

Perceptual versus attentional impairments of conscious access: Distinct neural mechanisms despite equal task performance

Reviewed Preprint

v2 • February 25, 2025

Revised by authors

Reviewed Preprint

v1 • July 8, 2024

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eLife Assessment

This **important** study provides new insights into the mechanisms that underlie perceptual and attentional impairments of conscious access. The paper presents **convincing** evidence of a dissociation between the early stages of low-level perception, which are impermeable to perceptual or attentional impairments, and subsequent stages of visual integration which are susceptible to perceptual impairment but resilient to attentional manipulations. This study will be of interest to scientists working on visual perception and consciousness.

<https://doi.org/10.7554/eLife.97900.2.sa4>

Abstract

This study investigates failures in conscious access resulting from either weak sensory input (perceptual impairments) or unattended input (attentional impairments). Participants viewed a Kanizsa stimulus with or without an illusory triangle within a rapid serial visual presentation of distractor stimuli. We designed a novel Kanizsa stimulus that contained additional ancillary features of different complexity (local contrast and collinearity) that were independently manipulated. Perceptual performance on the Kanizsa stimulus (presence vs. absence of an illusion) was equated between the perceptual (masking) and attentional (attentional blink) manipulation to circumvent common confounds related to conditional differences in task performance. We trained and tested classifiers on electroencephalogram (EEG) data to reflect the processing of specific stimulus features, with increasing levels of complexity. We show that late stages of processing (~200-250 ms), reflecting the integration of complex stimulus features (collinearity, illusory triangle), were impaired by masking but spared by the attentional blink. In contrast, decoding of local contrast (the spatial arrangement of stimulus features) was observed early in time (~80 ms) and was left largely unaffected by either manipulation. These results replicate previous work showing that feedforward processing is largely preserved under both perceptual and attentional impairments. Crucially however, under matched levels of performance, only attentional

impairments left the processing of more complex visual features relatively intact, likely related to spared lateral and local feedback processes during inattention. These findings reveal distinct neural mechanisms associated with perceptual and attentional impairments and thus contribute to a comprehensive understanding of distinct neural stages leading to conscious access.

Introduction

Conscious access to sensory input can be impaired in two distinct ways (Dehaene et al., 2006 [↗](#); Lamme, 2010 [↗](#); Mashour et al., 2020 [↗](#); Northoff & Lamme, 2020 [↗](#)). Sensory input may lack sufficient bottom-up strength, or top-down attention may be directed elsewhere. Despite both cases resulting in a failure to perceive a stimulus, their underlying neural mechanisms are thought to be remarkably different. Influential theories of consciousness such as global neuronal workspace and recurrent processing theory propose four stages of neural information processing associated with distinct levels of bottom-up signal strength and top-down attention. These four stages can be investigated empirically by crossing “perceptual” manipulations that degrade the strength of sensory input (e.g., reducing stimulus contrast, masking, continuous flash suppression) with “attentional” manipulations that affect top-down attention (e.g., attentional blink, inattention blindness, **Fig. 1A** [↗](#)).

According to these theoretical models, all stimuli elicit feedforward information transfer from lower- to higher-level brain regions (**Fig. 1A** [↗](#), bottom row), but recurrent interactions are initiated only for stimuli with sufficient bottom-up strength (**Fig. 1A** [↗](#), top row). If stimuli are sufficiently strong and top-down attention is available, neural processing crosses a threshold, triggering a process termed global ignition, facilitating widespread recurrent interactions between frontal, parietal and sensory cortices, yielding conscious access (**Fig. 1A** [↗](#), top left). Crucially, when top-down attention is lacking, frontoparietal network ignition is prevented, while local recurrent interactions within sensory brain regions remain relatively intact (“attentional blindness”, **Fig. 1A** [↗](#), top right) (Dehaene et al., 2003 [↗](#); Marti et al., 2015 [↗](#); Sergent et al., 2005 [↗](#); Zivony & Lamy, 2022 [↗](#)). Weak stimuli result in the absence, or a substantial reduction, of local recurrent interactions (“perceptual blindness”, **Fig. 1A** [↗](#), bottom left) (Fahrenfort et al., 2007 [↗](#); Joglekar et al., 2018 [↗](#); van Gaal et al., 2008 [↗](#); van Vugt et al., 2018 [↗](#)).

