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Asymmetric influences of temporally vs. nasally presented masked visual information: Evidence for collicular contributions to nonconscious priming effects☆

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Abstract

It was tested whether the retino-collicular projection allows for the processing of nonconsciously registered visual information in healthy individuals. Masked primes were presented to different visual hemifields. Because the retino-collicular projection is stronger for temporal than for nasal hemifields, priming should be stronger by temporal than by nasal primes. This pattern was tested in two experiments (Experiments 1 and 3). Further, with less peripheral primes, only available to weaker parts of the retino-collicular projection, hemifield asymmetries of priming vanished (Experiment 2). In conclusion, the study offers first evidence for collicular contributions to nonconscious priming effects by visual information in healthy individuals.

Keywords: Direct parameter specification; Metacontrast; Nonconscious processing; Priming; Sensorimotor processing; Superior colliculus; Visuospatial attention

1. Introduction

Patients that are blind for information presented to parts of the visual field that are covered by a lesioned area in V1, are sometimes able to point to, or to saccade to objects presented in the blind field (Cowey & Stoerig, 1991; Perenin & Rossetti, 1996; Pöppel, Held, & Frost, 1973; Weiskrantz, 1986; Weiskrantz, Warrington, Sanders, & Marshall, 1974; Zihl, 1980). This condition, known as "*blindsight*", was ascribed to the processing of visual information presented to the blind field by the spared retino-collicular projection that feeds into cortical areas of the visual processing network via the thalamic nucleus pulvinaris (Dodds, Machado, Rafal, & Ro, 2002; Ptito, Johannsen, Faubert, & Gjedde, 1999; Weiskrantz, 1986, see Fig. 1). Several studies suggested that the processing of nonconsciously registered information by blindsight patients is not restricted to information about the position of objects in the blind field, but that information about the shape or the orientation of objects might be available via the retino-collicular projection, too (De Gelder, Vroomen, Pourtois, & Weiskrantz, 1999; Perenin & Rossetti, 1996). For example, De Gelder and colleagues found that blindsight patients were able to extract emotional content from facial expressions presented to their blind fields.

Nonconscious registration of visual information can also be observed in healthy individuals. For example, masked visual information has an influence on reaction times (RTs) and error rates (Ansorge, Heumann, & Scharlau, 2002; Damian, 2001; Dehaene et al., 1998; Eimer & Schlaghecken, 1998; Klotz & Neumann, 1999; Klotz & Wolff, 1995; Naccache & Dehaene, 2001a; Neumann & Klotz, 1994; Schmidt, 2001, 2002). If masked primes indicate the same response as the following target (*congruent condition*) responses are faster and error rates are lower than if masked primes indicate another response

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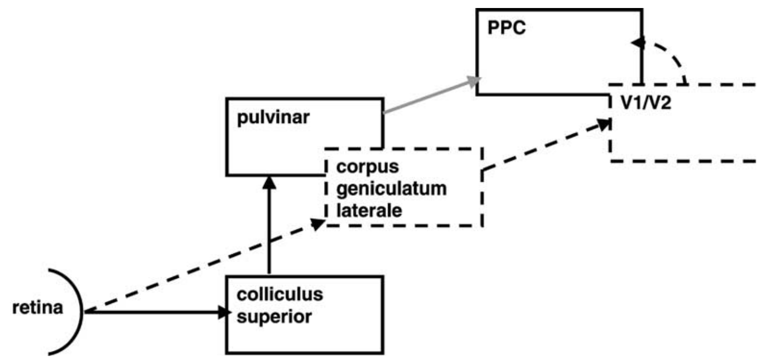

Fig. 1. Depicted are two possible projections from the retina to the cortex, the retino-collicular, and the retino-geniculate projection. (Structures underlying the retino-geniculate projection only, are indicated by broken lines of boxes and arrows.) The gray arrow between pulvinar and PPC indicates that the connection might be indirect (e.g., via V4). PPC, posterior parietal cortex; V1/V2, primary/secondary cortical visual area.

than the target (*incongruent condition*). Besides, the same differences (i.e., advantages for congruent, costs for incongruent conditions) are sometimes observed in comparison to *neutral conditions*, in which the primes do not indicate a response (e.g., Klotz & Wolff, 1995).

