

# The reversal of perceptual and motor compatibility effects differs qualitatively between metacontrast and random-line masks

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**Abstract** In masked priming tasks, participants typically respond faster to compatible than to incompatible primes, an effect that has been dubbed as the positive compatibility effect (PCE). However, when the interval between the prime and the mask is relatively long, responses are faster to incompatible than to compatible primes. This inversion is called the negative compatibility effect (NCE). Two main origins of the NCE have been proposed. The *object-updating* theory holds that when the masks share stimulus features with the primes, both perceptual and motor processes generate an NCE. As an example, for masks composed of overlaid left and right prime arrows, the NCE is thought to be positive priming induced by the arrow of the mask pointing in the opposite direction of the prime. In contrast, the *motor inhibition* theories hold that the origin of the NCE is purely motor and can be demonstrated when masks do not share features with primes. To test both hypotheses, the present study aims at delineating the respective contributions of perceptual and motor components of the NCE in the context of different types of masks. Consistent with the object-updating hypothesis, we found both perceptual and motor NCEs at the long SOA with metacontrast masks (with internal contours corresponding

to left and right overlaid arrows). Consistent with the motor inhibition hypothesis, we found motor NCE but no perceptual NCE at the long SOA with random-line masks (containing no prime features). The study thus suggests that the origin of the NCE depends on the type of mask.

## Introduction

The influence of unconscious stimuli on behavior has been observed at many levels of processing and through many different suppression techniques (Dehaene & Changeux, 2011; Kim & Blake, 2005; van Gaal & Lamme, 2012). Despite the diversity of existing methods, unconscious influences remain essentially studied with the masked priming task, in which responses to a target stimulus are influenced by the prior presentation of a prime stimulus rendered invisible by a temporally adjacent mask stimulus (for a review, see Kouider & Dehaene, 2007). Typically, masked priming effects consist of faster and more accurate responses when the prime is similar to the subsequent target than when the prime is different (Atas, Vermeiren, & Cleeremans, 2013; Dehaene, Naccache, Le Clec, Koechlin, Mueller, & Dehaene-Lambertz, 1998; Klotz & Neumann, 1999; Neumann & Klotz, 1994; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003). However, the similarity between prime and target might sometimes disfacilitate target processing rather than improving it (e.g., Eimer & Schlaghecken, 2003). This reversed pattern has been called “the negative compatibility effect,” distinguishing it from the more familiar “positive compatibility effect”.

Eimer and Schlaghecken (1998) were the first to discover the existence of this effect by manipulating the Mask-Target SOA, that is, the interval between the offset

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of the prime and the onset of the target. In their studies, participants were instructed to respond as fast as possible to the direction of the arrow they perceived, which could either point to the left or to the right ( $\ll$  or  $\gg$ ). This target stimulus was preceded by a masked prime that could either point in the same direction as the target (compatible condition) or in the opposite direction (incompatible condition). When the Mask-Target SOA was short (about 0–40 ms), responses were faster and more accurate in the compatible trials than in the incompatible trials (Positive Compatibility Effect, PCE). In contrast, when the Mask-Target SOA was long (about 100–200 ms), responses were slower and less accurate in compatible trials than in incompatible trials (Negative Compatibility Effect, NCE). This pattern of results—i.e., a PCE for short SOAs followed by an NCE for long SOAs—has now been replicated by many authors with different types of masks and stimuli (e.g., Boy & Sumner, 2010; Klapp & Hinkley, 2002; Lingnau & Vorberg, 2005; Lleras & Enns, 2004; Mattler, 2006).

Many studies have attempted to elucidate the cause of the NCE. At present, two opposing theories of the NCE have received empirical support: the *object-updating* theory and the *motor inhibition* theory. The *object-updating* theory holds that when masks share stimulus features with primes, both perceptual and motor processes generate an NCE. In contrast, the *motor inhibition* theory holds that the origin of the NCE is purely motor and can be demonstrated when masks do not share stimulus features with primes. Taking both theories into account, recent studies on NCE assume that the NCE origin can be both perceptual and motor. However, depending on the types of masks and stimuli used, one component (perceptual vs. motor) may play a more prominent role than the other (Boy & Sumner, 2010; McBride, Boy, Husain, & Sumner, 2012). This important assumption has not yet been directly tested. Therefore, the present study aimed to delineate the perceptual and motor components that, respectively, contribute to the NCE for different types of masks and stimuli.

In more detail, the Object-Updating Theory (also known as the Mask-Induced Priming Hypothesis), which was proposed by Lleras and Enns (2004, 2006) and by Verleger, Jaśkowski, Aydemir, van der Lubbe, and Groen (2004), assumes that each new object presented to an observer becomes integrated into an already existing scene. This integration results in an updated version of that scene: If the scene changes, the existing scene is replaced by the most recent update. Object updating is likely to occur in priming studies that use pattern masks constructed by superimposing the two alternative prime stimuli (Eimer & Schlaghecken, 1998; Schlaghecken & Eimer, 2000), as well as in studies that use metacontrast masks, in which the internal contours correspond to the contours from the

superimposition of the two alternative primes (Eimer, 1999; Lingnau & Vorberg, 2005; Mattler, 2006). The theory holds that the rapid succession of the prime (e.g., a right-pointing arrow) and the mask (i.e., composed of both right-pointing and left-pointing arrow-like features) decreases the saliency of those features of the mask that are also present in the prime (i.e., the right-pointing arrow) and increases the saliency of those features of the mask that are not present in the prime (i.e., the left-pointing arrow). In other words, the updated object is the novel element added to the scene: the left-pointing arrow. When the updated object (i.e., the left-pointing arrow) calls for the opposite response than that already initiated by the prime (i.e., the right-pointing arrow), participants change their response accordingly: the prime-triggered motor activation is stopped and motor activation of the updated object (i.e., the left-pointing arrow) is initiated. The observation of the Negative Compatibility Effect simply reflects that (1) the updated arrow always points in the opposite direction to the prime arrow, and that (2) the compatibility conditions are designed in accordance with the relation between the prime and the target. Thus, an *incompatible* trial according to the prime target relation is actually a *compatible* trial according to the updated object-target relation. This also implies that the origin of the NCE is both perceptual and motor: the updated arrow causes a classical positive compatibility effect with both perceptual and motor facilitation when the updated arrow is compatible with the target arrow (and the prime incompatible to the target arrow). Importantly, masks must share stimulus features with primes to observe object updating. For the sake of simplicity, these masks are called “relevant” with respect to the features of the primes.

It is important to note, however, that object updating cannot account for all the results observed in more recent studies (Boy & Sumner, 2010; Klapp, 2005; Schlaghecken & Eimer, 2006; Sumner, 2008). For instance, a significant NCE was found with pattern masks that contained no relevant features, such as vertical and horizontal random lines when the primes and targets were left-pointing and right-pointing double arrows ( $\ll/\gg$ ; Schlaghecken & Eimer, 2006). An NCE was also found when pattern masks were composed of oblique lines and the primes and targets were horizontal or vertical double lines ( $=//$ ; Boy & Sumner, 2010; Sumner, 2008). For pattern masks constructed by combining all the possible line orientations, random-line masks, an NCE was also observed when primes and targets were left-pointing and right-pointing double arrows (used in e.g., Eimer & Schlaghecken, 2002; Praamstra & Seiss, 2005; Schlaghecken & Eimer, 2002, 2004; Seiss & Praamstra, 2004). This random-line mask is not fully irrelevant because it might be composed of oblique lines of the same orientation as that of the arrow stimuli. However, Sumner, (2008) found that the NCE was not different

between classical random-line masks and random-line masks that did not contain oblique lines of the same orientation as that of the arrow stimuli. This finding suggests that object updating might not play a major role in the NCE with random-line masks.

In such cases, the NCE is likely to be the result of Motor Inhibitory Mechanisms (Eimer, 1999; Eimer & Schlaghecken, 2002, 2003; Jaśkowski, 2008; Jaśkowski, Bialunska, Tomanek, & Verleger, 2008; Jaśkowski & Przekoracka-Krawczyk, 2005; Jaśkowski & Verleger, 2007; Schlaghecken & Eimer, 2000, 2002). According to this account, the NCE is caused by an inhibitory mechanism in the motor system which suppresses the initial premature motor activation evoked by the prime. Thus, when the target appears, it is more difficult to produce the corresponding prime response (inhibited) than the alternative response, which has not been inhibited. Importantly, this form of motor inhibition is assumed to take place automatically and without any voluntary intention to suppress the prime response. Indeed, participants are generally not aware of the brief task-irrelevant stimulus, and are not instructed to employ response inhibition (Boy, Husain, & Sumner, 2010c; McBride et al., 2012). Supporting the *motor locus* of the inhibitory mechanism, several studies using irrelevant masks (mainly random-line masks) have shown that the SMA may be the source of the inhibition process, that is, the brain area that causes suppression (Boy, Evans, Edden, Singh, Husain, & Sumner, 2010a; Sumner, Nachev, Morris, Peters, Jackson, & Kennard, 2007). The SMA is an area interconnected with the primary motor cortex. This area is specialized in motor control and is unlikely to inhibit perceptual influences elicited by the prime. Taken together, current empirical evidence suggests that the NCE with irrelevant masks is the result of automatic inhibition of the motor activation elicited by the prime. The *negative* compatibility effect takes place because the motor representation of the prime is selectively inhibited, while the perceptual representation of the prime is not the target of inhibition.

The present study aims at delineating the respective contributions of perceptual vs. motor components of the NCE in the context of relevant masks (metacontrast masks) and irrelevant masks (random-line masks). This will provide direct evidence that (1) when the masks share relevant stimulus features with the prime, the NCE origin is both perceptual and motor because it is due to a classical positive compatibility effect when the updated arrow is compatible to the target arrow—and the prime incompatible to the target arrow; and that (2) when the masks share no relevant stimulus features with the prime, the NCE origin is purely motor because it is due to selective motor inhibition. To test this hypothesis, we manipulated the Mask-Target SOA (i.e., 0, 70, 140 and 200 ms) and used a task that

involves four stimuli (upleft, downleft, upright, downright arrows) mapped onto two responses (left and right button presses). Participants were instructed to respond with their left index when the target was pointing in the left direction (i.e., upleft and downleft arrows), and to respond with their right index when the target was pointing in the right direction (i.e., upright and downright arrows). This design was inspired by the flanker study of Eriksen and Eriksen (1974), who originally proposed to use four stimuli (H, K, S, C) mapped onto two responses (left for H, K and right for S, C) to separate perceptual from motor compatibility effects in the flanker task.