Although this framework is at the heart of influential theories of consciousness, the four stages of the model and their underlying neural mechanisms have rarely been investigated simultaneously within the same study (for an exception see Fahrenfort et al., 2017 [↗](#)). One challenge with comparing results across different studies, or even within a study, is that perceptual manipulations tend to impair overall task performance more than attentional manipulations, so that it may not be surprising to find that perceptual manipulations interrupt recurrent interactions to a greater extent than attentional manipulations. Given the right parameter settings, perceptual manipulations can be used to induce chance-level performance, while it is not possible to use attentional manipulations to drive behavioral performance down to chance, even when they are optimized fully. For this reason, attentional manipulations are often combined with post-hoc selection of a subset of “blind” trials (e.g., attentional blink [AB]) or subjects (e.g., inattention blindness) based on subjective awareness reports, a methodologically questionable practice that is susceptible to criterion confounds and introduces sampling bias that leads to underestimation of consciousness (Fahrenfort et al., 2024 [↗](#); Peters & Lau, 2016 [↗](#); T. Schmidt, 2015 [↗](#); Shanks, 2017 [↗](#)).

Thus, when comparing perceptual to attentional manipulations, any (neural) effect could reflect differences in task performance rather than genuine differences between manipulations and hence stages in the model depicted in **Figure 1A** [↗](#). While these issues with comparing conditions that differ in task performance in consciousness research have been acknowledged (Lau, 2022 [↗](#)),