Whereas the masked primes have reliable effects in RT tasks, they are not discriminated (and even less perceived) as indicated by the performance in signal detection (SD) tasks. For example, using metacontrast (a form of visual backward masking where primes are spatially adjacent to masks, which follow at a short Stimulus Onset Asynchrony [SOA] of approximately 50–70 ms; e.g., Breitmeyer, 1984), participants often performed at chance level if asked to tell conditions with primes (congruent and incongruent conditions) from conditions without a prime (neutral condition) (e.g., Ansorge, Klotz, & Neumann, 1998; Klotz & Wolff, 1995; Klotz & Neumann, 1999; Neumann & Klotz, 1994). Therefore, the effect of masked primes has been ascribed to the processing of nonconsciously registered visual information in the RT task. This pattern of an effect of masked primes in an RT task, on the one hand, and the evident failure to discriminate the primes, on the other hand, was called the *metacontrast dissociation* (Neumann, Ansorge, & Klotz, 1998; Neumann & Klotz, 1994; Steglich & Neumann, 2000).

At least a part of the primes' effect is presumably due to the processing of masked visual information in the sensorimotor domain. Leuthold and Kopp (1998) demonstrated that incongruent, masked primes led to the temporary activation of the alternative response in the lateralized readiness potential of the EEG (see also Dehaene et al., 1998; Eimer & Schlaghecken, 1998). Moreover, nonconscious primes or cues influence RT via the orienting of attention (e.g., Jaśkowski, van der Lubbe, Schlotterbeck, & Verleger, 2002; Lambert, Naikar, McLachlan, & Aitken, 1999; Mattler, in press; McCormick, 1997). In situations where the position of the target is not known in advance, a peripheral prime or cue can be used to direct attention to one of the possible positions. With short SOAs between the cue and the target, a valid peripheral cue at the position of the target leads to an appropriate orienting of attention and to faster responses (facilitation), and an invalid peripheral cue at an alternative position leads to a deflection of attention away from the target and to slower responses (interference) (Jonides, 1981; Posner, 1980). This pattern can be obtained with masked primes or cues, too (Neumann, Esselmann, & Klotz, 1993; Scharlau, 2002; Scharlau & Neumann, in press; Steglich & Neumann, 2000).

The purpose of the present study was to test whether the RT effect of masked primes in metacontrast dissociation could have been brought about by the *retino-collicular projection* of the visual system in healthy individuals—the same structure that is presumably contributing to the nonconscious processing in blindsight patients (Weiskrantz et al., 1974). To this end, the RT effects of masked primes that were presented briefly in the periphery of the visual field were studied under monocular viewing conditions. In each block, one eye of the participant was patched. In these conditions, an RT effect of the masked prime that is brought about by the retino-collicular projection should be stronger for primes presented to the temporal visual hemifield than for primes presented to the nasal visual hemifield (Fig. 2), because the superior colliculi receive a stronger input from the temporal compared to the nasal hemifield (Dodds et al., 2002; Rafal, Henik, & Smith, 1991; Simion, Valenza, Umiltà, & Dalla Barba, 1995; Stein, 1982). In contrast, under the appropriate conditions, if nonconscious priming effects originate cortically no such temporal/nasal asymmetry should be observed (e.g., Paradiso & Carney, 1988). [1]

2. Experiment 1

It was tested whether the effect of masked primes on RT and error rates obtained by Neumann and Klotz

[1] At least for stimulus eccentricities <10–20° of visual angle, sensitivity is about the same for nasal and temporal, retinal and cortical hemifields (e.g., Paradiso & Carney, 1988).

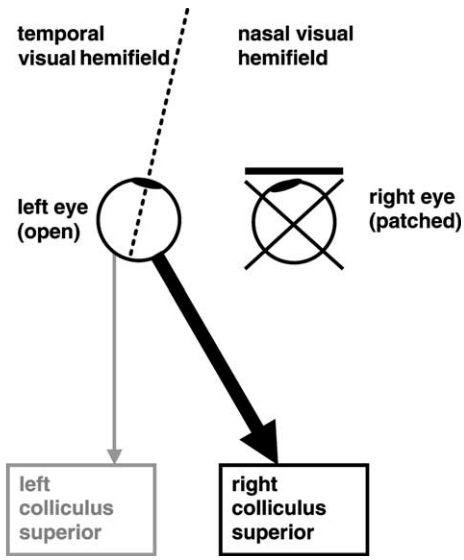

Fig. 2. Schematic picture of the anatomical basis of the experimental rationale (for the left eye). If one eye is patched (e.g., the right one), information presented briefly and peripherally to the temporal hemifield of the open eye (e.g., the left one) will be available to the stronger part of the retino-collicular projection (bold black arrow) than information presented briefly and peripherally to the nasal hemifield of the open eye. This weaker projection strength is indicated by the thin gray arrow.