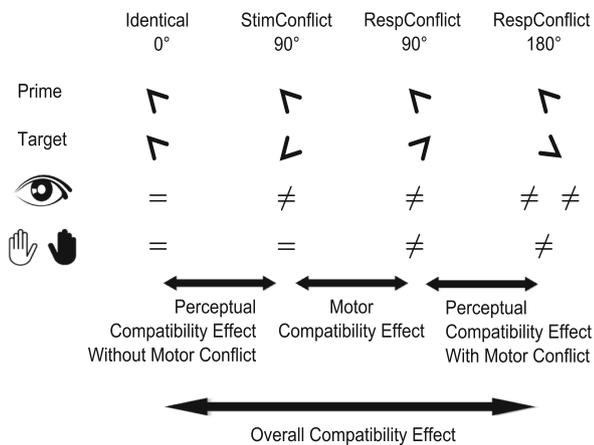
The mapping used in the present study makes it possible to compare four levels of conflict between the prime and the target (see Fig. 1a).

In the Identical trials, the prime arrow was identical to the target arrow (e.g., both the prime and the target were an upleft pointing arrow). In the StimConflict trials, the prime arrow was visually different from the target but evoked the same response (e.g., the prime was an upleft pointing arrow and the target was a downleft pointing arrow). In the RespConflict 90° trials, the prime arrow was visually different from the target, and they also evoked a different response (e.g., the prime was an upleft pointing arrow and the target was an upright pointing arrow). In the RespConflict 180° trials, the prime arrow was even more “visually different”<sup>1</sup> from the target arrow than in the RespConflict trials 90°, also evoking a different response (e.g., the prime was an upleft pointing arrow and the target was a downright pointing arrow). These manipulations allow for dissociation between perceptual and motor compatibility effects.

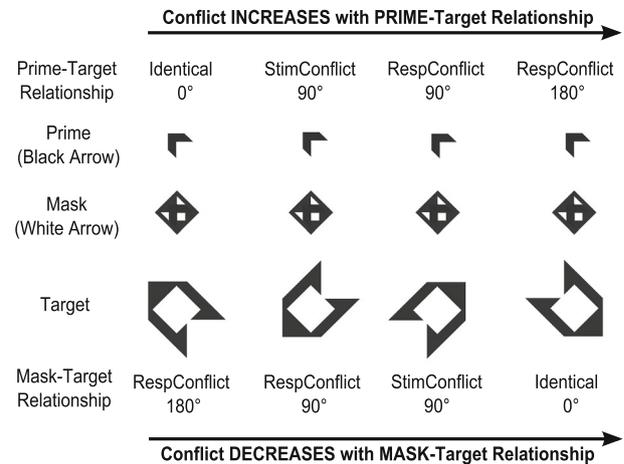
*The perceptual compatibility effect without motor conflict* was quantified by subtracting the reaction times/error rates of the identical trials from the reaction times/error rates of the StimConflict trials. In both cases, the primes evoked the same response as those of the targets but were only perceptually identical in the Identical trials. The motor compatibility effect was assessed by subtracting the reaction times/error rates of the StimConflict 90° trials from the reaction times/error rates of the RespConflict 90° trials. In

<sup>1</sup> For arrow stimuli, the relevant perceptual information is the orientation of the arrowhead, not the orientation of the lines that composed the head. By saying even more “visually different”, we refer to the orientation of the arrowhead. As a matter of fact, in RespConflict 180° trials, prime and target are composed of lines with identical orientation (a line rotated by 180° has the same orientation as a non-rotated line), only the spatial arrangement of the lines relative to each other differs. In contrast, in RespConflict 90° trials, the lines making up the target are at a 90° angle to those making up the prime. However, this is not the relevant perceptual information in the task. Also, the prime and target were never presented in the same location so that the influence of low-level similarity of line orientation is reduced.

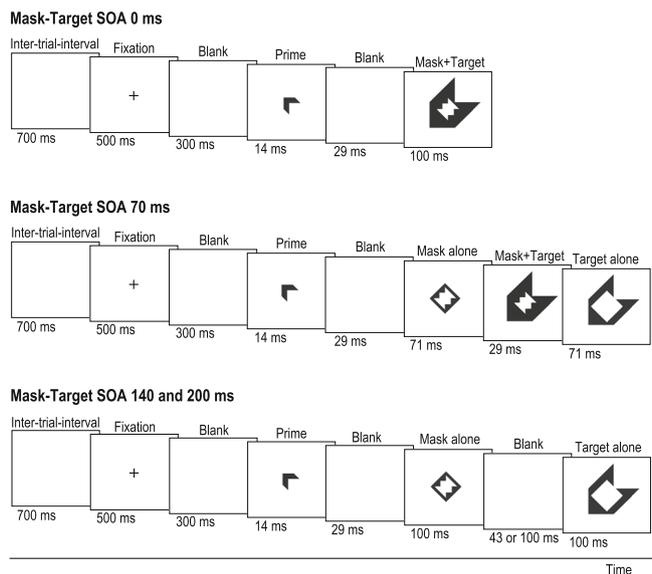
**a Prime-Target Relationship**



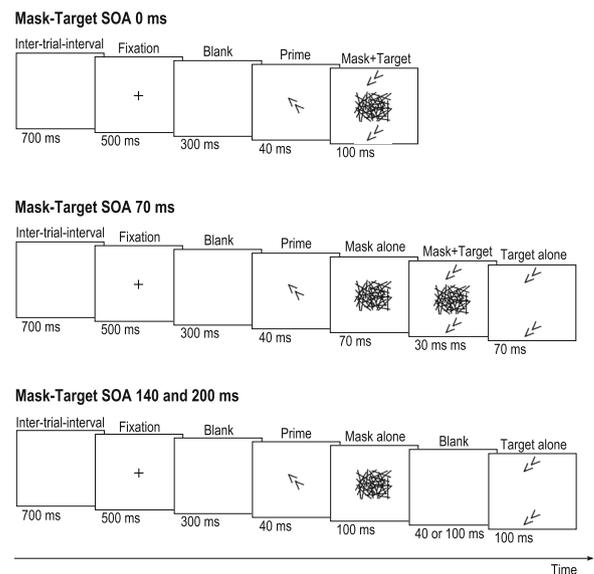
**b Prime-Mask Interaction with Metacontrast Mask**



**c Metacontrast Mask**



**d Random Line Mask**



**Fig. 1** Trial procedure of the priming task. **a** In each trial of the priming task, participants had to make quick and accurate responses with a left- or right-hand key press to the *leftward* and *rightward* orientation of the *arrow* target, while the prime and target stimuli were *upleft*, *upright*, *downleft* and *downright*. With this two responses/four stimuli mapping, four levels of conflict between the prime and the target were possible. In the Identical trials, the prime arrow was identical to the *target* arrow. In the StimConflict trials, the *prime* arrow was visually different from the target but evoked the same response. In the RespConflict 90° trials, the prime arrow was visually different from the target and also evoked a different response. In the RespConflict 180° trials, the *prime* arrow was even more visually different from the *target* arrow than in the RespConflict trials 90° but also evoked a different response. Comparing Identical to StimConflict trials allows extracting the perceptual compatibility effect without motor conflict. Comparing StimConflict to

RespConflict trials allows isolating the motor compatibility effect. Finally, comparing StimConflict to RespConflict trials allows extracting the perceptual compatibility effect with motor conflict. **b** For metacontrast masking, the object-updating hypothesis assumes that the *white* arrow (i.e., the percept resulting of prime-mask interaction) is the information that induces priming at longer Mask-Target SOAs. All the *arrow* directions and levels of conflict are completely reversed between the priming by the actual prime (the *black* arrow) and the priming by the mask (the *white* arrow). **c, d** The Mask-Target SOA and the Type of Mask were systematically manipulated. In Mask-Target SOA 0 blocks, targets appeared together with the mask. In Mask-Target SOA 70, the mask was presented alone and then presented together with the target, which remained alone on the screen after the offset of the mask. In Mask-Target SOA 140 and 200 blocks, targets appeared 40 or 100 ms after the offset of the mask

both cases, the primes were perceptually different from the targets with an angle difference of  $90^\circ$ , but only evoked a different response in the RespConflict  $90^\circ$  trials. The *perceptual compatibility effect with motor conflict* was quantified by subtracting the reaction times/error rates of the RespConflict  $90^\circ$  trials from the reaction times/error rates of the RespConflict  $180^\circ$  trials. In both cases, the primes evoked the opposite response from that of the target, but primes are perceptually more different than the targets in RespConflict  $180^\circ$  than in RespConflict  $90^\circ$  trials. Finally, the *overall compatibility effect* was quantified by subtracting the reaction times/error rates of the Identical trials from the reaction times/error rates of the RespConflict  $180^\circ$  trials.

The primes and targets were presented in black on a white background. For random-line masks, the rapid succession of the prime and the mask is unlikely to create a new “updated” arrow given that the lines of the mask were oriented randomly. In contrast, for metacontrast masking, the rapid succession of the prime and the mask is likely to create a white arrow: the empty area resulting from the superimposition of the prime and the mask. Thus, for metacontrast masking, if we consider that the white arrow is the information that induces priming at longer Mask-Target SOA rather than the black arrow (i.e., the actual prime stimulus), then, all the arrow directions and levels of conflict are “reversed” for these SOAs (see Fig. 1b). In other words, the upleft-“black arrow” prime becomes a downright-“white arrow” mask, the upright-“black arrow” prime becomes a downleft-“white arrow” mask, the downleft-“black arrow” prime becomes an upright-“white arrow” mask, and the downright-“black arrow” prime becomes an upleft-“white arrow” mask. Similarly, Identical trials with respect to the prime–target relation (“black arrow”) becomes RespConflict  $180^\circ$  trials with respect to the mask–target relation (“white arrow”). StimConflict  $90^\circ$  trials with respect to the prime–target relation (“black arrow”) become RespConflict  $90^\circ$  trials with respect to the mask–target relation (“white arrow”). RespConflict  $90^\circ$  trials with respect to the prime–target relation (“black arrow”) become StimConflict  $90^\circ$  trials with respect to the mask–target relation (“white arrow”). Finally, RespConflict  $180^\circ$  trials with respect to the prime–target relation (“black arrow”) become Identical trials with respect to the mask–target relation (“white arrow”).