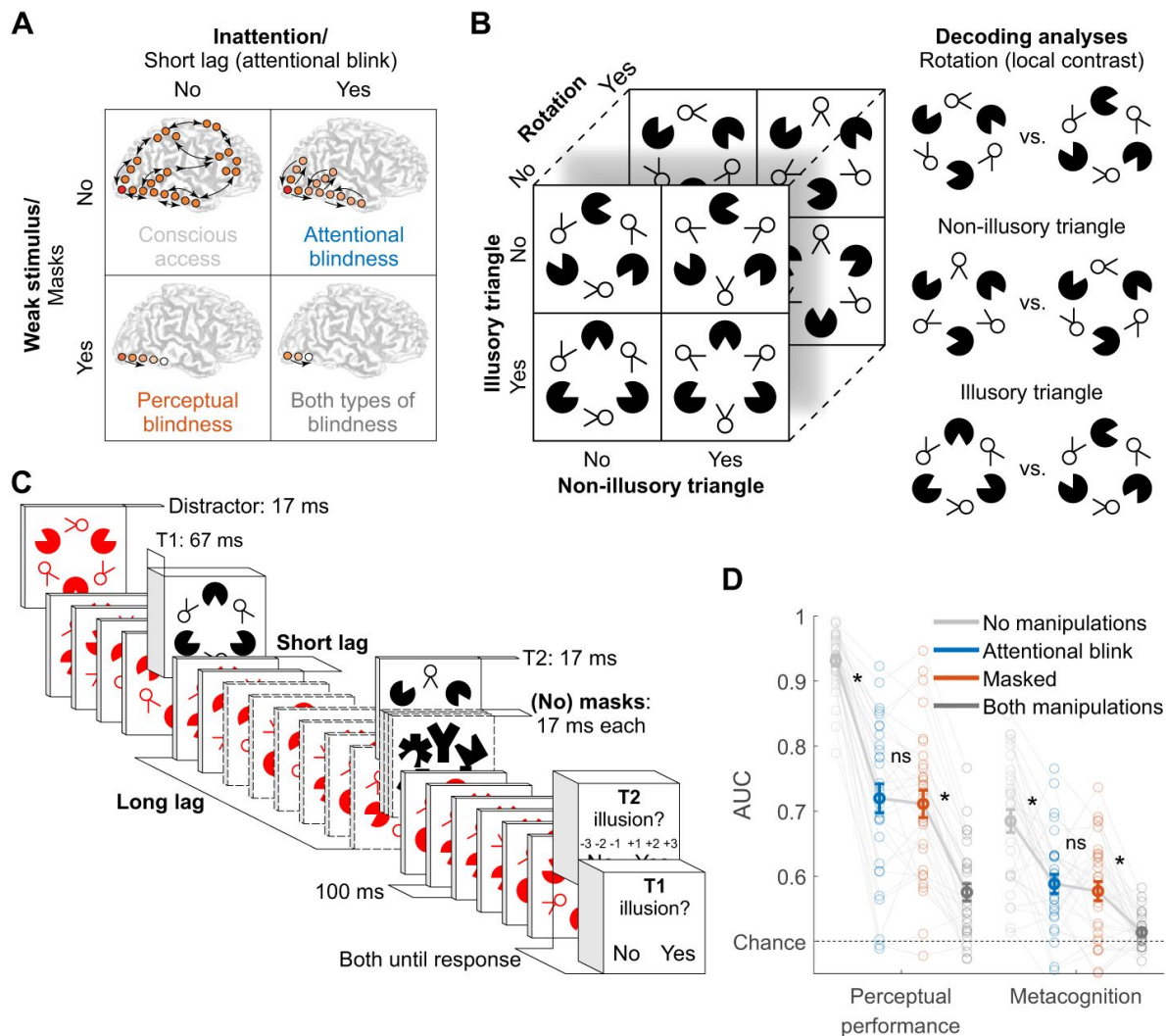


Figure 1.

Experimental design and behavior.

(A) Perceptual vs. attentional blindness in the four-stage model. A stimulus with low bottom-up strength (masked) is thought to interrupt local recurrent processing in sensory areas while leaving feedforward processing largely intact, while inattention (induced by the attentional blink) is thought to interrupt global recurrent processing between frontoparietal areas and sensory areas, while leaving local recurrent processing within sensory areas largely intact. Reprinted from Dehaene et al. (2006) with permission from Elsevier. (B) Target stimulus set and decoding analyses. (C) Trial design. Note that the central fixation cross is not displayed for readability. (D) Perceptual performance refers to participants' ability to detect the Kanizsa illusion. Metacognition refers to participants' ability to evaluate their own performance using confidence judgments. Both perceptual performance and metacognition are measured as the area under the receiver operating characteristic curve (AUC). Error bars are mean $\pm$ standard error of the mean. Individual data points are plotted using low contrast. Ns is not significant ($P \geq 0.477$, $BF_{01} \geq 4.05$). $*P \leq 0.001$.

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they have rarely been addressed experimentally (Kanai et al., 2010 [↗](#); Lau & Passingham, 2006 [↗](#); Meuwese et al., 2014 [↗](#)). For example, Fahrenfort and colleagues (2017) [↗](#) found that illusory surfaces could be decoded from electroencephalogram (EEG) data during the AB but not during masking. This was taken as evidence that local recurrent interactions, supporting perceptual integration, were preserved during inattention but abolished by masking. However, masking had a much stronger behavioral effect than the AB, effectively reducing task performance to chance level. Indeed, a control experiment using weaker masking, which resulted in behavioral performance well above chance similar to the main experiment's AB condition, revealed some evidence for preserved local recurrent interactions also during masking. However, these conditions were tested in separate experiments with small samples, precluding a direct comparison of perceptual vs. attentional impairments at matched levels of behavioral performance. To test and further refine the four-stage model of consciousness in humans, the present study compared all stages within the same experimental setup, analyzing all trials and including all participants while carefully matching task performance between a perceptual manipulation (masking) and an attentional manipulation (attentional blink).

To reveal neural mechanisms associated with perceptual and attentional impairments, we combined a novel visual stimulus with features of different complexity with time-resolved decoding of these visual features from EEG data (**Fig. 1B** [↗](#)). The target stimulus differed along three dimensions (illusory triangle, non-illusory triangle, and local contrast) that were independently manipulated. First, “Pac-Man” stimuli could create either the perception of an illusory surface in the shape of a Kanizsa triangle when aligned, or not, when misaligned. Second, additional “two-legged white circles” could form either a non-illusory triangle when their line segments were aligned, or not, when the “legs” were misaligned. Third, for the local contrast manipulation, the whole stimulus was rotated by 180 degrees, so that the same retinotopic positions had high contrast in one spatial configuration and low contrast when flipped 180 degrees.