(1994) might have been due to processing in a network that received input from the retino-collicular projection. Targets were presented either to the left or to the right of the center of the screen. In the RT task, spatially compatible responses to the position of the target were required. If the target was on the right a right response, and if the target was on the left a left response was to be given. Prior to the targets, masked primes were shown. In the congruent condition, primes appeared at the position of the target. In the incongruent condition, primes were presented on the opposite side of the target. Finally, in the neutral condition, no prime was shown. In the congruent condition, RT should be reduced compared to the incongruent condition.

As the participants had one eye patched, and fixated the center of the screen, the primes and the targets were either presented in the temporal or in the nasal part of the visual field. For example, with only the left eye open, a prime to the left was presented in the temporal field, and a prime to the right was presented in the nasal field. If the primes were processed via the retino-collicular projection, the RT effect should be stronger for primes presented temporally than for primes presented nasally.

2.1. Method

2.1.1. Participants

Sixteen students of Bielefeld University participated in Experiment 1. The participants had a mean age of 25.1 years. Here and in the following experiments, participants had normal or corrected-to-normal vision, and were paid for their participation.

2.1.2. Apparatus

The experiment was controlled by a PC. Stimuli were presented on a 15-in. color monitor. The responses were registered via a serial mouse. Latency was measured from the beginning of the target. The participants were seated in a dimly lit and sound-attenuated room, 65 cm in front of the screen with their line of gaze straight ahead.

2.1.3. Procedure

An example of the sequence in a trial is shown in Fig. 3. The stimuli were displayed bright (48 cd/m^2) on a dark background (<1 cd/m^2). To draw the attention of the participants to the center of the screen, squares were shown at the beginning of each trial in the corners of the screen that moved on diagonal trajectories towards the center where they merged and disappeared. This fixation aid took 800 ms. Immediately after the fixation aid, two precues (area: $0.5° \times 0.6°$ of visual angle) were shown at both possible positions of the target (5.7° to the right and to the left of the center) for 17 ms, followed by a blank interval of 17 ms. Next, two neutral cues (small rectangles $0.5°$ high $\times$ $0.12°$ long) at the two possible positions, and in congruent and incongruent conditions, a prime consisting of two small black bars (one above and one below the neutral cue) at one of the two positions were presented simultaneously for 17 ms. Finally, with an SOA between the prime and the target of 51 ms two black bars (3 pixels strong), one above, the other one below the position formerly occupied by the cue, were presented as a target in one of the positions, and masks (rectangles subtending $0.9° \times 0.9°$) were shown in both possible positions for 128 ms.

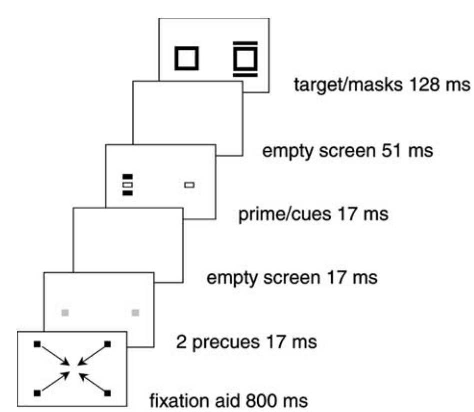

Fig. 3. The sequence of events in an example trial of Experiment 1. Depicted is an incongruent trial (starting from the bottom). The arrows in the lower frame indicate the direction of the motion of the squares.