Based on the object-updated theory, we predict that for metacontrast masks, the black arrow—the prime—will be the information that influences target processing at the short SOAs, while the white arrow—the percept resulting from the prime-mask interaction—will be the information that influences target processing at the long SOAs. Importantly, a task-irrelevant arrow information—

regardless of whether it is the actual prime or an updated object—can induce (1) perceptual conflict when the processing of the irrelevant stimulus features interferes with the processing of the target stimulus features; and (2) motor conflict when the prepotent response elicited by the task-irrelevant stimulus interferes with the response to the task-relevant stimulus. Therefore, we expect to observe both perceptual and motor compatibility effects for short and long Mask-Target SOAs. Notably, these effects will be positive when the SOA is short because they are caused by the black arrow prime, while these effects will be negative when the SOA is long because they are caused by the updated white arrow that points in the opposite direction than the prime arrow.

Based on the motor inhibition theory, we predict that for random-line masks, the black arrow—the prime—will always be the information that influences target processing. The influence of the prime on target processing will be the same for both types of masks (metacontrast and random-line) at short Mask-Target SOAs. However, at the long SOAs, an inhibitory mechanism will exert its influence on the motor activation elicited by the prime, but not on the perceptual representation. Therefore, the irrelevant motor activation triggered by the prime will be selectively inhibited, resulting in a purely motor NCE. Under such inhibition, the *correct* response is inhibited on the StimConflict trials (i.e., motor compatible trials), resulting in *slower* responses to the target, whereas the *incorrect* response is inhibited on the RespConflict  $90^\circ$  trials (i.e., motor incompatible trials), which *facilitate* responses to the target. Importantly, the perceptual representation will not be inhibited, resulting in an absence of perceptual reversal (i.e., no NCE). At long Mask-Target SOAs, the perceptual compatibility effect (StimConflict<sub>RT</sub>–Identical<sub>RT</sub>) will be either positive because perceptual identity between the prime and target may still facilitate target response, or null because the perceptual representation of the masked prime may passively decay when the Mask-Target SOA exceeds a few hundred milliseconds (Ferrand, 1996; Greenwald, Draine, & Abrams, 1996; Naccache, Blandin, & Dehaene, 2002).

## Method

### Participants

Twenty-nine students (17 females; mean age = 21) from the Université Libre de Bruxelles served as participants. They participated in two sessions, 1 h in length, separated by 24 h. Participants reported normal or corrected-to-normal vision and were unaware of the purpose of the experiment. They were paid €16 for their participation.

## Apparatus and stimuli

Stimuli were displayed on a CRT monitor (Philips 107T). Subjects viewed the screen from a distance of 70 cm. Responses were executed with the index fingers of both hands and collected through the two extreme keys of a button box (E-prime 1.1, PST software, Pittsburgh, USA). All stimuli were black and displayed at the center of the screen on a white background.

### Stimuli of the metacontrast mask condition (relevant mask)

Stimuli were displayed at a resolution of  $1024 \times 768$  and at a refresh rate of 70 Hz. The prime was a small upleft, downleft, upright or downright pointing arrow subtending a visual angle of approximately  $0.9 \times 0.9^\circ$  and fitting exactly into the inner contours of the mask. Importantly, to improve the effectiveness of both masking and object updating, the inner contours of the mask did not correspond to the external contours of all the four possible primes. Instead, two different masks were created: one mask with inner contours corresponding to the external contours of upleft and downright primes (as in Fig. 1b, c), and the other with inner contours corresponding to the external contours of downleft and upright primes. The target was a large upleft, downleft, upright or downright pointing arrow, subtending a visual angle of approximately  $2.9 \times 2^\circ$ . The different arrow directions were made by tilting the stimulus '<' at the angles of 45, 135, 225 and  $315^\circ$ . The fixation cross subtended a visual angle of approximately  $0.6 \times 0.6^\circ$ . For the Mask-Target SOA of 0 ms, the mask and the target were merged, forming a single stimulus. For the Mask-Target SOA of 140 and 200 ms, the outer shape of the mask was a square subtending a visual angle of approximately  $1.2 \times 1.2^\circ$  (see Fig. 1c). The mask fit into the inner contours of the target without touching it. For the Mask-Target SOA of 70 ms, the mask alone, the target alone, and the mask and target forming a single stimulus were all used.

### Stimuli of the random line mask condition (irrelevant mask)

Stimuli were displayed at a resolution of  $800 \times 600$  and at a refresh rate of 100 Hz. Both prime and target stimuli were upleft, downleft, upright and downright pointing double arrows subtending a visual angle of approximately  $1.6 \times 0.7^\circ$ . The different arrow directions were produced by tilting the stimulus '<<' at the angles of 45, 135, 225 and  $315^\circ$ . Masks were made up of 35 randomly orientated lines of different length positioned on a virtual grid of  $3.3 \times 2.7^\circ$ . Sixty different masks were created and one of them was randomly selected on each trial. The fixation

cross subtended a visual angle of approximately  $0.6 \times 0.6^\circ$ . The fixation cross, the prime and the mask stimuli appeared at the center of the screen, whereas the target was presented in duplicate, either just above and below the mask or at just the left and right of the mask (the distance from the center of the screen to the center of the target arrow subtended a visual angle of  $2.5^\circ$ ; see Fig. 1d). The vertical and horizontal presentations of the two targets relative to the mask were randomly selected over trials.

## Design and procedure

In the priming task, participants had to make quick and accurate responses with a left- or right-hand key press to the leftward and rightward orientations of the arrow target, respectively. Each trial started with a fixation cross that was presented for 500 ms, followed by a blank screen for 300 ms. For the Metacontrast Masking condition, the prime was presented at the center of the screen for 14 ms and was followed by a mask (100 ms) after a blank screen for 29 ms. For the Random-Lines Masking condition, the prime was presented at the center of the screen for 40 ms and was followed immediately by a mask (100 ms). The target was presented for 100 ms. The interval between the offset of the prime and the onset of the target (the Mask-Target SOA) was systematically manipulated. We used four Mask-Target SOAs conditions: 0, 70, 140 and 200 ms. After the offset of the target, a blank screen was displayed until participants responded. The inter-trial interval was a blank screen presented for 700 ms. The two masking conditions were tested in two different sessions, separated by exactly 24 h. The order of the Mask-Type between the two sessions was counterbalanced over participants. Each session consisted of 16 experimental blocks of 80 trials each, separated by short breaks of a minimum of 20 s. Each block contained only trials with one specific Mask-Target SOA condition. The order of the blocks was counterbalanced between participants. Each block contained an equal number of trials of the Identical, StimConflict, RespConflict  $90^\circ$  and RespConflict  $180^\circ$  prime-target relations, presented in a randomized order. Performance feedback was presented after each block (mean reaction times and percentage of correct responses to the target). A practice block of 20 trials preceded the experimental blocks.

At the end of the second session, prime visibility was evaluated by a discrimination test on the arrow prime. Prime and mask stimuli were presented in the same way as in the main experiment but the target was removed. After the offset of the mask, either the question "left?" or "right?" was displayed until participants responded which was completed without time pressure. Participants had to respond "yes" with the left index if the direction of the arrow prime corresponded to the question or "no" with the

right index if the direction of the arrow prime did not correspond to the question. The direction of the prime arrow did not correspond to the hand response to minimize the influence of automatic motor activation or inhibition during the visibility task. The visibility task consisted of two blocks of 48 trials, both performed at the end of the second session. One block contained the Metacontrast Masking and the other the Random-Lines Masking. The order of the blocks was counterbalanced between participants. The different prime–target–question relations were all equally represented and randomly presented.

## Results

The first trial of each block<sup>2</sup> and RTs < 100 and > 1000 were excluded from the analysis (< 1 %). Mean reaction times from correct responses (96.5 % of trials) and mean error percentages were each submitted to a repeated-measures analysis of variance (ANOVA) with Mask-Type (Metacontrast and Random Lines), Mask-Target SOA (0, 70, 140 and 200 ms) and Compatibility (Identical, StimConflict, RespConflict 90° and RespConflict 180°) as within-subject factors. Results of these analyses are represented in Figs. 2. For the RT analysis, the main effect of Mask-Type was not significant ( $F(1, 28) = 1.99, p = 0.169$ ). In contrast, we observed significant main effects of Mask-Target SOA ( $F(3, 84) = 5.22, p = 0.002$ ) and Compatibility ( $F(3, 84) = 8.65, p < 0.001$ ). We also observed significant 2-way interactions between Mask-Type and Mask-Target SOA ( $F(3, 84) = 22.07, p < 0.001$ ), Mask-Type and Compatibility ( $F(3, 84) = 10.90, p < 0.001$ ), and between Mask-Target SOA and Compatibility ( $F(9, 252) = 88.22, p < 0.001$ ). Crucially, the 3-way interaction was also significant,  $F(9, 252) = 5.61, p < 0.001$ , indicating that the modulation of the compatibility effect by the SOA condition was not the same for the Metacontrast masking and the Random-Lines Masking. Similar results were observed for the error analysis. The main effect of Mask-Type was not significant ( $F(1, 28) = 0.54, p = 0.818$ ). The main effect of Mask-Target SOA was significant ( $F(3, 84) = 4.29, p = 0.007$ ) and the main effect of Compatibility was also significant ( $F(3, 84) = 7.39, p < 0.001$ ). The 2-way interaction between Mask-Type and Mask-Target SOA was not significant ( $F(3, 84) = 1.70, p = 0.174$ ). The 2-way interactions between Mask-Type and Compatibility ( $F(3, 84) = 3.51, p = 0.019$ ) and between Mask-Target SOA

and Compatibility ( $F(9, 252) = 20.17, p < 0.001$ ) were significant. Similarly to the RT analysis, the 3-way interaction was also significant ( $F(9, 252) = 2.00, p = 0.040$ ). This further showed that the modulation of the compatibility effect by the SOA condition was not the same for the Metacontrast masking and the Random-Lines Masking. We then tested whether the four relevant compatibility effects were significant for each Mask-Target SOA condition and for each Mask-Type condition.

