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Early visual processing allows for selective behavior, shifts of attention, and conscious visual experience in spite of masking

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ABSTRACT

Object-substitution masking (OSM) occurs when a briefly displayed target in a search array is surrounded by a mask, which remains onscreen after the target has disappeared. It has been suggested that OSM results from a specific interference with reentrant visual processing, while the initial feedforward processing is left intact. Here, we tested the prediction that the fastest saccadic responses towards a masked target, supposedly triggered before the onset of reentrant processing, are not impaired by OSM. Indeed, saccades faster than 350 ms “escaped” the influence of the mask. Notably, participants’ judgements of subjective awareness indicated that stimulus processing during this early stage is not entirely devoid of conscious awareness. Furthermore, the N2pc event-related potential component indicated shifts of spatial attention towards the masked targets on trials with correct fast saccades, suggesting that both target detection and spatial attention can be based on the computations accomplished during the initial feedforward sweep.

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1. Introduction

The perceptual and neural mechanisms necessary for visual awareness are greatly debated, but several theories assume that, among other mechanisms, reentrant processing plays a key role in the process (Dehaene & Changeux, 2011; Lamme, 2006; Overgaard & Mogensen, 2014; Tononi & Koch, 2015). Visual brain areas are heavily interconnected, and most of these connections are reciprocal. The term “reentrant processing” or “recurrent processing” refers to neural activity arising due to feedback from higher areas and lateral connections, allowing the integration of information from outside the neuron’s classical receptive field, reducing ambiguity and increasing tolerance to variability in low level features. The role of reentrant processing has been demonstrated by a number of physiological and psychophysical studies, which suggest that reentrant processing is crucial for figure-ground segmentation and contour integration (Bullier, 2001; Scholte, Jolij, & Lamme, 2006), as well as for selective attention (Macknik & Martinez-Conde, 2009). Several authors have proposed that reentrant processing is also crucial for visual awareness, implying that information processed during the feedforward sweep remains unconscious if

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reentrance is disrupted, e.g. by masking or TMS (Boehler, Schoenfeld, Heinze, & Hopf, 2008; Di Lollo, Enns, & Rensick, 2000; Lamme, 2006; Silvanto, Lavie, & Walsh, 2005).

In psychophysics, the interplay between feedforward and reentrant processing has been studied using visual masking (Bachmann, 2006; Breitmeyer & Ogmen, 2006). Specifically, object substitution masking (OSM), stands as particularly relevant to that aim. OSM occurs when a briefly presented target in a search array is surrounded by small dots that remain visible after the target disappears (Di Lollo et al., 2000). This delayed offset of the four-dot mask strongly reduces target visibility. Thus, unlike pattern masking or meta-contrast masking, the masking effect results from the delayed mask *offset* rather than its delayed *onset*. In fact, Francis and Cho (2007) have demonstrated that any delay between target and mask onset obliterates the masking effect and that models of backward masking do not account for this finding. Therefore, OSM is also referred to as “common onset masking”. Di Lollo et al. (2000) proposed that the representation of the target-plus-mask initially proceeds undisturbed through the feedforward sweep, and that OSM occurs when a mismatch arises between the reentrant signal representing target-plus-mask and the new incoming information at the lower level representing the mask alone. This mismatch results in the replacement of the target-plus-mask representation with the mask-alone representation. While it is still debated whether the performance impairment under OSM is due specifically to object substitution, authors agree that OSM affects some later processes beyond the initial feedforward signal (Di Lollo, 2014; Francis & Hermens, 2002; Goodhew, Pratt, Dux, & Ferber, 2013; Pöder, 2013). Thus, in contrast to other forms of backward masking, OSM has been claimed to selectively disrupt reentrant processing while leaving the initial feedforward sweep intact (Di Lollo et al., 2000; Enns, 2004).

Numerous studies have used OSM as a proxy for a selective disruption of reentrant processing. The reasoning is that if performance on a task is impaired by OSM, this task is assumed to require reentrant processing. By contrast, if performance is not impaired, it is assumed that this task is based on the unimpaired feedforward sweep (e.g. Bouvier & Treisman, 2010; Dux, Visser, Goodhew, & Lipp, 2010; Koivisto, 2012; Ro, Breitmeyer, Burton, Singhal, & Lane, 2003). For example, several studies have demonstrated that even when the target cannot be consciously identified under OSM, its low-level, unbound stimulus features can be detected (Bouvier & Treisman, 2010; Chen & Treisman, 2009) consistent with the notion that these processes do not require recurrent processing.

Recently, a number of event-related potentials (ERP) studies have investigated target processing under OSM by investigating the N2pc component of the ERP. The N2pc (N2-posterior-contralateral) is a negative-going deflection of the ERP at posterior channels contralateral to a relevant stimulus with an onset latency of approximately 200 ms, which indicates top-down selection of a stimulus according to its task-relevant properties (Eimer, 1996). For example, Woodman and Luck (2003) found that even though OSM reduced target visibility, the N2pc was not reduced by OSM and was equivalent on trials with correct and incorrect responses. Similar findings were reported in subsequent studies (Harris, Ku, & Woldorff, 2013; Prime, Pluchino, Eimer, Dell’Acqua, & Jolicœur, 2011; Woodman, 2010). Taken together, these findings confirm a central tenet of the object-substitution account by showing that early target processing is yet undisturbed by the mask and allows for target detection and a subsequent shift of attention (see Woodman & Luck, 2003). Thus, the perceptual impairment under OSM occurs only later when information transfer to higher-level processing is disrupted by the mask. However, given that the first feedforward sweep reaches occipito-temporal areas within the first 100 ms (Schmolesky et al., 1998) and given that the N2pc occurs only after 200 ms, “early processing” as indicated by an intact N2pc under OSM may not be identical with feed-forward activation in low-level sensory areas.

However, most demonstrations of intact task performance or differential electrophysiological effects would be equally consistent with the notion that OSM represents simply a weak form of perceptual impairment that affects all stages of stimulus processing, and that the residual information surviving this impairment is sufficient to perform certain rather simple tasks such as detecting simple visual features. This interpretation is supported by a large number of behavioral experiments (e.g. Overgaard, 2006; Overgaard, Feh, Mouridsen, Bergholt, & Cleeremans, 2008; Overgaard & Sandberg, 2012) and ERP experiments (Tagliabue, Mazzi, Bagattini, & Savazzi, 2016) showing that consciousness should not be conceived of as a dichotomous “either-or” but as a gradual phenomenon. Theoretically, the idea that the ability to solve tasks of different degrees of complexity relates to the degree of consciousness has been predicted by the REF-CON framework (see Overgaard & Mogensen, 2014).