Participants were told to keep their fixation at the center of the screen throughout the experiment. As the targets were presented unpredictably either to the left or to the right, keeping fixation at the center was a beneficial strategy. Moreover, as primes were presented for only 17 ms and the prime-target SOA was 68 ms, there was no time to saccade to one of the alternative positions after the prime and prior to the target. In the RT task, the participants had to give fast and accurate spatially compatible responses to the targets. They had to press the left mouse key with the left index finger if the target was on the left, and the right mouse key with the right index finger if the target was on the right. As the primes were smaller variants of the targets, the primes were apt to activate a response in the RT task (Leuthold & Kopp, 1998; Neumann & Klotz, 1994). In the SD task, participants had to decide whether or not a prime was presented. Half of the participants gave right hand responses if they saw (evidence for) the prime, and left hand responses if not, whereas this mapping was reversed for the other half of the participants. As the SOA between the primes and the masks was short and the outer contours of the prime fitted exactly into the inner contours of the mask, the primes were metacontrast masked by the masks (Breitmeyer, 1984; Breitmeyer & Ogmen, 2000). Prior to the SD task, the primes were shown in slow motion. The participants knew that primes were presented in half of all trials and were encouraged to guess whether a prime was presented if they did not perceive it during the SD task.

2.1.4. Design

All participants worked through two sessions on two different days. In session one, they received the RT task and in session two they received the SD task, in that order. In each session, the participants worked through two separate blocks. Either the right eye or the left eye was patched in the first block, whereas the other eye was patched in the second block. Which eye was patched first was balanced across participants. Half of the trials in each block was neutral, a quarter of the trials was congruent, and a quarter of the trials was incongruent. The four conditions with primes (2 positions of the target $\times$ 2 positions of the prime) were repeated 20 times per block. The two conditions without a prime were repeated 40 times per block. The sequence of the resulting 160 trials within each block was randomized. Together with approximately 40 trials practice prior to each block, and short rests between the blocks of one session, the whole experiment took about 90 min.

2.1.5. Analyses and predictions

Judgments with a latency of less than 100 ms and RTs with a latency of less than 100 ms and greater than 1000 ms were excluded. The performance in the SD blocks was evaluated by averaging individual indices of d' (Green & Swets, 1966). Values of mean d' close to zero indicate good masking. A d' of zero indicates chance discrimination performance. The individual median latencies of correct responses and the arc-sine transformed error rates from the RT blocks were subjected to separate repeated-measures ANOVAs with the factors of *hemifield* of the prime (temporal vs. nasal) and *priming* (congruent vs. incongruent).

It was expected that RT and error rates would be reduced in the congruent compared to the incongruent condition. Moreover, if primes presented in the temporal hemifield yield stronger effects than primes in the nasal hemifield, an interaction of hemifield and priming was expected, with stronger priming in the temporal than in the nasal-hemifield condition.

2.2. Results

2.2.1. RT task

In the RT task, 0.2% of the trials were discarded. The only significant factor in the RT analysis was priming, $F(1,15) = 244$, $p < .001$. RT was shorter in congruent (340 ms) than in incongruent (414 ms) conditions. Significant effects of priming, $F(1,15) = 60.24$, $p = .001$, and hemifield, $F(1,15) = 7.28$, $p < .05$, and most noteworthy, an interaction between these factors, $F(1,15) = 7.85$, $p < .05$, were obtained in the error analysis. Error rates were higher in incongruent (8.2%) than in congruent (0.2%), and in temporal (5.1%) compared to nasal conditions (3.3%). The interaction of priming and hemifield was produced by the increased error rate in the incongruent/temporal (10%) compared to the incongruent/nasal condition (6.4%, $t[15] = 3.076$, $p < .05$, Bonferroni-adjusted), whereas the corresponding difference for the congruent condition was not significant ($t[15] = 0.1$), see also Table 1. Note, that the resulting stronger priming effect in the temporal condition could not have been due to a speed-accuracy tradeoff, because RT tended to be higher in the incongruent/temporal than in the incongruent/nasal condition.

2.2.2. SD task

In the SD task, 0.9% of the trials were discarded. The primes were well masked as indicated by a low mean $d' = 0.09$ (individual values ranged from −0.15 to 0.304). None of the participants reported to have seen the primes. Although mean d' was significantly different from zero,

Table 1
RT in milliseconds and mean percent errors (in brackets) as a function of congruence/incongruence and hemifield in Experiment 1

Hemifield	Congruence/Incongruence		
	Congruent	Neutral	Incongruent
Temporal	340 (0.2)	375 (1.0)	418 (10.0)
Nasal	340 (0.2)	375 (1.2)	411 (6.4)

$t(15) = 2.74$, $p < .01$ (one-tailed test), indicating some residual capacity to discriminate primes, a regression of individual priming indices (100 × [incongruent RT − congruent RT]/congruent RT) as a function of individual d' scores (Greenwald, Draine, & Abrams, 1996; Naccache & Dehaene, 2001a) had a significant positive intercept with a priming index of 23.3 ($p < .001$) at $d' = 0$, whereas no significant correlation between priming and d' was revealed ($r = -.175$, $F[1, 14] = 0.441$).