Overall compatibility effect: the difference between identical and RespConflict 180° trials

RT analysis for the Metacontrast Masking showed that the overall compatibility effect was significant and positive at the SOA 0 ms ( $t(28) = 18.21, p < 0.001$ ; RespConflict 180°–Identical = 58 ms), non-significant at the SOA 70 ms ( $t(28) = 0.92, p = 0.368$ ; difference = 7 ms), and significant and negative at both the SOA 140 ms ( $t(28) = -7.90, p < 0.001$ ; difference = -42 ms) and the SOA 200 ms ( $t(28) = -3.70, p = 0.001$ ; difference = -22 ms). Error analysis for this masking condition showed a similar pattern: the overall compatibility effect was significant and positive at the SOA 0 ms ( $t(28) = 5.48, p < 0.001$ ; RespConflict 180°–Identical = 5.8 %), non-significant at the SOA 70 ms ( $t(28) = 1.28, p = 0.211$ ; difference = 1.8 %), significant and negative for the SOA 140 ms ( $t(28) = -4.64, p < 0.001$ ; difference = -4.5 %), and marginally significant and negative at the SOA 200 ms ( $t(28) = -2.01, p = 0.054$ ; difference = -1.6 %).

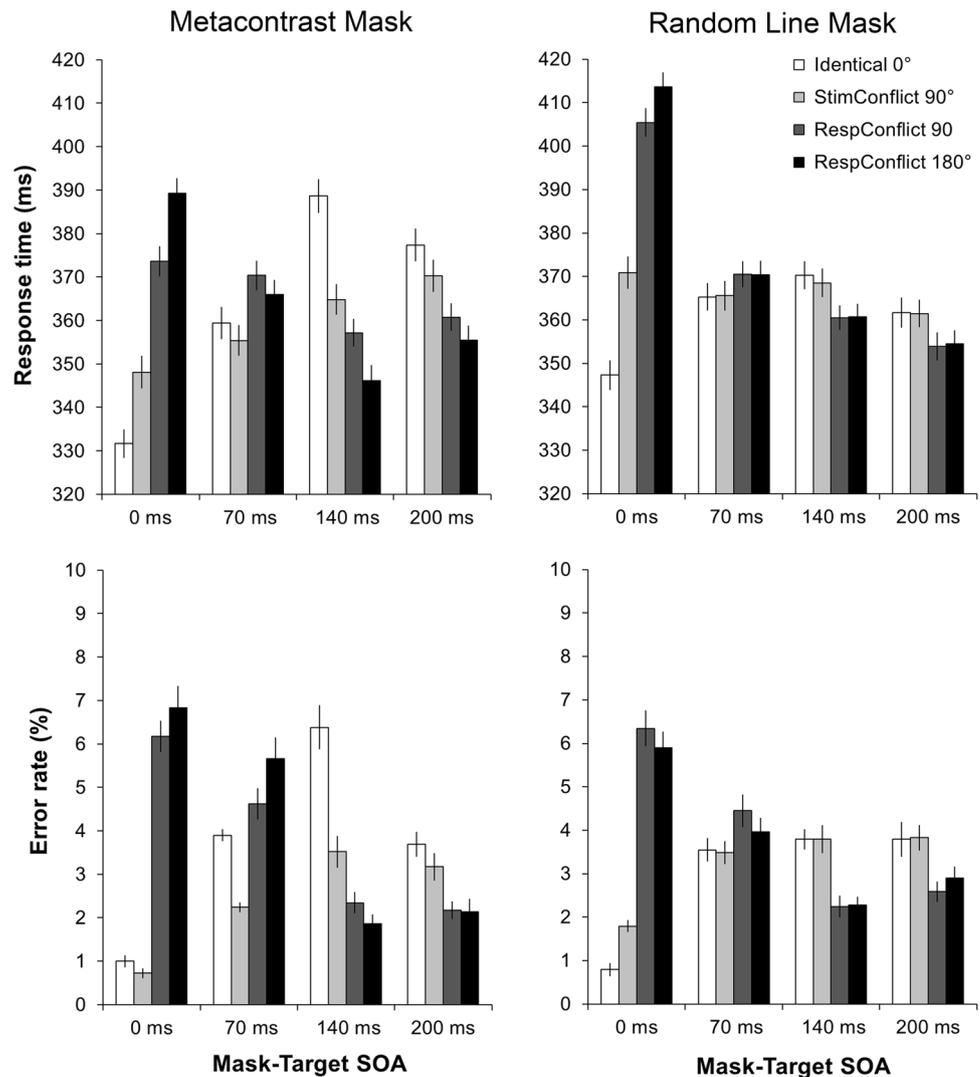
RT analysis for the Random-lines Masking showed that the overall compatibility effect was significant and positive at the SOA 0 ms ( $t(28) = 20.29, p < 0.001$ ; difference = 66 ms), non-significant at the SOA 70 ms ( $t(28) = 1.17, p = 0.252$ ; difference = 5 ms), and significant and negative at both the SOA 140 ms ( $t(28) = -3.10, p = 0.004$ ; difference = -10 ms) and the SOA 200 ms ( $t(28) = -2.40, p = 0.023$ ; difference = -7 ms). Similarly, error analysis for this masking condition showed that the overall compatibility effect was significant and positive at the SOA 0 ms ( $t(28) = 6.73, p < 0.001$ ; difference = 5.1 %), non-significant at the SOA 70 ms ( $t(28) = 0.52, p = 0.610$ ; difference = 0.4 %), significant and negative at the SOA 140 ms ( $t(28) = -2.72, p = 0.011$ ; difference = -1.5 %) and non-significant at the SOA 200 ms ( $t(28) = -1.16, p = 0.258$ ; difference = -0.9 %).

Perceptual compatibility without motor conflict: the difference between identical and StimConflict trials (see Fig. 3)

RT analysis for the Metacontrast Masking showed that the perceptual compatibility was significant and positive at the

<sup>2</sup> Because participants started each block by pressing the spacebar of the keyboard and then responded to target by choosing between the two extreme keys of the button box, the RT of the very first trial was affected by the changing of device. For this reason, it was systematically not analyzed.

**Fig. 2** Mean reaction times (ms) and mean error percentages (%) for Identical, StimConflict, RespConflict 90° and RespConflict 180° trials as function of the Mask-Target SOA and the Type of Mask. Error bars represent  $\pm 1$  SE



SOA 0 ms ( $t(28) = 7.07, p < 0.001$ ; StimConflict–Identical = 16 ms), non-significant at the SOA 70 ms ( $t(28) = -0.77, p = 0.446$ ; difference = -4 ms), significant and negative at both the SOA 140 ms ( $t(28) = -6.78, p < 0.001$ ; difference = -24 ms) and the SOA 200 ms ( $t(28) = -2.53, p = 0.017$ ; difference = -7 ms). Error analysis for this masking condition indicated that the perceptual compatibility was non-significant at the SOA 0 ms ( $t(28) = -0.95, p = 0.348$ ; StimConflict–Identical = -0.3 %), marginally significant at the SOA 70 ms ( $t(28) = -1.92, p = 0.064$ ; difference = -1.7 %), significant and negative at the SOA 140 ms ( $t(28) = -3.63, p = 0.001$ ; difference = -2.9 %), and non-significant at the SOA 200 ms ( $t(28) = -1.26, p = 0.219$ ; difference = -0.5 %).

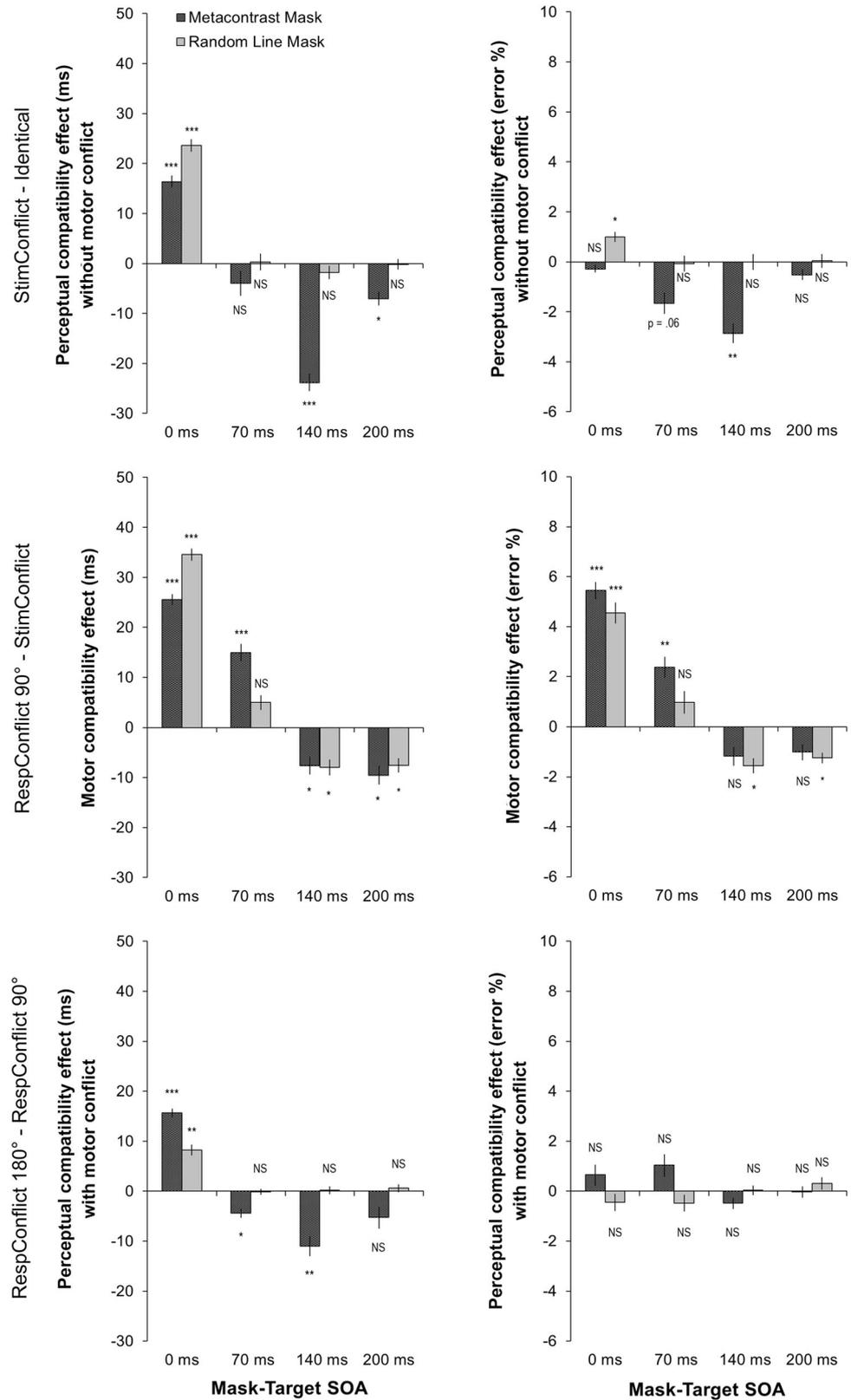
RT analysis for the Random-lines Masking showed that the perceptual compatibility was significant and positive at the SOA 0 ms ( $t(28) = 9.40, p < 0.001$ ;