The hypothesis that OSM is associated with an intact feedforward sweep, while later recurrent processing is disrupted, predicts a specific temporal pattern of task performance that cannot be explained by a weak perceptual impairment: the accuracy of behavioral responses under OSM should strongly depend on the time when these responses are initiated. Specifically, OSM should not affect the accuracy of particularly fast responses, which were already initiated during the first, intact feedforward sweep and before recurrent processing was disrupted by the mask. By contrast, if the response is delayed, e.g. because the target was not located rapidly enough in the search display, the mask may disrupt recurrent processing before a response is initiated. Thus, OSM should primarily impair the accuracy of slow responses, which were initiated after the mask had already disrupted recurrent processing. To test this hypothesis, we recently established a masking paradigm in which two critical items (one target and one lure) are embedded in a search array and surrounded by four-dot masks. Unlike previous OSM studies that emphasized response accuracy over speed, we asked observers to make a saccade as fast as possible towards the target item. We found that OSM and backward masking impaired performance predominantly for slower saccades, while the fastest saccades under masking were as accurate as comparably fast saccades without a mask. This sparing of the fastest saccades cannot be explained by a generic, time-independent performance impairment. Rather, it suggests that early processing stages, which may coincide with the early feedforward sweep, are not impaired by masking. By contrast, a

simple reduction of stimulus contrast yielded a comparable reduction of response accuracy but was independent of response speed, demonstrating that a general perceptual impairment affects all processing stages equally (Crouzet, Overgaard, & Busch, 2014).

In the present study, we extended the paradigm used by Crouzet et al. (2014) with three main aims. First, we sought to replicate our previous finding that speeded saccades can “escape” OSM (Crouzet et al., 2014). Second, we tested the claim that processing during early visual processing stages is unconscious. According to this claim, speeded saccades initiated during the early processing sweep should be associated with low subjective visibility, even when correct. Since Crouzet et al. (2014) only collected response time and accuracy data, we additionally collected ratings of subjective visibility in the present study. Third, we tested the hypothesis that shifts of spatial attention, indicated by the N2pc, can be elicited during early visual processing stages. This hypothesis predicts the presence of an N2pc under masking, specifically for trials with speeded saccades. Thus, we combined the behavioral paradigm used by Crouzet et al. (2014) with additional EEG recordings, allowing us to analyze saccadic response time distributions along with electrophysiological correlates of stimulus processing and attention.

2. Methods

2.1. Participants

A total of 23 participants were tested after giving signed informed consent. All participants reported to be free of neurological or psychiatric disorders and had normal or corrected-to-normal visual acuity. The experimental protocol was approved by the ethics committee of the German Psychological Society (DGPS). Three participants were excluded from all analyses due to insufficient quality of the EEG data or because saccades could not be determined reliably from their data. Four additional subjects were excluded due to chance performance, leaving a total of 16 participants for analysis (mean age: 24.6; SD 3.5 years; 6 women).

2.2. Stimuli and procedure

Observers sat in an electrically shielded, silent and dimly lit room at a viewing distance of 57 cm. To improve eye tracking accuracy, a chin-rest was employed to maintain a stable head position and restrict head movements. We presented stimuli on a gamma-linearized CRT monitor with 100 Hz refresh rate. Stimulus presentation was controlled using MATLAB R2010 (The Mathworks, Inc. Natick, USA, 2010) with the Psychophysics Toolbox 3 (Brainard, 1997).

The procedure combined a standard OSM paradigm with a 2AFC saccadic choice task (Crouzet, Kirchner, & Thorpe, 2010; Crouzet et al., 2014). Throughout the experiment, the background luminance was set to dark gray (32.1 cd/m²). Contrast was defined as $(\text{stimulus luminance} - \text{background luminance}) / \text{background luminance}$. A black fixation cross appeared in the center of the monitor for 800–1200 ms, followed by a blank screen lasting for 200 ms.¹ A search array was then flashed for one frame (10 ms), consisting of the display of 16 l, each covering $0.83^\circ \times 0.83^\circ$ of visual angle. The letters were shown in light gray; the exact contrast was determined by a staircase procedure (see below). The letters were placed at random locations in two 7×9 virtual arrays covering $9.96^\circ \times 11.62^\circ$ in each hemifield with the restriction that each hemifield always contained 8 stimuli. The minimum center-to-center offset between two letters was 1.1° . The offset between screen center and grid center was 7.43° . One of the 16 letters was designated the target (letter “O”); the other 15 letters were designated distractors (letter “X”). The target and a lure (one of the distractors in the opposite hemifield) were surrounded by a set of four white (contrast: 1.55) dots (0.21° each), centered on the imaginary corners of a $1.66^\circ \times 1.66^\circ$ square surrounding the letter. Target and lure positions were selected at random from the 8 stimuli in each hemifield. In addition to target, distractor and mask stimuli, two black saccade target markers were displayed concurrently at 14.48° to the left or right of fixation. Line thickness of letters, fixation cross, and saccade target markers was approximately 0.1° (see Fig. 1 for an illustration).

The following frames varied by condition: (i) a condition with common offset of the four dots and search array (no masking) or (ii) object-substitution masking (OSM), where the four dots remained on the screen for an additional 300 ms after the search array’s offset. Each trial was followed by a 1000 ms blank intertrial interval. The factors condition and target hemifield were counterbalanced across trials. The experiment consisted of 200 trials of each combination of condition and hemifield presented in pseudorandomized order (800 trials total).

Participants were instructed to fixate on the central fixation cross at the start of a trial. After stimulus presentation, they were to make a saccade as quickly and accurately as possible to the saccade target marker on the side containing the target item. No instructions for fixation or eye movements were provided for the subsequent report phase. Next, they indicated by a mouse click on which hemisphere the target was located (accuracy emphasized). Accuracy in this manual task served to compare the strength of the masking effect to previous studies, most of which used unspeeded manual responses, and as feedback for the adaptive staircase procedure (see below). Finally, they reported their experience of the target using the Per-

¹ This blank screen served to elicit the “gap effect”: reduced saccadic reaction times resulting from a brief blanking of the display before the onset of a saccade target (Fischer & Ramsperger, 1984).