Human neuroimaging and direct neural recordings in animals have shown that the Kanizsa illusion is supported by both lateral and feedback connections (Halgren et al., 2003 [↗](#); Kok et al., 2016 [↗](#); Kok & de Lange, 2014 [↗](#); Lee & Nguyen, 2001 [↗](#); Pak et al., 2020 [↗](#); Wokke et al., 2013 [↗](#)), while the processing of collinear line elements (as in the non-illusory triangle) primarily relies on lateral connections (Bosking et al., 1997 [↗](#); Gilbert & Wiesel, 1979 [↗](#); Li, 1998 [↗](#); Liang et al., 2017 [↗](#); K. E. Schmidt et al., 1997 [↗](#); Stettler et al., 2002 [↗](#)). Differences in local contrast are processed early in the visual system through feedforward connections and are resistant to masking (Fahrenfort et al., 2007 [↗](#), 2017 [↗](#); Kandel et al., 2000 [↗](#); Lamme & Roelfsema, 2000 [↗](#)). Decoding the stimulus conditions of the illusory triangle, non-illusory triangle, and local contrast at different points in time, in combination with the associated topography, therefore served as putative markers of these distinct neural processes (**Fig. 1B** [↗](#)) and allowed us to test whether the effects of masking and the attentional blink followed the predictions of the four-stage model of consciousness.

Results

Masking and the attentional blink were matched in perceptual performance and metacognition

We recorded the EEG signal of 30 participants who identified the presence or absence of an illusory surface (triangle) in two black target stimuli (T1 and T2) that were presented amongst red distractors in a rapid serial visual presentation task (**Fig. 1C** [↗](#)). We manipulated the visibility of T2 in two ways: masking the stimulus and manipulating attention, resulting in a 2×2 factorial design (**Fig. 1A** [↗](#)). Specifically, T2 could be either masked or unmasked (perceptual manipulation), and T2 could be presented at either a long interval (900 ms) or a short interval (200

or 300 ms) after T1, inducing an attentional blink (AB) effect for the short T1-T2 intervals (Raymond et al., 1992). This design resulted in four conditions, which we from now on refer to as the masked condition (T2 masked at the long T1-T2 interval), AB condition (T2 unmasked at the short T1-T2 interval), no-manipulations condition (T2 unmasked at the long T1-T2 interval), and both-manipulations condition (T2 masked at the short T1-T2 interval). At the end of a trial, participants indicated whether each target (T1 and T2) contained an illusory surface or not. Importantly, mask contrast in the masked condition was adjusted using a staircasing procedure to match performance in the AB condition, ensuring comparable perceptual performance in the masked and the AB condition across participants (see Methods for more details).

Conscious access can be assessed not only based on perceptual performance but also through metacognitive sensitivity, the ability to evaluate one's own performance (Brown et al., 2019; Dienes, 2007; Fleming & Lau, 2014; Lau & Passingham, 2006; Merikle et al., 2001; Seth et al., 2008). Participants in our study provided confidence ratings on a 3-point scale (low, medium, high) for their responses to T2. To ensure that the distribution of confidence ratings in the performance-matched masked and AB condition was not influenced by participants anchoring their confidence ratings to the unmatched very easy and very difficult conditions (no and both manipulations condition, respectively), the masked and AB condition were presented in the same experimental block, while the other block type included the no- and both-manipulations condition.

We used area under the receiver operating characteristic (ROC) curve (AUC) as a shared metric for perceptual performance (detection of the Kanizsa illusion), metacognitive sensitivity, and EEG decoding (see Methods for details on the calculation of these measures). A repeated-measures (rm) ANOVA with the factors masking (present/absent) and T1-T2 lag (short/long) revealed, as expected, that both masking and the short T1-T2 lag impaired perceptual performance ($F_{1,29}=344.24$, $P<10^{-15}$, $BF_{10}=2.76\times 10^{13}$ and $F_{1,29}=427.54$, $P<10^{-15}$, $BF_{10}=3.67\times 10^{13}$) as well as metacognitive sensitivity ($F_{1,29}=50.78$, $P<10^{-7}$, $BF_{10}=1.18\times 10^5$ and $F_{1,29}=47.83$, $P<10^{-6}$, $BF_{10}=3.28\times 10^4$). Importantly, paired t-tests showed that we successfully matched the key conditions, the masked condition (masked, long lag) and the AB condition (unmasked, short lag) for perceptual performance ($t_{29}=0.62$, $P=0.537$, $BF_{01}=4.30$, **Fig. 1D**, left) as well as for metacognitive sensitivity ($t_{29}=0.72$, $P=0.477$, $BF_{01}=4.05$; **Fig. 1D**, right, see **Fig. S1** for signal detection theory related measures of performance). Thus, whereas in previous studies task performance was considerably higher during the AB than during masking (e.g., Fahrenfort et al., 2017), in the present study the masked and the AB condition were matched in both measures of conscious access.