2.3. Discussion

Masked visual primes had an effect on RT and error rates. A regression method suggested priming by non-consciously registered information. A substantial priming effect was present even at chance performance levels in the SD task (Greenwald et al., 1996; Naccache & Dehaene, 2001a, 2001b). Most importantly, the strength of the error effect of the primes depended on the hemifield to which the primes were presented. Incongruent primes in the temporal hemifield interfered stronger than incongruent primes in the nasal hemifield. This pattern is in line with an extrageniculate, retino-collicular contribution to the priming effect.

The strength of the retino-collicular projection decreases with decreasing retinal eccentricity (Perry & Cowey, 1984). Consequently, if the interaction between priming and hemifield was indeed due to processing in the retino-collicular projection, it should be diminished or even abolished if primes and targets are presented less peripherally. This prediction was tested in Experiment 2.

3. Experiment 2

Experiment 2 was a replication of Experiment 1 with one exception. The stimuli were presented less peripherally (3.7°) than in Experiment 1. This might lead to a diminution or an elimination of the interaction of priming and hemifield, if this interaction is due to processing in the retino-collicular projection.

3.1. Method

3.1.1. Participants

Twelve students of Bielefeld University with a mean age of 25.3 years participated.

Apparatus, procedure, and design were equal to Experiment 1 with the sole exception that stimuli were presented 3.7° to the left or to the right of fixation.

3.2. Results

3.2.1. RT task

In the RT task, 0.2% of the trials were discarded. In the analyses of RT and error rates only priming had a significant influence, RT: $F(1, 11) = 96.61$, $p < .001$, error rates: $F(1, 11) = 13.19$, $p < .01$. Responses were faster in congruent (353 ms) than in incongruent conditions (411 ms), and error rates were higher in incongruent (6.5%) than in congruent conditions (0.4%). The interaction of priming and hemifield was not significant in both analyses, RT: $F(1, 11) = 0.02$, error rates: $F(1, 11) = 1.97$, $p = .19$. RT was virtually identical in congruent/temporal and congruent/nasal on the one hand, and in incongruent/temporal and incongruent/nasal conditions on the other hand (see Table 2). Likewise, in the error rates, priming effects were not significantly different for the nasal and the temporal hemifields, respectively.

3.2.2. SD task

In the SD task, 1.3% of the trials were discarded. The primes were well masked as indicated by a mean $d' = 0.05$ (individual values ranged from −0.138 to 0.345), and mean d' was not significantly different from zero, $t(11) = 1.104$, $p = .15$ (one-tailed test). Again, no participant reported to have seen the primes, and a significant positive intercept with a priming index of 18.4 ($p < .001$) at $d' = 0$ for a regression of priming indices as a function of d' resulted, whereas no significant correlation between priming and d' was obtained ($r = -.334$, $F[1, 10] = 1.253$, $p = .29$).

3.3. Discussion

The masked primes produced a pronounced effect on RT and error rates. Yet, the size of the priming effect was not modified by whether the primes were presented to the temporal or to the nasal part of the visual field. This was expected because primes were presented less peripherally in Experiment 2, thereby reducing contributions of the retino-collicular projection to overall effects.

The question arises whether the temporal–nasal hemifield asymmetry obtained for the priming effect in Experiment 1 was due to attentional orienting (Zackon, Casson, Zafar, Stelmach, & Racette, 1999), or whether it could have been due to sensorimotor congruence/incongruence. In Experiment 1, *congruence/incongruence* (sensorimotor effects) and *validity* (effects of shifting attention) were confounded. Incongruent conditions were also invalid. Presenting the prime opposite to the

Table 2
RT in milliseconds and mean percent errors (in brackets) as a function of congruence/incongruence and hemifield in Experiment 2