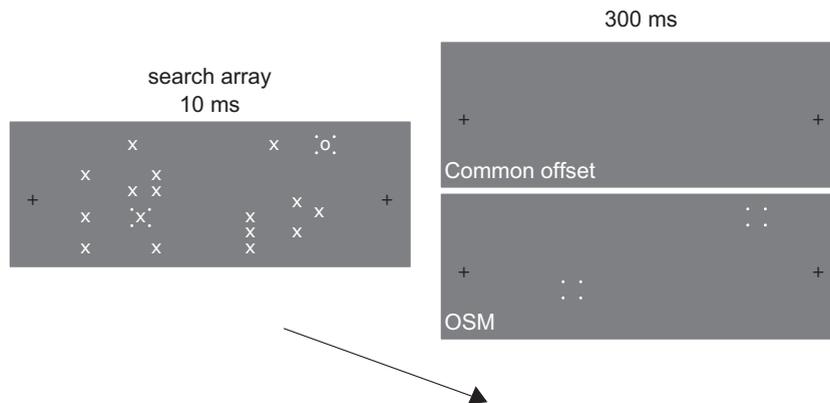


Fig. 1. Schematic illustration of the experimental paradigm. A search array containing 16 letters was presented for 10 ms. One lure stimulus (“x”) and a target stimulus (“o”) were surrounded by a four-dot mask. In the common offset condition, the search array was followed by a blank screen. In the OSM condition, the four-dot mask remained on the screen for another 300 ms. Observers made speeded saccades towards the location of the target and subsequently indicated the location of the target with a button press and rated their subjective awareness of the target.

ception Awareness Scale (PAS; Ramsøy & Overgaard, 2004; Sandberg & Overgaard, 2015). This scale describes the subjective visual experience using four levels:

1. “No experience”: No impression of the stimulus. All answers are experienced as mere guesses.
2. “A weak experience”: A feeling that something has been shown; not characterized by any content and cannot be specified any further.
3. “An almost clear experience”: Ambiguous experience of the stimulus. Some stimulus aspects are experienced more vividly than others and are accompanied by a feeling of being almost certain about one’s answer.
4. “A clear experience”: Non-ambiguous experience of the stimulus. No doubt in one’s answer.

To ensure that the task was challenging, but not too difficult, and to reduce the variability between subjects, we used an adaptive staircase procedure (QUEST; Watson & Pelli, 1983) to control the contrast of target, lure, and distractor stimuli throughout the experiment. Based on the accuracy of participants’ manual responses in the common offset condition, the staircase estimated each participant’s contrast threshold and “recommended” on each trial a contrast value that would most likely yield a performance of 82% in the common offset condition. Notably, while this estimate was only based on performance in common offset trials, the same contrast recommendations were applied on OSM trials.

2.3. EEG acquisition, preprocessing, and analysis

EEG was recorded using a Biosemi Active Two system (Biosemi, Amsterdam, the Netherlands) with 64 active electrodes arranged according to the extended 10–20 system. Additional electrodes were placed at the two mastoids. Furthermore, the electro-oculogram (EOG) was recorded with electrodes above and below the right eye as well as lateral to the left and right outer canthus. The recording was referenced to the CMS-DRL ground, a feedback loop that keeps the montage potential close to amplifier zero (<http://www.biosemi.com>). Signals were sampled at 2048 Hz.

After recording, signals were downsampled to 512 Hz, converted to an average reference, and epoched from –2000 to 2000 ms time-locked to stimulus onset. After removing large artifacts such as electrode drifts and muscle activity, independent component analysis (ICA) was applied to the unaveraged raw data to correct the scalp channels (but not the EOG channels) for eye blinks and eye movements using the EEGLAB toolbox for Matlab and the extended infomax ICA algorithm (Delorme & Makeig, 2004). Raw data were baseline-corrected according to the 200 ms-interval preceding stimulus onset.

Event-related potentials (ERP) were analyzed with a specific focus on the N2pc component, i.e. a difference between ipsilateral and contralateral channels relative to the position of the target stimulus. The N2pc, averaged across the time interval from 200–320 ms at lateral posterior channels (Left: P3, P5, P7, P9, PO3, PO7; Right: P4, P6, P8, P10, PO4, PO8), was analyzed with repeated measures analyses of variance (ANOVA), using the Greenhouse-Geisser correction for non-sphericity where appropriate. We report the uncorrected degrees of freedom along with the corrected *p*-values. Two-tailed *t*-tests were computed as post hoc tests to investigate significant interaction effects.

2.4. Analysis of behavioral data

2.4.1. Saccade detection

Saccadic Response Times (SRT) were measured using the horizontal EOG signal, which was derived from the left and right EOG electrodes. To detect accurately the onset time and direction of the first saccade after stimulus presentation, we used a

standard eye-tracking method based on position (here: potential in μV) and velocity (derivative of position) thresholds. We used a two-pass analysis to adjust the position and velocity threshold independently for each subject based on their own data. In the first-pass, position and velocity distributions were obtained from all the EOG data points of a given participant. These distributions were multimodal, with a main peak corresponding to fixation times. The position threshold of each participant was then defined as the value corresponding to the start of the second distribution peak among position values, and the velocity threshold was defined to exclude the higher 5% velocity values. Once the thresholds were derived from the data, a saccade was defined as a period of time where both the position and velocity thresholds were passed. Since eye movement recordings using EOG are spatially less precise than infra-red eyetracking devices, no spatial criterion (e.g. saccade landing in the target area, minimum visual angle) were used. The saccadic reaction time (SRT) was defined as the onset of the saccade. Only SRT below 600 ms were considered in the analysis (no further outlier removal was performed). Trials for which no saccade onset could be determined were excluded from further analysis. After rejecting trials without clear saccade onset and trials with strong EEG artifacts (see above), an average of 352 common onset trials and 332 OSM trials per subject were included in the analysis. This data-driven EOG saccade detection method gave results that were similar to a standard manual procedure (as used in Crouzet et al., 2010) with the advantage of being fast and reproducible. The MATLAB function implementing the saccade detection procedure is available for download at <https://gist.github.com/scrouzet/5170257>.

2.4.2. Analysis of saccadic response times and accuracy

The relationship between SRT and accuracy was analyzed with an exponentially weighted moving average (EWMA; Milosavljevic, Madsen, Koch, & Rangel, 2011; Roberts, 1959). We performed this analysis for each subject separately and additionally with all trials of all subjects pooled together to achieve stronger statistical power (Fig. 3A). Accuracy data were rank ordered according to each trial's SRT from fastest to slowest and the EWMA was computed as follows:

$$EWMA_i = \lambda X_i + (1 - \lambda)EWMA_{i-1}$$

where X_i denotes the accuracy (correct = 1; incorrect = 0) of the i th ordered trial and the parameter λ determines how much weight is given to faster SRT in the moving average. When $\lambda = 1$, the EWMA for a given trial represents the accuracy of only that trial. For $\lambda < 1$, previous trials (i.e. trials with faster SRT) are given more weight. Thus, the EWMA provides an estimate of how accuracy changes as a function of response speed. Intuitively, we expect that accuracy should be at chance for unreasonably fast responses (e.g. SRT < 100 ms) and should gradually increase with increasing SRT, as subjects take more time to process the stimulus and prepare their response. Above-chance performance is determined by comparing the EWMA to a confidence interval given by:

$$CI_i = \mu \pm N\sigma \sqrt{\frac{\lambda}{2-\lambda} (1 - (1-\lambda)^{2i})}$$

where μ represents chance performance under the null hypothesis ($p_{\text{correct}} = 0.5$), σ represents the standard deviation of X under the null hypothesis (0.5), and N is the width of the confidence interval in units of σ . We chose $N = 3$ and $\lambda = 0.01$ for analysis of single subjects and $\lambda = 0.0005$ for the analysis of all pooled trials (to account for the larger number of trials). Since above-chance performance is indicated by $EWMA_i > CI_i$, we defined minimal SRT (minSRT) as the fastest SRT exceeding this limit.