difference = 24 ms) and non-significant at all the other SOA conditions (all  $p_s > 0.500$ ). Similarly, error analysis for this masking condition indicated that the perceptual compatibility was significant and positive at the SOA 0 ms ( $t(28) = 2.52, p < 0.001$ ; difference = 1 %) and non-significant for all the other SOA conditions (all  $p_s > 0.900$ ).

Motor compatibility on RTs: the difference between StimConflict and RespConflict 90° trials (see Fig. 3)

RT analysis for the Metacontrast Masking indicated that the motor compatibility effect was significant and positive at both the SOA 0 ms ( $t(28) = 12.09, p < 0.001$ ; StimConflict–RespConflict 90° = 26 ms) and at the SOA 70 ms ( $t(28) = 4.41, p < 0.001$ ; difference = 15 ms), while it was significant and negative at both the SOA 140 ms ( $t(28) = -2.11, p = 0.044$ ; difference = -8 ms)

**Fig. 3** (Upper panel) The Perceptual Compatibility Effect without motor conflict (i.e., StimConflict–Identical trials) on RTs and on errors as a function of the Type of Mask and the Mask-target SOA; (Middle panel) The Motor Compatibility Effect (i.e., RespConflict 90°–StimConflict trials) on RTs and on errors as a function of the Type of Mask and the Mask-target SOA; (Lower panel) The Perceptual Compatibility Effect with motor conflict (i.e., RespConflict 180°–RespConflict 90° trials) on RTs and on errors as a function of the Type of Mask and the Mask-target SOA. Error bars represent  $\pm 1$  SE. The asterisk(s) indicate(s) a significant compatibility effect (\* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ )



and the SOA 200 ms ( $t(28) = -2.50$ ,  $p = 0.019$ ; difference = -10 ms). Error analysis for this masking condition also showed that the motor compatibility effect was

significant and positive at both the SOA 0 ms ( $t(28) = 8.10$ ,  $p < 0.001$ ; StimConflict–RespConflict 90° = 5.4 %) and the SOA 70 ms ( $t(28) = 2.89$ ,

$p = 0.007$ ; difference = 2.4 %). The effect was non-significant at both the SOA 140 ms ( $t(28) = -1.55$ ,  $p = 0.132$ ; difference = -1.2 %) and the SOA 200 ms ( $t(28) = -1.48$ ,  $p = 0.151$ ; difference = -1 %).

RT analysis for the Random-lines Masking showed that the motor compatibility effect was significant and positive at the SOA 0 ms ( $t(28) = 14.17$ ,  $p < 0.001$ ; difference = 35 ms), non-significant at the SOA 70 ms ( $t(28) = 1.7$ ,  $p = 0.100$ ; difference = 5 ms), and significant and negative at both the SOA 140 ms ( $t(28) = -2.49$ ,  $p = 0.019$ ; difference = -8 ms) and the SOA 200 ms ( $t(28) = -2.68$ ,  $p = 0.012$ ; difference = -8 ms). Error analysis for this masking condition showed a similar pattern: the motor compatibility effect was significant and positive at the SOA 0 ms ( $t(28) = 5.39$ ,  $p < 0.001$ ; difference = 4.6 %), non-significant at the SOA 70 ms ( $t(28) = 1.06$ ,  $p = 0.297$ ; difference = 1 %), significant and negative at both the SOA 140 ms ( $t(28) = -2.62$ ,  $p = 0.014$ ; difference = -1.6 %) and the SOA 200 ms ( $t(28) = -2.95$ ,  $p = 0.006$ ; difference = -1.2 %).

Perceptual compatibility with motor conflict on RTs, i.e., the difference between RespConflict 90° and RespConflict 180° trials (see Fig. 3)

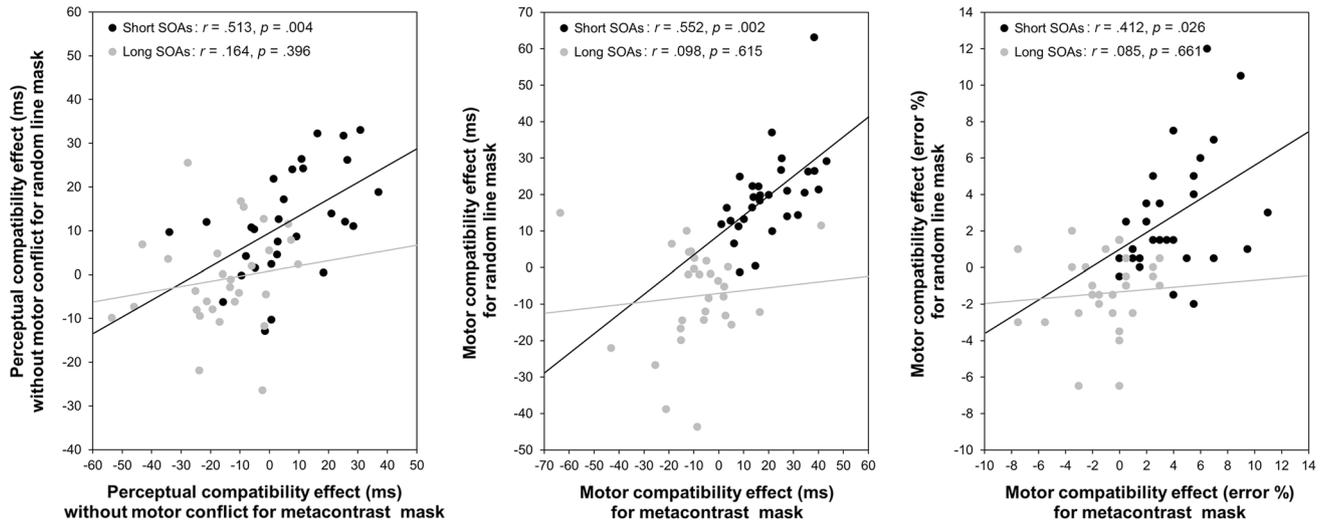
RT analysis for the Metacontrast Masking indicated that the perceptual compatibility effect was significant and positive at the SOA 0 ms ( $t(28) = 8.75$ ,  $p < 0.001$ ; RespConflict 180°–RespConflict 90° = 16 ms), significant and negative at both the SOA 70 ms ( $t(28) = -2.51$ ,  $p = 0.018$ ; difference = -4 ms) and the SOA 140 ms ( $t(28) = -2.79$ ,  $p = 0.009$ ; difference = -11 ms), and non-significant at the SOA 200 ms ( $t(28) = -1.21$ ,  $p = 0.235$ ; difference = -5 ms). RT analysis for the Random-lines Masking showed that the perceptual compatibility was significant and positive at the SOA 0 ms ( $t(28) = 3.77$ ,  $p = 0.001$ ; difference = 8 ms) and non-significant at all the other SOA conditions (all  $p_s > 0.700$ ). None of the effects was significant for the errors (all  $p_s > 0.250$ ).

Correlation of the compatibility effects between the two types of masks (see Fig. 4)

For the shortest SOAs (SOAs of 0 and 70 ms), the different sub-components (perceptual, motor) of the compatibility effect are not yet reversed and each are assumed to reflect the same process across the two types of masks. That is, the perceptual compatibility effect (StimConflict–Identical) reflects perceptual processing of the prime stimulus for both types of masks, while the motor compatibility effect (RespConflict90°–StimConflict) reflects the initial motor activation elicited by the prime for both types of masks.

For this reason, we expect that the perceptual compatibility effect will correlate between the two types of masks, and that the motor compatibility effect will also correlate between the two types of masks for the shortest SOAs. In contrast, for the longest SOAs (SOAs of 140 and 200 ms), we assumed that the negative compatibility effects reflect two different processes (object updating vs. motor inhibition) across the two types of masks. For this reason, we expect that the compatibility effects (perceptual or motor) will not correlate across the two types of masks for the longest SOAs. To demonstrate this, it is not sufficient to show that one correlation is significant (i.e., with short SOAs) and another is not (i.e., with long SOAs), one also needs to show that those correlations are significantly different from each other (Nieuwenhuis, Forstmann, & Wagenmakers, 2011). We thus used the ZPF statistic proposed by Raghunathan, Rosenthal, and Rubin (1996) to test the difference between two coefficient correlations in the situation where there is no variable in common between the two correlations (e.g.,  $r_{1,2}$  : motor compatibility effects between metacontrast and random-line masks at the short SOAs, and  $r_{3,4}$  : motor compatibility effects between metacontrast and random-line masks at the long SOAs), and both correlations were computed on the same participants. For these analyses, data of the SOAs 0 and 70 ms were regrouped as “Short SOAs”, while data of the SOAs 140 and 200 ms were regrouped as “Long SOAs”.