Hemifield	Congruence/Incongruence		
	Congruent	Neutral	Incongruent
Temporal	355 (0.6)	378 (0.9)	413 (6.3)
Nasal	352 (0.2)	383 (0.3)	409 (6.7)

target did not only induce response conflict as the prime indicated an alternative response compared to the target, but also deflected attention away from the target. Likewise, congruent conditions were also valid. If the prime was at the position of the target, both prime and target indicated the same response, but an attention shift to the prime would have been to the position of the target, too. Therefore, it is not clear which of these processes was responsible for the priming effect. In Experiment 3, both congruent and incongruent primes were presented at the same position as the following target (Ansorge et al., 1998; Klotz & Wolff, 1995). Thereby, influences of validity and congruence were unconfounded.

4. Experiment 3

In each trial, either a square or a diamond was presented as the target at one of the alternative target positions (5.7° left or right of fixation). One of the targets (e.g., the square) required a right, the other one (e.g., the diamond) a left hand response. Prior to the target and at the target's position, a prime was presented which was masked by the target. In congruent conditions, the prime had the same shape as the target, indicating the same response (e.g., a square-shaped prime preceded a square-shaped target). In incongruent conditions, the prime had a different shape than the target, indicating a different response (e.g., a square-shaped prime preceded a diamond-shaped target). Finally, in neutral conditions a circular prime appeared prior to the target.

Again, RT should be shorter in congruent than in incongruent conditions. Moreover, as the stimuli were presented peripherally and the participants had always one eye patched, an interaction of hemifield (temporal vs. nasal) and priming was expected with stronger priming effects in the temporal condition, if processing in the retino-collicular projection contributes to sensorimotor congruence effects. However, if processing in the retino-collicular projection only mediates the orienting of attention, no interaction was expected because in Experiment 3 all conditions were valid (i.e., the prime was always at the position of the target).

4.1. Method

4.1.1. Participants

Sixteen students of Bielefeld University with a mean age of 27 years participated.

4.1.2. Apparatus, procedure, and design

In each trial, the target was either a square or a diamond. The prime was a small square or diamond (congruent and incongruent conditions), or a small circle (neutral condition), see also Fig. 4. The prime-target sequence appeared 5.7° to the right or to the left of the screen center. Targets had a side length of 1.6°, and the primes' outer contours fitted exactly into the inner contours of the targets. Squares and diamonds were presented as targets with equal probabilities. In the RT task, the participants either pressed the left mouse key with their left index finger in response to a square, and the right mouse key with their right index finger in response to a diamond, or vice versa (balanced across participants).

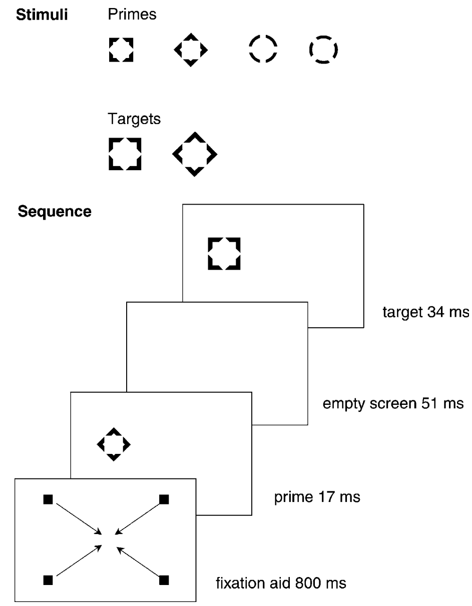

Fig. 4. The stimuli and the sequence of events in an example trial of Experiment 3. Depicted is an incongruent trial (starting from the bottom). The arrows in the lower frame indicate the direction of the motion of the squares.

A trial started with a fixation aid. Immediately afterwards a prime was presented for 17 ms. Next, the screen was blank for 51 ms, after which the target was presented at the prime's position for 34 ms. Congruent and incongruent conditions comprised half of the trials, and the other half were neutral trials.

The experiment consisted of two sessions. Like before, participants had to work through an RT session and an SD session, both consisting of two blocks, and had one of their eyes patched in each block, and changed the patched eye between blocks. In this and all other respects, Experiment 3 was similar to the previous experiments.