The central objective of our study was to test the hypothesis that masking effects are dependent on the time at which a behavioral response is initiated, such that particularly fast responses can “escape” the masking effect. The relevant null hypothesis states that masking impairs performance, but does so uniformly over time. Thus, we compared the EWMA of accuracy under OSM to a surrogate EWMA, which was constructed to represent this null hypothesis.

We first determined the total number of trials obtained under OSM (NT_{OSM}) and common offset (NT_{comoff}) as well as the number of correct trials under OSM (NC_{OSM}) and common offset (NC_{comoff}), using the data pooled from all subjects. Note that data of each trial include an SRT and accuracy (0 or 1). The surrogate data consisted of the trials from the common offset condition plus a number of “synthetic trials”—trials with an overall accuracy of 0.5 (i.e. chance performance) and a uniform distribution of response times ranging from the fastest to the slowest measured SRT. The number of synthetic correct and incorrect trials N_{synth} was determined as:

$$N_{\text{synth}} = \frac{NT_{\text{OSM}} * NC_{\text{comoff}} - NC_{\text{OSM}} * NT_{\text{comoff}}}{2 * NC_{\text{OSM}} - NT_{\text{OSM}}}$$

For example, imagine subjects performed correctly on 60 out of 100 ($p_{\text{correct}} = 0.6$) OSM trials and 80 out of 100 ($p_{\text{correct}} = 0.8$) common offset trials. The surrogate data would comprise the trials from the common offset condition plus $N_{\text{synth}} = 100$ correct and the same number of incorrect trials, and each of these trials would be assigned a random SRT. Consequently, the surrogate data would comprise 180 “correct” out of a total of 300 trials ($p_{\text{correct}} = 0.6$). Thus, mean accuracy of the surrogate data exactly matched the measured accuracy under OSM. In other words, adding synthetic trials with overall chance performance mimicked the effect of object substitution masking on overall accuracy. Importantly, since the random SRT assigned to these synthetic trials were uniformly distributed across time, the surrogate data accurately represented the null hypothesis that OSM equally affects performance independent of response time. In the final step, the EWMA was computed for the surrogate data in the same way as for the observed data.

To test whether the EWMA of observed performance under OSM exceeded the performance expected under the null hypothesis, we repeated the construction of surrogate data by computing the surrogate's EWMA for 1,000 times, each time using a new random draw of SRT from the uniform distribution. This procedure yielded a distribution of EWMA expected under the null hypothesis (blue band in Fig. 3A). Performance observed under OSM was considered significantly better than expected under the null hypothesis if the observed EWMA exceeded the 95-percentile of the surrogate distribution.

Furthermore, accuracy data were analyzed with two-tailed *t*-tests or, where appropriate, with repeated measures analyses of variance (ANOVA), using the Greenhouse–Geisser correction for non-sphericity for ANOVA including factors with more than two levels. We report the uncorrected degrees of freedom along with the corrected *p*-values.

3. Results

3.1. Behavioral results

3.1.1. Accuracy and awareness ratings

Accuracy of manual responses was at .85 ($SD = .05$) in the common offset condition, indicating that the staircase successfully adjusted the stimulus contrast for this condition. At the end of the experiment, stimulus contrast was set to 0.78 on average ($SD = 0.19$). As expected, accuracy in the OSM condition using the same contrast was significantly lower at .62 ($SD = .07$; $t(15) = 15.46$; $p < .001$).

Saccades were accurately directed towards the target side (rather than towards the lure in the opposite hemifield) in 79% of trials in the common offset condition and in 60% of trials in the OSM condition (Fig. 2A). Thus, the delayed mask offset under OSM significantly reduced the accuracy of saccades relative to common offset ($t(15) = 12.24$; $p < .001$).

The frequencies of awareness ratings were analyzed using a 2×4 ANOVA with factors *condition* (common offset vs. masked) and *awareness* (awareness levels 1–4). For both conditions, participants used the lower awareness categories more often (*awareness*: $F(3, 45) = 10.12$; $p < .001$). Moreover, participants reported their awareness as lower under OSM. Thus, OSM trials received ratings of 1 (“no visual experience”) more often and ratings of 3 (“almost clear”) and 4 (“clear experience”) less often than common offset trials (*condition* \times *awareness*: $F(3, 45) = 27.70$; $p < .001$; Fig. 2B).

The proportions of correct saccadic responses were analyzed using a 2×4 ANOVA with factors *condition* (common offset vs. masked) and *awareness* (awareness levels 1–4). Accuracy was higher on trials with high awareness ratings in both conditions (*awareness*: $F(3, 45) = 37.21$; $p < .001$; Fig. 2C). The ANOVA also confirmed that accuracy was superior in the common offset condition (*condition*: $F(1, 15) = 23.79$; $p < .001$). No *awareness* \times *condition* interaction was found ($F < 1$). This association between subjective awareness and objective accuracy suggests that in general, the perceptual processes resulting in accurate saccadic responses also support the vividness of the subjective experience.

Saccadic response times We tested whether accuracy of saccadic responses under OSM depended on the time when these responses were initiated. Saccadic response times (SRT) were analyzed based on an exponentially weighted moving average (EWMA) which represents how accuracy evolved as a function of SRT.

When trials from all subjects were pooled, the fastest SRT at which accuracy was significantly above chance was observed at 145 ms for common offset and 174 ms under OSM. Estimates for subjects' individual SRT were delayed due to the smaller number of trials per subject, resulting in smaller statistical power compared to the pooled data: 256 ms for common offset and at 274 ms under OSM ($t(15) = -1.58$; $p = .13$). Accuracy for SRT faster than approximately 200 ms was virtually indistinguishable between conditions. In the common offset condition, performance improved further as SRT increased and reached a plateau at approximately 400 ms. This pattern reflects the simple fact that without masking, performance benefits from holding the response while information about the stimulus is accumulated (Ratcliff & McKoon, 2008). By contrast, performance under OSM improved much less with increasing SRT and leveled off very quickly after approximately 300 ms (Fig. 3A).