We only examined the perceptual compatibility effect on RTs since the error measure is not sufficiently sensitive to the perceptual processing. We found that the perceptual effect without motor conflict (i.e., StimConflict–Identical trials) significantly correlated between the two types of masks at the Short SOAs ( $r(29) = 0.513$ ,  $p = 0.004$ ), but did not correlate between the two types of masks at the Long SOAs ( $r(29) = 0.164$ ,  $p = 0.396$ ). The difference between these two correlations was marginally significant ( $ZPF = 1.45$ ,  $p = 0.074$ , one-tailed test). We examined the motor compatibility effect on both RTs and errors since both measures were strongly sensitive to the motor processing elicited by the prime. Results on RTs showed that the motor compatibility effect (RespConflict90°–StimConflict) significantly correlated between the two types of masks at the Short SOAs ( $r(29) = 0.552$ ,  $p = 0.002$ ), but did not correlate between the two types of masks at the Long SOAs ( $r(29) = 0.098$ ,  $p = 0.615$ ). The difference between these two correlations was significant ( $ZPF = 1.89$ ,  $p = 0.03$ , one-tailed test). Similarly, results on errors showed that the motor compatibility effect (RespConflict90°–StimConflict) significantly correlated between the two types of masks at the Short SOAs ( $r(29) = 0.412$ ,  $p = 0.026$ ), but did not correlate between the two types of masks at the Long SOAs ( $r(29) = 0.085$ ,  $p = 0.661$ ). We found a small trend toward significance for



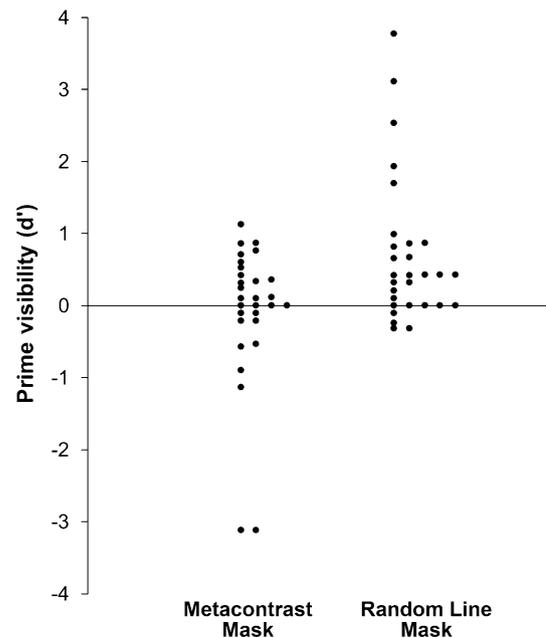
**Fig. 4** (Left panel) Black dots Correlation of the Perceptual effect without motor conflict (i.e., StimConflict–Identical trials) on RTs between the two types of masks at the Short SOAs (0 and 70 ms); Grey dots Correlation of the Perceptual effect without motor conflict (i.e., StimConflict–Identical trials) on RTs between the two types of masks at the Long SOAs (140 and 200 ms); (Middle panel) Black dots Correlation of the Motor Compatibility Effect (i.e., RespConflict 90°–StimConflict trials) on RTs between the two types of masks at the Short SOAs (0 and 70 ms); Grey dots Correlation of the Motor

Compatibility Effect (i.e., RespConflict 90°–StimConflict trials) on RTs between the two types of masks at the Long SOAs (140 and 200 ms); (Right panel) Black dots Correlation of the Motor Compatibility Effect (i.e., RespConflict 90°–StimConflict trials) on errors between the two types of masks at the Short SOAs (0 and 70 ms); Grey dots Correlation of the Motor Compatibility Effect (i.e., RespConflict 90°–StimConflict trials) on errors between the two types of masks at the Long SOAs (140 and 200 ms)

the difference between these two correlations ( $ZPF = 1.27, p = 0.10$ , one-tailed test).

Prime visibility (see Fig. 5)

Mean  $d'$  values on the visibility measure were  $-0.09$  for the Metacontrast Masking (with a mean accuracy performance of 49.7 %), and  $0.69$  for the Random-lines Masking (with a mean accuracy performance of 61.3 %). The mean  $d'$  value was not significantly different from zero for Metacontrast Masking ( $t(28) = -0.48, p = 0.638$ ) and differed significantly from zero for Random-lines Masking ( $t(28) = 3.67, p < 0.001$ ). This result suggests that participants were unable to perceive consciously the prime arrows with Metacontrast Masking, whereas they were able to do so with Random-Line Masking. However, a closer look at the individual performances indicates that the number of participants able to perceive consciously arrow information was very similar between the two types of masking (see Fig. 4). Indeed, for the Metacontrast Masking condition, 3 participants had a strong negative  $d'$  ( $-3.11, -3.11$  and  $-1.13$ ), and 4 other participants had a strong positive  $d'$  ( $1.13, 0.87, 0.86$  and  $0.76$ ). For the Random Line Masking, 9 participants had a strong positive  $d'$  ( $3.78, 3.11, 2.53, 1.93, 1.70, 0.99, 0.87, 0.86$  and  $0.81$ ), and no participant had a strong negative  $d'$  (the smallest  $d'$  value was  $-0.32$ ).



**Fig. 5**  $d'$  scores of each participant for the Metacontrast Masking and the Random-Line Masking conditions in the prime visibility test

**Discussion**

The purpose of this study was to investigate whether the origin of the negative compatibility effect (NCE) depends

directly on the type of mask. Two main theories have been proposed to explain the NCE. The motor inhibition theory considers that the NCE is caused by an inhibitory mechanism in the motor system, which suppresses the initial premature motor activation evoked by the prime (Eimer, 1999; Eimer & Schlaghecken, 2002, 2003; Jaśkowski, 2008; Jaśkowski et al., 2008; Jaśkowski & Przekoracka-Krawczyk, 2005; Jaśkowski & Verleger, 2007; Schlaghecken & Eimer, 2000, 2002). This theory holds that the origin of the NCE is purely motor and can be demonstrated when masks do not share perceptual features with their primes. Alternatively, the object-updating theory considers that the NCE is due to positive priming induced by the feature of the mask that was not present in the prime (Lleras & Enns, 2004; 2006). In other words, the negative compatibility effect is produced not by the inhibition of the primed response, but by positive priming of the opposite direction of the prime. Importantly, masks must share stimulus features with primes to observe object updating. If this is the case, then both perceptual and motor processes generate an NCE.

For metacontrast masking (i.e., with internal contours corresponding to left and right overlaid arrows), the rapid succession of the black arrow prime and the black mask is likely to create an updated white arrow: the empty area resulting from the superimposition of the prime and the mask. If object updating is the main source of the NCE for the metacontrast mask, the priming induced by the prime at the short Mask-Target SOA would be the reversal of the priming induced by the updated white arrow at long Mask-Target SOA, because the white updated arrow always points in the opposite direction of the prime (see Fig. 1). Importantly, the actual black arrow prime and the updated white arrow are both task-irrelevant arrows that can each induce (1) perceptual conflict when the processing of the irrelevant stimulus features interferes with the processing of the target stimulus features, and (2) motor conflict when the prepotent response elicited by the task-irrelevant stimulus interferes with the response to the task-relevant stimulus. Therefore, we expect to observe both perceptual and motor compatibility effects for short and long Mask-Target SOAs. Notably, these effects will be positive when the SOA is short because they are caused by the arrow prime, while these effects will be negative when the SOA is long because they are caused by the updated white arrow that points in the opposite direction than the prime arrow.

For random-line masks (i.e., pattern masks constructed by combining all the possible line orientations), the rapid succession of the prime and the mask is unlikely to create a new updated arrow given that the lines of the mask were randomly oriented. Based on the motor inhibition theory, we predict for the random-line mask that the black arrow—the prime—will always be the information that influences

target processing. The prime's influence on target processing will be the same for both types of masks (metacontrast and random line) at short Mask-Target SOAs. However, at the long SOAs for random line mask, an inhibitory mechanism will exert its influence on the motor representation of the prime, but not on the perceptual representation. Therefore, the irrelevant motor activation triggered by the prime will be selectively inhibited, resulting in a purely motor NCE. Under such inhibition, the *correct* response is inhibited on StimConflict trials (i.e., motor compatible trials), resulting in *slower* responses to the target, whereas the *incorrect* response is inhibited on RespConflict 90° trials (i.e., motor incompatible trials), which *facilitates* responses to the target.

To test these hypotheses, we manipulated the Mask-Target SOA (i.e., 0, 70, 140 and 200 ms) and we used a 4-stimuli 2-responses mapping that makes it possible to dissociate perceptual from motor compatibility effects. This design allows comparisons among four levels of conflict between the prime and the target (see Fig. 1a): Identical, StimConflict 90°, RespConflict 90° and RespConflict 180° trials. The perceptual compatibility effect without motor conflict was quantified by subtracting reaction times/error rates of the Identical trials from the reaction times/error rates of the StimConflict trials. The *motor compatibility effect* was assessed by subtracting the reaction times/error rates of the StimConflict trials from the reaction times/error rates of the RespConflict 90° trials. The perceptual compatibility effect with motor conflict was quantified by subtracting reaction times/error rates of the RespConflict 90° trials from the reaction times/error rates of the RespConflict 180° trials. Finally, the overall compatibility effect was quantified by subtracting reaction times/error rates of the Identical trials from the reaction times/error rates of the RespConflict 180° trials.