4.2. Results

4.2.1. RT task

In the RT task, 2.8% of the trials were discarded. In the analysis of RT, a significant main effect of priming, $F(1,15) = 11.99$, $p < .01$, and a significant interaction of priming and hemifield, $F(1,15) = 5.9$, $p < .05$, resulted. RT was shorter in congruent (492 ms) than in incongruent conditions (513 ms), and this priming effect (RT incongruent–RT congruent) was stronger for temporally (31 ms) than for nasally presented stimuli (12 ms, $t[15] = 2.43$, $p < .05$), see also Table 3. Only priming had a significant effect in the error analysis, $F(1, 15) = 11.23$, $p < .01$, with higher error rates in incongruent (8.3%) than in congruent conditions (5.7%).

4.2.2. SD task

In the SD task, 1.4% of the trials were discarded. The primes were well masked as indicated by a low mean $d' = 0.004$ (individual values ranged from -0.288 to 0.232), which was not significantly different from zero, $t[15] = 0.1$, $p = .42$ (one-tailed test). Besides, no participant reported to have seen the primes, and a significant positive intercept with a priming index of 5.7 ($p < .01$) at $d' = 0$ for a regression of priming indices as a function of d' resulted, whereas no significant correlation between priming effects and d' was obtained ($r = .05$, $F[1, 15] = 0.35$).

4.3. Discussion

A priming effect for nonconsciously registered (completely masked) primes resulted that was stronger for temporally than for nasally presented stimuli. As congruent and incongruent conditions were realized by presenting primes and targets at the same positions, the interaction of priming and hemifield was not due to shifts of attention. Rather, it seemed as if effects of sensorimotor congruence/incongruence of nonconsciously registered information depended on processing mediated via the retino-collicular projection.

5. General discussion

In the present study, a stronger effect of masked visual primes presented in the temporal hemifield was obtained. In Experiment 1, presenting masked primes laterally displaced by 5.7° produced a hemifield asymmetry of the priming effect, indicative of a collicular contribution to the priming effect. Presenting masked primes less peripherally in Experiment 2 abolished the hemifield asymmetry. As less peripheral information does not tap into the retino-collicular projection-asymmetry that much, this result substantiates the claim that hemifield differences of priming effects in Experiment 1 were mediated by retino-collicular processing. In Experiment 3, a stronger priming effect by primes presented to the temporal hemifield was found with primes and targets at the same location in each trial. Therefore, it seems as if processing in the retino-collicular projection mediates the effect of sensorimotor congruence/incongruence between prime and target, and that collicular contributions are not restricted to attention shifts.

Evidence suggests that not only gaze, but also arm movements are coded in the superior colliculi (e.g., Bell, Everling, & Munoz, 2000; Stuphorn, Bauswein, & Hoffmann, 2000), and such sensorimotor coding might have contributed to the priming effects of the nonconsciously registered visual primes. This does not mean that the priming effects in the current study depended on processing by the retino-collicular projection alone. For example, the superior colliculi are known to have strong reciprocal connections to the posterior parietal cortex (PPC), a structure presumably also involved in the processing of nonconscious visual information for action (Goodale & Milner, 1992; Milner & Goodale, 1995). Therefore, information from the superior colliculi might be directly transferred to PPC, and onwards, bypassing the processing in primary cortical visual areas. Evidence for the processing of nonconsciously registered, masked visual primes in PPC has been obtained just recently by functional magnetic resonance imaging (Naccache & Dehaene, 2001b). Alternatively, priming effects might have been due to top-down influences from higher brain centers such as the PPC on sensorimotor relay neurons in the colliculi.

Finally, as priming effects in Experiment 3 were due to the shapes of primes and targets, and participants seemed to be completely unaware of the primes as indicated by their chance performance in the SD task, the results of the current study substantiated the claim by others (e.g., De Gelder, Pourtois, van Raamsdonk, Vroomen, & Weiskrantz, 2001; Perenin & Rossetti, 1996) that nonconsciously registered visual information apart from stimulus position, namely information about the shape or the orientation of visual objects, can be extracted in processes that are mediated via the retino-collicular projection.

Table 3
RT in milliseconds and mean percent errors (in brackets) as a function of congruence/incongruence and hemifield in Experiment 3

Hemifield	Congruence/Incongruence		
	Congruent	Neutral	Incongruent
Temporal	487 (5.7)	499 (5.3)	518 (8.0)
Nasal	496 (5.6)	503 (5.6)	508 (8.5)

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