While reduced accuracy under OSM compared to common offset is expected, the crucial question is whether the performance impairment due to masking depended on the latency of a response. In other words, did masking spare particularly fast saccades? To answer this question statistically, we compared the EWMA observed under OSM to a distribution of surrogate EWMA (gray band in Fig. 3A). These surrogate data represent the null hypothesis of a response time-independent performance impairment due to OSM (see Methods). In the interval between 172 and 348 ms, saccadic responses were significantly more accurate than predicted by the surrogate data. In other words, the fastest responses under OSM showed no sign of a masking-induced impairment, while the detrimental effect of masking was observed only at longer latencies.

We then tested how saccade speed affected perceptual awareness under common offset and OSM. For each condition (common offset, OSM) separately, we computed how often each of the four PAS levels was reported on fast and on slow trials, relative to the number of trials in each condition. These data were then analyzed using a *speed* (faster vs. slower than 348 ms) \times *condition* (common offset, OSM) \times *awareness* (awareness ratings 1–4) ANOVA (Fig. 3B). Overall, slow saccades were more frequent than fast saccades (*speed*: $F(1, 15) = 5.77$; $p = .030$), low awareness ratings were more frequent than high awareness ratings (*awareness*: $F(3, 45) = 9.98$; $p < .001$), particularly under OSM (*awareness* \times *condition*: $F(3, 45) = 27.48$; $p < .001$). These results confirmed the findings of the previous analysis, which did not take speed into account (see Fig. 2). Importantly, we found a *speed* \times *awareness* \times *condition* interaction ($F(3, 45) = 3.62$; $p = .020$). Follow-up ANOVAs showed that

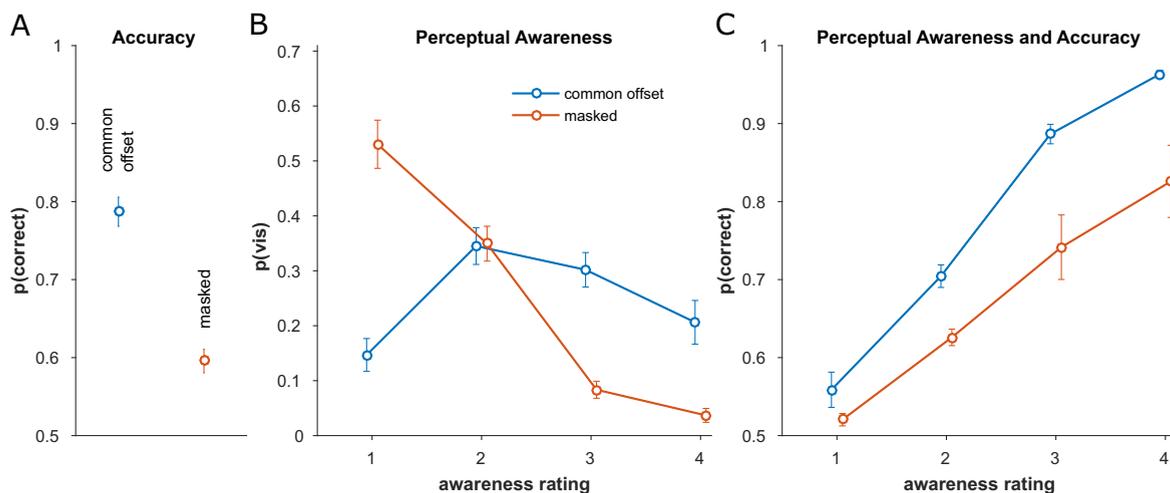


Fig. 2. (A) proportion of correct saccadic responses for common offset and OSM trials. All error bars represent standard error of the mean. Masking reduced accuracy by approximately 20%. (B) proportion of trials on which participants reported each of the four levels of the perceptual awareness scale. OSM strongly reduced participants' subjective awareness of the target stimulus. (C) proportion of correct responses increased with increasing awareness rating in both conditions.

under OSM, subjects rated awareness as lower when saccades were slow compared to fast saccades ($F(3,45) = 3.21$; $p = .032$). No such interaction was found for common offset ($F(3,45) = 1.72$; $p = .18$).

The EWMA analysis showed that fast responses under masking had a chance to “escape” the effect of the mask. Were subjects aware of targets on those trials? Our analysis described above showed that overall, awareness is rated as higher when responses were correct. Does this association between awareness and accuracy exist even for fast saccades under OSM? To answer this question, we computed for each condition (common offset, OSM) how often each of the four PAS levels was reported on correct and on incorrect trials, relative to the number of correct and incorrect trials in each condition. These data were then analyzed using a *correctness* (correct vs. incorrect) \times *condition* (common offset, OSM) \times *awareness* (awareness ratings 1–4) ANOVA, using only trials with fast saccades (Fig. 3C). As before, a main effect of *awareness* indicated that low awareness reports were more frequent than high reports ($F(3,45) = 14.76$; $p < .001$), especially under OSM (*awareness* \times *condition*: $F(3,45) = 24.14$; $p < .001$). In both conditions, awareness was reported as higher in correct trials (*correctness* \times *awareness*: $F(3,45) = 12.44$; $p < .001$), especially for common offset trials (*correctness* \times *awareness* \times *condition*: $F(3,45) = 3.65$; $p = .014$). Importantly, when fast OSM trials were tested alone, a *correctness* \times *awareness* interaction indicated that participants' were subjectively aware of target stimuli when they made fast correct responses ($F(3,45) = 8.46$; $p < .001$).

3.2. EEG results

The response to display onsets was lateralized such that ERPs were more negative-going at contralateral than at ipsilateral posterior channels (see topography in Fig. 4B). A pronounced lateralization in the time interval between 200 and 300 ms resembled the N2pc component as previously reported in the literature (Fig. 4A). The magnitude of this N2pc was strongly dependent on the targets' subjective visibility.

To quantify this impression statistically, we conducted a repeated measures ANOVA with factors *hemisphere* (ipsilateral vs. contralateral) \times *condition* (common offset vs. OSM) \times *awareness* (no experience, weak, clear). Visibility ratings of 3 (“almost clear”) and 4 (“clear experience”) were combined in this analysis because participants rarely gave ratings of 4, especially under OSM (less than 10 trials on average). A main effect of *hemisphere* confirmed the presence of an N2pc ($F(1,15) = 11.00$; $p = .005$). However, a *hemisphere* \times *awareness* interaction ($F(2,30) = 10.36$; $p < .001$) indicated that lower awareness was associated with a smaller N2pc. In fact, follow-up ANOVAs did not find any significant N2pc, i.e. a main effect of *hemisphere*, for awareness level 1 ($F(1,15) = 1.92$; $p = .18$) or awareness level 2 ($F(1,15) = 1.29$; $p = .27$). Only awareness level 3&4 yielded a significant N2pc ($F(1,15) = 13.00$; $p = .003$).