The pattern of results we observed at the short SOA of 0 ms was similar across both metacontrast and random-line masking conditions: reaction times increased gradually as a function of the degree of conflict. More specifically, we observed a positive perceptual compatibility effect when no additional motor conflict was present, that is, faster RTs for Identical trials than for StimConflict. The motor compatibility effect by itself was also positive and significant: RTs were faster for StimConflict 90° trials than for RespConflict 90°. These results replicate findings from previous studies that had separately examined perceptual and motor processing of masked primes (Kouider & Dehaene, 2009; Mattler, 2006; Naccache et al., 2002), and are very similar to studies that have separated perceptual and motor compatibility effects in the Eriksen flanker task (Eriksen & Eriksen, 1974; Nigbur, Cohen, Ridderinkhof, & Sturmer, 2012; Van Veen & Carter, 2002; van Veen, Cohen, Botvinick, Stenger, & Carter, 2001). Furthermore, we also

observed a significant perceptual influence of the prime even when an embedded motor conflict was also present: RTs were faster for RespConflict 90° trials than for RespConflict 180°. We thus extend previous results by showing that a positive perceptual influence of the masked prime can take place irrespective of whether an additional motor conflict is present or not.

Crucially, at the long SOAs of 140 and 200 ms, the patterns of results were qualitatively different between the two types of masks. For metacontrast masking, the two forms of perceptual effects and motor effect were all significantly negative. Thus, all the compatibility effects induced by the prime at the short SOA were reversed at the long SOAs. The observed results strongly suggest that object updating was the main source of the NCE for metacontrast masking: the perceptual and motor negative effects seem to correspond to positive effects elicited by the white arrow (i.e., the percept resulting from prime-mask interaction, see Fig. 1b). Indeed, the object-updating theory considers that the NCE would have both a perceptual and a motor origin just like the positive priming induced by the prime, because it is also positive priming from arrow information (Lleras & Enns, 2004, 2006). Moreover, our results reconcile the apparent contradictory results observed in the previous studies using fully relevant masks, and suggest that each of these results fits partially with the object-updating theory. Thus, Eimer (1999), Klapp and Hinkley (2002), and Schlaghecken and Eimer (2000) found a motor source for the NCE because their paradigm aimed at isolating the motor component, whereas Krüger, Klapötke and Mattler (2011) and Mattler (2006) demonstrated a perceptual source for the NCE because their paradigm was more adequate to isolate the perceptual component.

For random-line masking, however, only the motor effect was negative and significant at the long SOAs, whereas the two forms of perceptual effects were both null. Previous studies systematically found that the influence of the masked prime disappears when the delay between the offset of the prime and the onset of the target (i.e., the Mask-Target SOA) exceeds a few hundred milliseconds (Ferrand, 1996; Greenwald et al., 1996; Naccache et al., 2002). This can explain the fact that the perceptual effect vanishes when the Mask-Target SOA is increased. Interestingly, the absence of a perceptual effect co-occurring with a significant negative motor effect is predicted by the self-generated motor inhibition hypothesis proposed by Eimer and colleagues (Bowman, Schlaghecken, & Eimer, 2006; Eimer, 1999; Eimer & Schlaghecken, 1998, 2002, 2003; Schlaghecken & Eimer, 2000, 2002, 2004, 2006). Indeed, according to this hypothesis, the NCE reflects the operation of an inhibitory process through which the activated response elicited by the prime becomes automatically

inhibited if the perceptual evidence for its response is suddenly removed by the mask. While the self-generated motor inhibition hypothesis provides a plausible account of the NCE when the prime is strongly masked, it does not provide a convincing explanation of the origin of the NCE. Several studies have shown that the NCE occurs even if the primes were not effectively masked; suggesting that suppression of perceptual evidence by the mask is unlikely to be the cause of the NCE (Jaśkowski, 2008; Jaśkowski et al., 2008; Jaśkowski & Przekoracka-Krawczyk, 2005; Jaśkowski & Verleger, 2007). For instance, NCEs have been observed when random-line mask stimuli were presented after the prime but not in the same location, so that the prime was perfectly visible (e.g., Jaśkowski, 2008). According to the mask-triggered inhibition hypothesis proposed by Jaśkowski and colleagues, the motor activation elicited by the prime is not self-inhibited, but instead the presentation of the mask after the prime (i.e., each non-target stimulus presented after the prime, regardless of whether it effectively masks the prime or not) is the cause of the automatic inhibition. The authors assumed that when the participants were awaiting a target, the presence of the non-target stimulus (more often a mask) just after the prime might inform the system that the ongoing action was possibly premature and wrongly prepared. Note that Eimer and colleagues as well as Jaśkowski and colleagues agreed that the NCE is the result of a purely motor inhibition, which is presumably caused by the SMA (Boy et al., 2010a; Boy, Husain, Singh, & Sumner, 2010b; Sumner et al., 2007). According to this general view, a positive perceptual compatibility effect co-occurring with a negative motor compatibility effect might be observed at long Mask-Target SOAs when the prime is not sufficiently masked, because the perceptual trace would be preserved over time but would not be the focus of inhibition.

The fact that we did not observe a significant negative perceptual effect for random-line masks excludes the prime-mask interaction as being the main cause of the NCE. Indeed, the percept generated by the interaction of the prime and mask visual features should at least generate a (negative) perceptual influence on target processing if it was the main source of the behavioral effect. The pure negative motor effect we found with random-line masks is thus explained mainly by an automatic motor inhibitory mechanism. It is important to note that the random-line masks we used are not fully irrelevant regarding the features of the prime because they still contained oblique lines and arrow-like intersections. Lleras and Enns (2004, 2006) assumed that even with these types of masks, the object updating is a potential source of the NCE. However, our results suggest that the impact of object updating is heavily reduced with random-line masks; otherwise we would have obtained a significant negative perceptual effect. Our result

is also consistent with the study of Sumner (2008). The author examined whether the NCE observed with “fully irrelevant masks” was different from the NCE observed with more classical random-line masks, so-called “partially irrelevant masks”. He found that the NCE was not different between fully irrelevant and partially irrelevant mask, suggesting that object updating might not play a major role in NCE with random-line masks.

The correlational analyses provide additional support that CEs reflect the same processes across the two types of masks at short SOAs, but become qualitatively different at the long SOAs. Indeed, each specific sub-component of the compatibility effect (perceptual or motor) significantly correlated between the two types of masks at the short SOAs, but did not correlate at the long SOAs (see Fig. 4). The difference between the two correlations ( $r$  for short SOAs vs.  $r$  for long SOAs) was marginally significant for perceptual effects, and significant for motor effects (at least on the RT measure). These results thus suggest that (1) the perceptual compatibility effects reflect the same initial visual processing elicited by the prime across the two types of masks at short SOAs, but different processes (object updating vs. a decay of the perceptual trace) across the two types of masks at long SOAs, and (2) the motor compatibility effects reflect the same initial motor activation elicited by the prime across the two types of masks at short SOAs, but different processes (object updating vs. motor inhibition) across the two types of masks at long SOAs.

Finally, results of the visibility tests were quite different between the two types of masks (see Fig. 5). Indeed, for the metacontrast masking condition, the averaged performance between participants was near to 50 %, indicating chance level performance. However, individual performances indicated that three participants had a strong negative  $d'$ , which may suggest that they discriminated above chance level the white arrow resulting from the prime-mask interaction, and four other participants had a strong positive  $d'$ , which may suggest that they discriminated above chance level the black prime arrow. In contrast, for the random line masking condition, the averaged performance between participants was 61 %, indicating a visibility performance above chance level, and in favor of seeing a black arrow. Indeed, individual performances indicated that nine participants had a strong positive  $d'$ , suggesting that they discriminated above chance level the black prime arrow, and no participant had a strong negative  $d'$ .

Note that the visibility test with metacontrast masking in which some participants showed a negative  $d'$  has to be distinguished from free choice tasks in which participants showed a tendency to select a response that was opposite to the prime when they had to respond to targets requiring no specific response (Schlaghecken & Eimer, 2004;

Schlaghecken, Klapp, & Maylor, 2009). Indeed, these free choice tasks are influenced only indirectly by the masked prime and the effects observed are restricted to blocks in which free-choice neutral targets are intermixed with left-pointing and right-pointing arrow target with a specific Stimulus-Response mapping in the context of a priming task. When free-choice targets are blocked, the effect completely disappeared (Schlaghecken & Eimer, 2004). Thus, unconscious/implicit influences are likely to be the main source of these effects. In contrast, in our visibility test, the task was directly focused on the prime and the direction of the prime arrow did not correspond to the hand response to minimize the influence of automatic processing. Further research using a greater number of visibility trials and participants is necessary to confirm the between-subject variability in the visibility results for the metacontrast mask, and to determine why some participants might show a negative  $d'$  and the others a positive  $d'$  with this type of mask when no target is used.

For random-line masks, the prime discrimination performance was above chance, with 61 % of correct responses. This result is in line with studies showing a reliable NCE with random-line masks even when the primes are visible (e.g., Jaśkowski, 2008). In fact, although the role of prime visibility on automatic motor inhibition has been controversial for a decade (for a review, see Sumner, 2007), a recent study clarifies this issue by examining the relationship between priming and visibility both within and between participants (Boy & Sumner, 2014). The authors also used random-line masks with a constant Mask-Target SOA of 150 ms and showed that the compatibility effect correlated with prime visibility when factors influencing prime visibility (prime duration, prime brightness, mask brightness, mask density) were systematically manipulated within participants. However, importantly, no correlation between visibility and CE was found across participants. Consistent with our study, results of the within participants analysis showed an NCE when visibility performances were about 60 % or less, but a PCE when visibility performances were about 70 % or more.

## Conclusion

We showed that comparing four levels of conflict in a masked priming task was an efficient method to determine the cause of the NCE with different types of masks. With both metacontrast masks (relevant) and random-line masks (irrelevant), we found that positive perceptual effects co-occurred with positive motor effects at the short Mask-Target SOA. In contrast, at the long Mask-Target SOAs, the patterns of results were qualitatively different between the two types of masks. For metacontrast masking,

negative perceptual effects co-occur with a negative motor effect. Therefore, object updating is likely to be the main cause of the NCE observed with metacontrast masking. In contrast, for random-line masking, null perceptual effects co-occur with a negative motor effect at the long Mask-Target SOAs. This suggests that automatic motor inhibition was the main source of the NCE observed with random-line masks. Finally, the correlation analyses provide additional support that CEs were qualitatively different across the two types of masks at the long SOAs only. Taken together, the results of the present study demonstrate that the NCE origin is twofold and depends directly on the type of mask used.

