime and a relevant mask and is independent of prime visibility. According to this view, the present findings are related to the NCE-P and highlight a nonmotor component in this version of inverse priming.

Object Updating Accounts for Perceptual Inverse Priming Effects

According to this new distinction, the object updating hypothesis suggested by Lleras and Enns (2004) is a viable account for the perceptual version of inverse priming effects (Klapp, 2005; Lleras & Enns, 2005). This hypothesis proposes that an updating process leads to benefits for objects that correspond to those features of the mask that differ from the prime. Lleras and Enns (2004) examined this hypothesis and presented the prime and mask sequence at a different location from where the target subsequently appeared, to isolate the interaction between the prime and the mask from possible interactions between prime, mask, and target. As predicted, the manipulation of the mask (either containing task-relevant or -irrelevant stimulus features) revealed that the mask plays a crucial role via its interaction with the prime. Irrelevant masks yielded positive priming effects, whereas relevant masks yielded inverse priming effects.

The present design, in contrast, does not allow a distinction between the effects of individual stimuli, because all three stimuli have been presented at the same location. Therefore, the present inverse priming effects possibly depend on one or more of the possible interactions between the three stimuli. For example, the prime might interact with the mask to form a new percept via object updating, and the new percept in turn interacts with the

target stimulus. Therefore, perceptual processing of a target stimulus might be hindered when the target is similar to the prime because the percept that is formed by object updating differs greatly from the prime. In addition, the prime might induce the preparation of same-as-prime responses, whereas the percept formed by object updating might induce the preparation of opposite-to-prime responses (Lleras & Enns, 2004). Thus, the observed behavioral effects of the three stimuli might result from an interaction of these three components, and each of the components might have a different weight in other experimental contexts.

Moreover, the mask used in the present experiments differs from those used in prior studies. Previous inverse target priming experiments used masks that contained relevant features of the two alternative visual target stimuli (e.g., Eimer & Schlaghecken, 1998; Klapp & Hinkley, 2002). For these masks, object updating predicts that the incongruent target object would benefit from the updating process. In the present experiments, however, the mask consisted of the superposition of all four alternative stimuli that could follow (see Figure 1). On the one hand, object updating could lead to a benefit for a single target alternative. In this case, one would expect that the two incongruent target objects should benefit more frequently from updating than would the single congruent target alternative, leading to shorter mean RTs on incongruent than on congruent trials. On the other hand, all three alternative target representations could benefit from updating in the present experiments, leading to no RT difference between dissimilar congruent and incongruent trials. The same null effect could result if updating were to leave the system tuned for a pattern hypothesis that included the entire difference between the prime and the mask that corresponded to a task-irrelevant object.

Another potentially important distinguishing feature of the present study has been pointed out by an anonymous reviewer. Whereas the prime was uncorrelated with the response in previous studies, in the present study the prime was correlated with the response because there were twice as many trials with same-as-prime responses (similar target trials and congruent target trials) as there were opposite-to-prime responses (incongruent trials). This unbalanced design might have modulated the size of the priming effect that was induced by the prime via motor preparation. This potential is suggested by the previous finding that irrelevant unattended stimuli induce response priming effects when they are correlated with a specific motor response (Miller, 1987; Mordkoff & Yantis, 1991). Therefore, the experimental imbalance between same-as-prime and opposite-to-prime trials might have contributed to the present results, because it might have increased the response preparation effect of the prime and counteracted the response preparation effect of the mask that resulted from updating. Further research is needed to clarify the issue of these potential interactions. Nonetheless, the findings of this study highlight the presence of a nonmotor component in this version of inverse priming effects.

The Role of Prime Visibility for Inverse Priming Effects

According to the distinction made by Klapp (2005), the NCE-NP crucially depends on low prime visibility (Eimer & Schlaghecken, 2002; Klapp & Hinkley, 2002), whereas the NCE-P is independent of prime visibility. Two of the experiments in the present study assessed prime visibility with a forced choice prime discrimination task. Experiment 2 showed that the primes used in the present study were visible when the mask was absent, but visibility was reduced by the mask and the type of target stimuli used in this experiment to the level of 69.2% correct responses in the condition with a 153-msec SOA and the presence of a mask. In Experiment 3, the accuracy of prime recognition performance was reduced to 56.6% correct responses in this condition. These findings correspond to comparable measures of prime visibility in previous studies (e.g., Klapp & Hinkley, 2002, Experiment 1 [59.0%–65.2% correct responses]; Klapp, 2005 [69% correct]; Lleras & Enns, 2004 [58%–92% correct]). Nonetheless, in the present study inverse target and cue priming effects were the same in participants with good and poor prime recognition performance. This finding accords with Klapp's distinction by showing that the NCE-P is independent of prime visibility (for similar findings, see Lleras & Enns, 2004; Mattler, in press). Thus, in this respect the perceptual version of inverse priming is comparable to positive priming, which is largely independent of prime visibility (see, e.g., Mattler, 2003; Vorberg et al., 2003).

Commonalities Between Target and Cue Priming

The present study contributes to the similarities discovered between target and cue priming effects (Mattler, 2003, 2005, in press). Previous studies have shown that target and cue priming exhibited a similar time course when the temporal interval between the prime and the following target or cue was varied (Mattler, 2003). Second, target and cue priming effects were dissociated from prime awareness by showing that the time course of priming effects differs from that of prime recognition performance (Mattler, 2003). In addition, target and cue priming effects have both been found in conditions with total masking (Mattler, 2003; Vorberg et al., 2003). Third, target and cue priming effects decayed when the target stimulus was delayed by about half a second (Mattler, 2005). Fourth, the present study showed that target and cue priming effects are affected by the similarity between primes and the following stimulus. However, a substantial part of positive target and cue priming effects is not due to perceptual similarity. Finally, both target and cue priming effects can be inverted when a separate mask follows the prime (Mattler, in press). In light of the present study, this version of inverse priming results from early perceptual interactions between the prime, the mask, and the following stimulus, and it is independent of prime visibility for both target and cue priming.

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NOTE

1. I thank Dirk Vorberg for motivating the fourth experiment.

(Manuscript received October 13, 2004;
revision accepted for publication September 15, 2005.)