To analyze how the N2pc covaried with saccade speed, we conducted ANOVAs with factors *hemisphere* \times *condition* \times *speed* (faster vs. slower than 348 ms) separately for correct and incorrect trials (Fig. 5). The early time window corresponds to the brief time range during which saccadic responses under OSM were significantly more accurate than predicted by the surrogate data (see behavioral analysis above), indicating that performance under OSM is not yet impaired by the mask in this time range.

For correct trials, a main effect of *hemisphere* confirmed the presence of an N2pc ($F(1,15) = 10.41$; $p = .006$). Furthermore, the N2pc was stronger on trials with fast saccades (*hemifield* \times *speed*: $F(1,15) = 13.11$; $p = .003$). We conducted post hoc *t*-tests to analyze this interaction further. For correct common offset trials, an N2pc was found both for fast saccades ($t(15)$

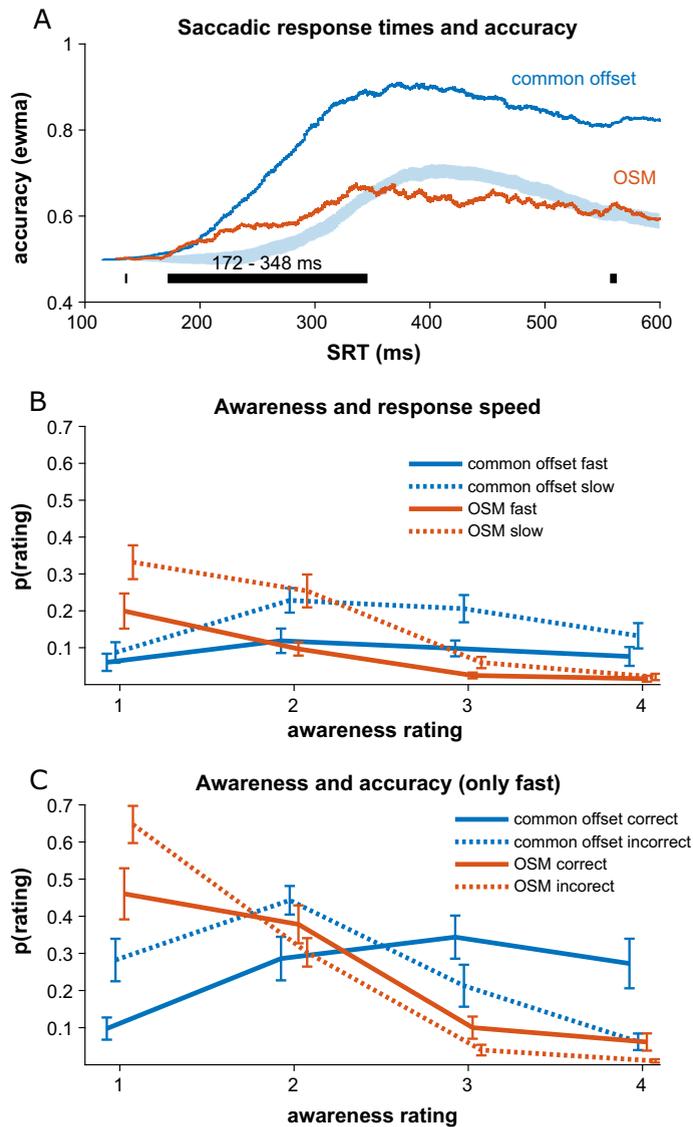


Fig. 3. (A) relationship between saccadic response time (SRT) and accuracy according to an exponentially weighted moving average (EWMA) computed on data pooled across all observers. Accuracy at a given time point corresponds to the proportion of correct responses among all SRT at least as fast as this value. The gray band indicates a confidence band computed according to the null hypothesis under object substitution masking (OSM), performance is impaired uniformly across time, i.e. independent of response speed. Note that the fastest saccades under OSM were as accurate as similarly fast saccades under common offset. Furthermore, faster saccades under OSM were significantly more accurate than predicted by the null hypothesis in the time range from 172 to 348 ms (black bar). (B) relationship between saccade speed and perceptual awareness. For each condition (common offset, OSM) separately, we computed how often each of the four PAS levels was reported on fast and on slow trials, relative to the number of trials in each condition. For common offset, high awareness ratings are more frequent for slow responses. By contrast, for OSM low awareness ratings are associated with slow responses. (C) proportion of trials on which participants reported each of the four levels of the perceptual awareness scale separately for correct and incorrect trials. Only trials with fast saccades are shown. Error bars represent standard error of the mean. Subjective awareness depends strongly on response accuracy, even for fast masked trials.

= 3.42; $p = .004$) and for slow saccades ($t(15) = 2.47$; $p = .026$). By contrast, OSM trials showed an N2pc only for fast saccades ($t(15) = 2.578$; $p = .021$), but not for slow saccades ($t(15) < 1$).

For incorrect trials, a weak main effect of hemisphere indicated the presence of an N2pc ($F(1, 15) = 4.83$; $p = .044$). Inspection of the ERP waveforms (Fig. 5) showed that this lateralization effect was actually due to a reversed N2pc: ERPs were more negative-going at ipsilateral than at contralateral channels. However, when each condition was tested separately, post hoc t -tests did not find a significant N2pc in incorrect fast common offset trials ($t(15) = -1.60$; $p = .13$), incorrect slow common offset ($t(15) = -1.25$; $p = .23$), incorrect fast OSM ($t(15) < 1$), or incorrect slow OSM trials ($t(15) < 1$). No additional interaction with *condition* or *speed* was found.