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## References

- Atas, A., Vermeiren, A., & Cleeremans, A. (2013). Repeating a strongly masked stimulus increases priming and awareness. *Consciousness and Cognition*, 22(4), 1422–1430.
- Bowman, H., Schlaghecken, F., & Eimer, M. (2006). A neural network model of inhibitory processes in subliminal priming. *Visual Cognition*, 13(4), 401–480.
- Boy, F., Evans, C. J., Edden, R. A., Singh, K. D., Husain, M., & Sumner, P. (2010a). Individual differences in subconscious motor control predicted by GABA concentration in SMA. *Current Biology*, 20(19), 1779–1785.
- Boy, F., Husain, M., Singh, K. D., & Sumner, P. (2010b). Supplementary motor area activations in unconscious inhibition of voluntary action. *Experimental Brain Research*, 206(4), 441–448.
- Boy, F., Husain, M., & Sumner, P. (2010c). Unconscious inhibition separates two forms of cognitive control. *Proceedings of the National Academy of Sciences USA*, 107(24), 11134–11139.
- Boy, F., & Sumner, P. (2010). Tight coupling between positive and reversed priming in the masked prime paradigm. *Journal of Experimental Psychology: Human Perception and Performance*, 36(4), 892–905.
- Boy, F., & Sumner, P. (2014). Visibility predicts priming within but not between people: a cautionary tale for studies of cognitive individual differences. *Journal of Experimental Psychology: General*, 143(3), 1011–1025.
- Dehaene, S., & Changeux, J. P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, 70(2), 200–227.
- Dehaene, S., Naccache, L., Le Clec, H. G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., et al. (1998). Imaging unconscious semantic priming. *Nature*, 395(6702), 597–600.
- Eimer, M. (1999). Facilitatory and inhibitory effects of masked prime stimuli on motor activation and behavioural performance. *Acta Psychologica (Amsterdam)*, 101(2–3), 293–313.
- Eimer, M., & Schlaghecken, F. (1998). Effects of masked stimuli on motor activation: behavioral and electrophysiological evidence. *Journal of Experimental Psychology: Human Perception and Performance*, 24(6), 1737–1747.
- Eimer, M., & Schlaghecken, F. (2002). Links between conscious awareness and response inhibition: evidence from masked priming. *Psychonomic Bulletin & Review*, 9(3), 514–520.
- Eimer, M., & Schlaghecken, F. (2003). Response facilitation and inhibition in subliminal priming. *Biological Psychology*, 64(1–2), 7–26.
- Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception and Psychophysics*, 16, 143–149.
- Ferrand, L. (1996). The masked repetition priming effect dissipates when increasing the inter-stimulus interval: evidence from word naming. *Acta Psychologica*, 91(1), 15–25.
- Greenwald, A. G., Draine, S. C., & Abrams, R. L. (1996). Three cognitive markers of unconscious semantic activation. *Science*, 273(5282), 1699–1702.
- Jaśkowski, P. (2008). The negative compatibility effect with nonmasking flankers: a case for mask-triggered inhibition hypothesis. *Consciousness and Cognition*, 17(3), 765–777.
- Jaśkowski, P., Bialunska, A., Tomanek, M., & Verleger, R. (2008). Mask- and distractor-triggered inhibitory processes in the priming of motor responses: an EEG study. *Psychophysiology*, 45(1), 70–85.
- Jaśkowski, P., & Przekoracka-Krawczyk, A. (2005). On the role of mask structure in subliminal priming. *Acta Neurobiol Exp (Wars)*, 65(4), 409–417.
- Jaśkowski, P., & Verleger, R. (2007). What determines the direction of subliminal priming. *Advances in Cognitive Psychology*, 3(1–2), 181–192.
- Kim, C. Y., & Blake, R. (2005). Psychophysical magic: rendering the visible ‘invisible’. *Trends in Cognitive Sciences*, 9(8), 381–388.
- Klapp, S. T. (2005). Two versions of the negative compatibility effect: comment on Lleras and Enns (2004). *Journal of Experimental Psychology: General*, 134(3), 431–435.
- Klapp, S. T., & Hinkley, L. B. (2002). The negative compatibility effect: unconscious inhibition influences reaction time and response selection. *Journal of Experimental Psychology: General*, 131(2), 255–269.
- Klotz, W., & Neumann, O. (1999). Motor activation without conscious discrimination in metacontrast masking. *Journal of Experimental Psychology: Human Perception and Performance*, 25, 976–992.
- Kouider, S., & Dehaene, S. (2007). Levels of processing during non-conscious perception: a critical review of visual masking. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, 362(1481), 857–875.
- Kouider, S., & Dehaene, S. (2009). Subliminal number priming within and across the visual and auditory modalities. *Experimental Psychology*, 56(6), 418–433.
- Krüger, D., Klapötke, S., & Mattler, U. (2011). PRP-paradigm provides evidence for a perceptual origin of the negative compatibility effect. *Consciousness and Cognition*, 20(3), 866–881.
- Lingnau, A., & Vorberg, D. (2005). The time course of response inhibition in masked priming. *Perception and Psychophysics*, 67(3), 545–557.
- Lleras, A., & Enns, J. T. (2004). Negative compatibility or object updating? A cautionary tale of mask-dependent priming. *Journal of Experimental Psychology: General*, 133(4), 475–493.
- Lleras, A., & Enns, J. T. (2006). How much like a target can a mask be? Geometric, spatial, and temporal similarity in priming: a reply to Schlaghecken and Eimer (2006). *Journal of Experimental Psychology: General*, 135(3), 495–500.
- Mattler, U. (2006). On the locus of priming and inverse priming effects. *Perception and Psychophysics*, 68(6), 975–991.

- McBride, J., Boy, F., Husain, M., & Sumner, P. (2012). Automatic motor activation in the executive control of action. *Frontiers in Human Neuroscience*, *6*, 82.
- Naccache, L., Blandin, E., & Dehaene, S. (2002). Unconscious masked priming depends on temporal attention. *Psychological Science*, *13*(5), 416–424.
- Neumann, O., & Klotz, W. (1994). Motor responses to nonreportable, masked stimuli: Where is the limit of direct parameter specification? In C. Umiltà & M. Moscovitch (Eds.), *Attention and performance XV: Conscious and nonconscious information processing* (pp. 123–150). Cambridge: MIT Press.
- Nieuwenhuis, S., Forstmann, B. U., & Wagenmakers, E. J. (2011). Erroneous analyses of interactions in neuroscience: a problem of significance. *Nature Neuroscience*, *14*(9), 1105–1107.
- Nigbur, R., Cohen, M. X., Ridderinkhof, K. R., & Sturmer, B. (2012). Theta dynamics reveal domain-specific control over stimulus and response conflict. *Journal of Cognitive Neuroscience*, *24*(5), 1264–1274.
- Praamstra, P., & Seiss, E. (2005). The neurophysiology of response competition: motor cortex activation and inhibition following subliminal response priming. *Journal of Cognitive Neuroscience*, *17*(3), 483–493.
- Raghunathan, T. E., Rosenthal, R., & Rubin, D. B. (1996). Comparing correlated but nonoverlapping correlations. *Psychological Methods*, *1*, 178–183.
- Schlaghecken, F., & Eimer, M. (2000). A central-peripheral asymmetry in masked priming. *Perception and Psychophysics*, *62*(7), 1367–1382.
- Schlaghecken, F., & Eimer, M. (2002). Motor activation with and without inhibition: evidence for a threshold mechanism in motor control. *Perception and Psychophysics*, *64*(1), 148–162.
- Schlaghecken, F., & Eimer, M. (2004). Masked prime stimuli can bias “free” choices between response alternatives. *Psychonomic Bulletin & Review*, *11*(3), 463–468.
- Schlaghecken, F., & Eimer, M. (2006). Active masks and active inhibition: a comment on Lleras and Enns (2004) and on Verleger, Jaśkowski, Aydemir, van der Lubbe, and Groen (2004). *Journal of Experimental Psychology: General*, *135*(3), 484–494.
- Schlaghecken, F., Klapp, S. T., & Maylor, E. A. (2009). Either or neither, but not both: locating the effects of masked primes. *Proceedings in Biological Sciences*, *276*(1656), 515–521.
- Seiss, E., & Praamstra, P. (2004). The basal ganglia and inhibitory mechanisms in response selection: evidence from subliminal priming of motor responses in Parkinson’s disease. *Brain*, *127*(Pt 2), 330–339.
- Sumner, P. (2007). Negative and positive masked-priming: implications for motor inhibition. *Advances in Cognitive Psychology*, *3*, 317–326.
- Sumner, P. (2008). Mask-induced priming and the negative compatibility effect. *Experimental Psychology (formerly “Zeitschrift für Experimentelle Psychologie”)*, *55*(2), 133–141.
- Sumner, P., Nachev, P., Morris, P., Peters, A. M., Jackson, S. R., Kennard, C., et al. (2007). Human medial frontal cortex mediates unconscious inhibition of voluntary action. *Neuron*, *54*(5), 697–711.
- van Gaal, S., & Lamme, V. A. (2012). Unconscious high-level information processing: implication for neurobiological theories of consciousness. *Neuroscientist*, *18*(3), 287–301.
- Van Veen, V., & Carter, C. S. (2002). The timing of action-monitoring processes in the anterior cingulate cortex. *Journal of Cognitive Neuroscience*, *14*(4), 593–602.
- van Veen, V., Cohen, J. D., Botvinick, M. M., Stenger, V. A., & Carter, C. S. (2001). Anterior cingulate cortex, conflict monitoring, and levels of processing. *Neuroimage*, *14*(6), 1302–1308.
- Verleger, R., Jaśkowski, P., Aydemir, A., van der Lubbe, R. H. J., & Groen, M. (2004). Qualitative Differences Between Conscious and Nonconscious Processing? On Inverse Priming Induced by Masked Arrows. *Journal of Experimental Psychology: General*, *133*(4), 494–515.
- Vorberg, D., Mattler, U., Heinecke, A., Schmidt, T., & Schwarzbach, J. (2003). Different time courses for visual perception and action priming. *Proceedings of National Academic Science USA*, *100*(10), 6275–6280.