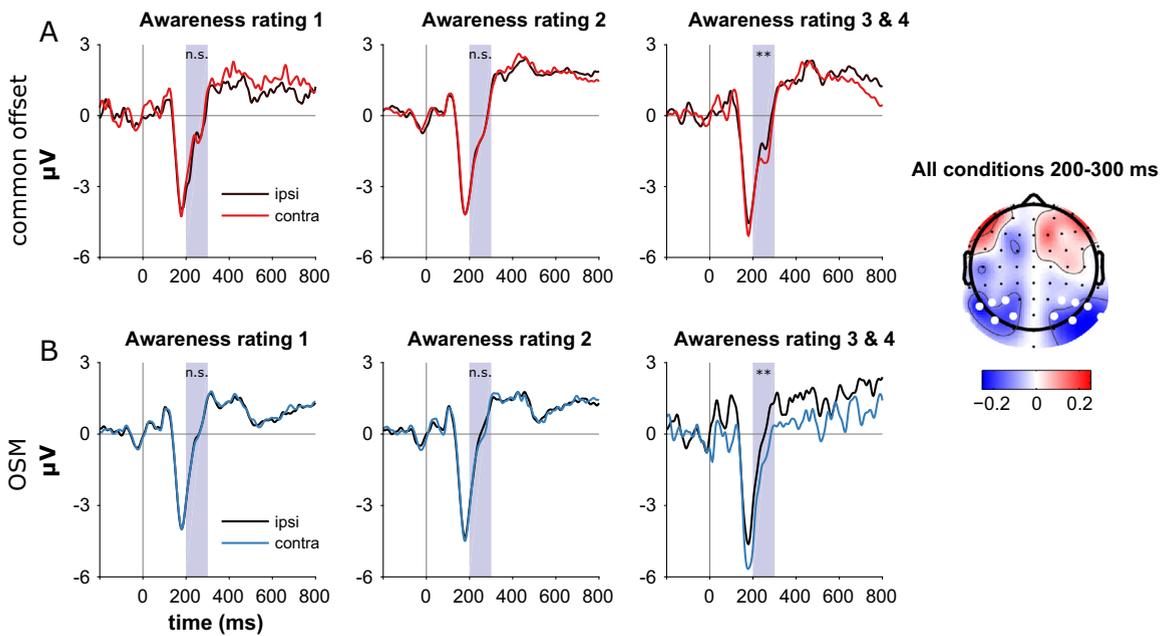


Fig. 4. A: grand-averaged ERPs time-locked to target onset at a group of lateral posterior channels (white electrode markers in B), shown separately for common offset (top) and OSM (bottom) trials and for different levels of perceptual awareness ratings. Ratings of 3 and 4 were combined due to the low number of trials for these categories. Differences between ipsilateral and contralateral channels from 200 to 320 ms (gray-shaded time range) on trials with high awareness ratings reflect an N2pc component. B: topography of the grand-averaged ERP, combined across all conditions, in the time range from 200 to 320 ms. Each channel shows the voltage difference between trials on which this channel is ipsilateral - contralateral relative to the target's location.

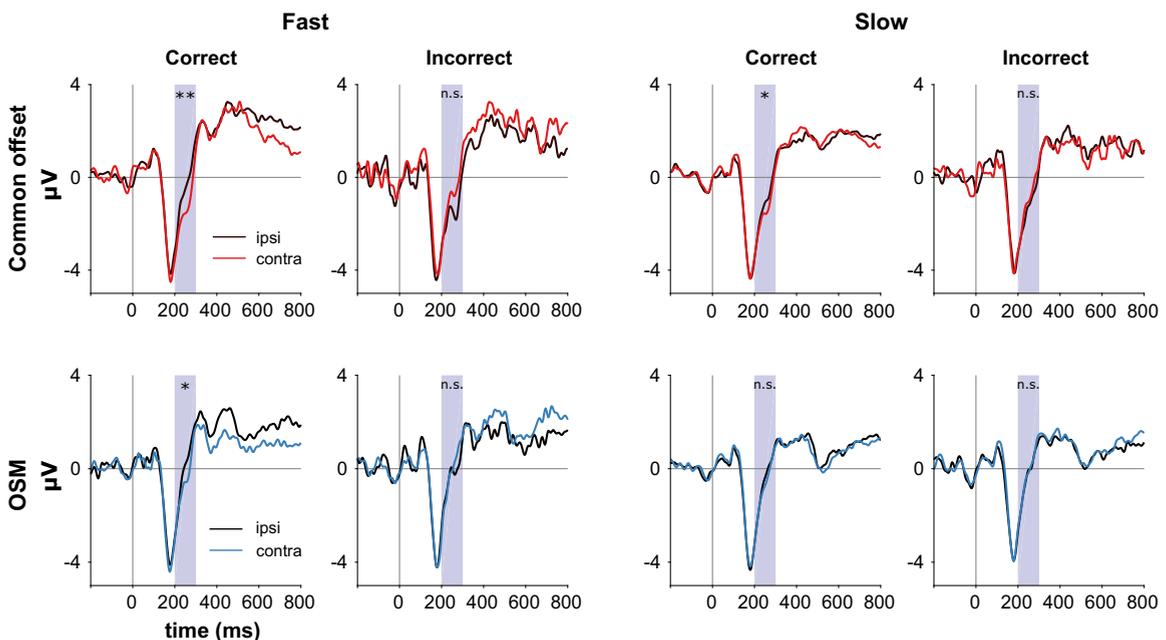


Fig. 5. Grand-averaged ERPs shown separately for common offset (top) and OSM (bottom) trials. Additionally, panels show ERPs separately for trials with fast and slow responses (i.e. saccades faster/slower 348 ms) and with correct and incorrect responses. N2pc was observed for all correct common offset trials and only for fast correct OSM trials.

4. Discussion

Numerous studies have demonstrated that various forms of masking cause an impairment of visual performance and have studied how mask properties (e.g. spatial arrangement or timing) affect this impairment (see Goodhew et al., 2013,

for a review). By contrast, much less is known about how the masking effect develops over time. In this study, we tested the hypothesis that object substitution masking (OSM) does not interfere with early visual processing, which may coincide with the initial feedforward sweep, thereby allowing for target detection and shifts of spatial attention, but interferes during a later processing stage, presumably during reentrant processing.

Observers were to detect target stimuli masked by a four-dot common-onset mask (Di Lollo et al., 2000) and to make a saccade as fast as possible to the target's location (Crouzet et al., 2014). As expected, OSM impaired performance in the saccadic choice task (Fig. 2A) and reduced objective performance and subjective awareness (Fig. 2B and C) compared to a common offset condition (no masking). To analyze how this impairment develops over time, we compared the response time distribution obtained under OSM to a surrogate condition, which represents the null hypothesis that the OSM-induced performance impairment is independent of response time. We found that the accuracy of fast saccades under OSM (RT < 348 ms) was less impaired by the mask than the accuracy of slower saccades (Fig. 3A), replicating the results of Crouzet et al. (2014). This finding indicates that OSM does not affect the accuracy of responses that are initiated during the first, intact feedforward sweep, before recurrent processing gets disrupted by the mask. However, OSM does impair the accuracy of slow responses, presumably because target information is no longer available once recurrent processing is disrupted by the mask. Note that this finding does not imply that the early processing stages responsible for fast correct saccades under OSM actually last up to 348 ms since this latency also includes the time necessary for saccade planning and execution.

Several authors have proposed that processing during the early feedforward sweep is not accessible to consciousness, such that stimuli remain unconscious if their processing is disrupted during later reentrant processing, e.g. by masking (Di Lollo et al., 2000; Lamme, 2006). In the context of the present study, an important question is whether stimuli that were successfully processed during early processing stages (as indicated by a correct fast saccade under OSM) are accessible to awareness. We addressed this question by comparing trials with fast correct responses to fast incorrect responses. If the information that triggered fast correct responses had remained unconscious, participants should be equally (un) aware on correct and incorrect trials. However, we found that awareness was reported as higher on fast correct trials than on fast incorrect trial, indicating that participants were well aware of the stimulus if they were correct (Fig. 3C). This finding is consistent with a study by Koivisto (2012) who demonstrated that confidence ratings discriminated between correct rejections on target-absent trials and misses on target-present trials, indicating that some sense of object-presence survived the disruption of the mask. He concluded that elementary conscious perception can be reached in purely feedforward manner. Together, these findings indicate that stimulus information computed during these early processing stages is not principally devoid of consciousness, as some authors have proposed (Lamme, 2006). As previously mentioned, this seemingly conflicting result could be a consequence of less sensitive measures of consciousness in previous experiments. As expected by other theoretical frameworks, different degrees of visual consciousness may relate to different neural correlates (Andersen, Pedersen, Sandberg, & Overgaard, 2015; Overgaard & Mogensen, 2014; Overgaard & Mogensen, 2015).

A number of studies have investigated neural signatures of target processing under object substitution masking by analyzing the N2pc component of the ERP (Harris et al., 2013; Prime et al., 2011; Woodman, 2010; Woodman & Luck, 2003). The N2pc is thought to reflect the attentional selection of a task-relevant visual stimulus following an attentional shift to the stimulus' location (Busch, Dürschmid, & Herrmann, 2010a; Busch, Fründ, & Herrmann, 2010b; Eimer, 1996). These studies demonstrated that object substitution-masked targets elicited an N2pc and thus a shift of spatial attention towards the target, even when the target could not be accurately reported. Woodman and Luck (2003) have interpreted this finding as showing that the shift of attention indicated by the N2pc is triggered during the initial feedforward sweep, before the mask interferes with the representation of the target stimulus. However, Woodman and Luck (2003) and subsequent studies of the N2pc under OSM had participants report target presence (Prime et al., 2011; Woodman & Luck, 2003) or identity (Harris et al., 2013) using delayed manual responses. Without access to informative response times, it is difficult to tell at what time and during which processing stage information about the target stimulus was present and when it was disrupted by the mask. Thus, the question remains whether the N2pc can be triggered during the initial feedforward processing stage. To address this question, we tested how the N2pc was related to response speed. As described above, we found that for OSM trials with fast saccades (SRT < 348 ms) performance was less impaired by the mask than for slower trials. Thus, fast responses may serve as a proxy for trials in which stimulus information was represented in an early processing sweep, and we tested if an N2pc was present on those trials. Indeed, we found an N2pc for correct OSM trials *only* for fast, but not for slow responses (Fig. 5), indicating that if target detection or response programming are delayed until after the mask has disrupted information about the target, an attentional shift towards the target is no longer possible. The N2pc on correct common offset trials was independent of response speed, indicating that without a mask, target information remains available for attentional shifts for a longer time. In contrast to previous studies, we found no significant N2pc on incorrect trials, except for a weak "N2pc" with reversed polarity (i.e. more negative ERP at ipsilateral channels). In fact, the magnitude of the N2pc across conditions was strongly dependent on participants' subjective awareness of the target, such that no N2pc was found when participants reported "no experience" or "weak glimpse" (Fig. 4). One important implication of this finding is that in our version of the OSM paradigm, the N2pc indeed reflects processing of the target stimulus. Had the N2pc reflected processes associated with saccade preparation or execution instead, every condition should have shown an N2pc, but the polarity should have been directly tied to the direction of the saccade (see Wauschkuhn et al., 1998, for a similar conclusion). The tight association between the N2pc and awareness and correctness does not necessarily indicate that allocation of attention at the target location was a requirement for target detection. In fact, the present study and previous studies on the N2pc

under OSM (Harris et al., 2013; Prime et al., 2011; Woodman, 2010; Woodman & Luck, 2003) used relatively salient target shapes that occurred nowhere else in the display. It is likely that performance in this task was primarily limited by the brief stimulus duration and by crowding, rather than the requirement for sequential shifts of attention from item to item until the target is found. This assumption is supported by recent studies demonstrating effective OSM even for single, attended targets (Filmer, Mattingley, & Dux, 2015), suggesting that the role of distractors for OSM is not to delay allocation of attention, but to crowd the target item (Camp, Pilling, Argyropoulos, & Gellatly, 2015). Thus, in this paradigm, the attentional shift indicated by the N2pc is most likely the *effect* of target detection rather than its cause or requirement.

Two characteristics of the present study might explain why the N2pc was so strongly dependent on accuracy and awareness here, but not in previous studies. First, target duration was much shorter (10 ms) than in most previous studies (83 ms in Prime et al., 2011; Woodman, 2010; Woodman & Luck, 2003). This might have increased the effectiveness of masking. In fact, Harris et al. (2013) used a brief target duration of 17 ms and found a significant, but strongly diminished N2pc on incorrect OSM trials. Moreover, in a detection task without an emphasis on response speed, trials can yield an incorrect response if (1) the target was detected during early processing stages, but the target representation was subsequently disrupted by the mask; (2) the target was detected, but participants decided they were not confident enough to report it; or (3) the target was never detected in the first place due to the high perceptual and attentional load of the task. It is conceivable that trials of type 1 and 2 have contributed to the significant N2pc effect for incorrect masked trials in previous studies. In contrast, by emphasizing response speed in the present study, trials of type 1 had a higher chance to yield a correct response. Additionally, by using a forced choice localization task, incorrect trials did not include type 2 trials because the decision does not depend on a response criterion. Thus, incorrect OSM trials in our study included mostly trials of type 3 without any target detection, and thus without any shift of attention that would elicit an N2pc.

In sum, we show that saccades faster than 348 ms can escape the influence of object substitution masking, while slower saccades were associated with reduced accuracy and reduced subjective awareness. Moreover, we found neural correlates of attentional shifts towards the masked targets, but only on fast trials. Correct performance on fast masked trials was associated with increased ratings of subjective awareness, indicating that stimulus representations established in this early phase is accessible to awareness. These early processing stages, which allow for target detection and selective shifts of attention, may coincide with the initial feedforward sweep. Thus, the findings support theories of object substitution masking, which assume that the delayed offset of the mask interferes with later visual processing while leaving early processing largely intact (Di Lollo et al., 2000; Francis & Cho, 2007).

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