Masking and the attentional blink leave local contrast decoding largely intact

To derive markers of the different neural processes from the EEG data, for each stimulus feature we trained linear discriminant classifiers on the T1 data and tested them on the T2 data. Classifiers used preprocessed EEG activity (see Methods) across all electrodes. To leverage the similarities between T1 and T2 in task and stimulus context, all main analyses used T1 training data for T2 decoding. This approach minimized possible differences in conscious access and working memory demands between the training and test datasets.

For local contrast decoding, the classifier categorized stimuli as either pointing upwards or pointing downwards, thereby effectively decoding the stimuli's local differences in contrast at the top vs. bottom of the stimulus. Classification performance (AUC) over time was obtained, with peak decoding accuracy in a 75-95 ms time window (**Fig. 2A** and **Fig. S2A**, top). The peak in decoding accuracy was occipital in nature (see the covariance/class separability map of **Fig. 2A**) (Haufe et al., 2014), consistent with previous findings (Fahrenfort et al., 2017). We focused our analyses on the averages of this time window. An rm ANOVA with the factors masking (present/absent) and T1-T2 lag (short/long) revealed a weak but statistically significant effect of masking on local contrast decoding, with the Bayes factor indicating only “anecdotal” evidence

($F_{1,29}=6.51$, $P=0.016$, $BF_{10}=1.31$), while the T1-T2 lag had no significant effect ($F_{1,29}=0.32$, $P=0.578$, $BF_{01}=3.45$). A paired t-test yielded no evidence for a difference between the performance matched conditions (masked vs. AB; $t_{29}=1.42$, $P=0.166$, $BF_{01}=2.08$; **Fig. 2C**, “Local contrast: 75-95 ms”). These results are in line with theoretical proposals and empirical findings that suggest limited effects of masking and attentional manipulations on perceptual processes that rely on feedforward connections (Dehaene et al., 2006; Fahrenfort et al., 2007, 2017; Lamme, 2010), contrasting with the robust effects of these consciousness manipulations on feedback processes reported in the following section.

Stronger effect of masking than the attentional blink on early but not on late illusion decoding

Next, we trained a linear classifier on the T1 data to discriminate between the presence and absence of the Kanizsa illusion and tested it on each of the four conditions of the T2 data. The average of all four conditions revealed two prominent peaks in decoding accuracy, consistent with previous research (Fig. S2C, top) (Fahrenfort et al., 2017). Based on this previous study, our analyses focused on the averages of the two time windows that encompassed these two peaks: specifically, from 200 to 250 ms and from 375 to 475 ms after target stimulus onset. The covariance/class separability maps (**Fig. 2B**) indicated that during the earlier time window (200–250 ms) classification mainly relied on occipital electrodes. Considering its timing, topology and previous findings, this neural event likely reflects early sensory processes and may thus represent a marker for local recurrent processing (Fahrenfort et al., 2017; Kok et al., 2016; Roelfsema, 2006; Wokke et al., 2013; Wyatte et al., 2014). The timing and topology of the later neural event (375–475 ms) overlapped with the event-related potential component P300 (Fig. S4), which is associated with conscious access (Fahrenfort et al., 2017; Sergent et al., 2005; Weaver et al., 2019) and may thus represent a marker for global recurrent processing.

We tested how the consciousness manipulations affected these putative markers of local and global recurrent processing (**Fig. 2C**), again conducting rm ANOVAs with the factors masking (present/absent) and T1-T2 lag (short/long) that we followed-up on with paired t-tests comparing the matched conditions (masked vs. AB). Importantly, we observed a distinct difference between the performance matched conditions in the first decoding peak, which was significantly impaired by both masking ($F_{1,29}=162.62$, $P<10^{-12}$, $BF_{10}=5.86\times10^{10}$) and T1-T2 lag ($F_{1,29}=78.07$, $P<10^{-8}$, $BF_{10}=6.03\times10^6$), but importantly, it was more affected by masking than by T1-T2 lag (interaction, $F_{1,29}=18.67$, $P<0.001$, $BF_{10}=149.92$) (**Fig. 2C**, “Illusory triangle: 200-250 ms”). Directly comparing the performance matched conditions, the first decoding peak was more strongly impaired by masking than by the AB ($t_{29}=4.66$, $P<10^{-4}$, $BF_{10}=3.81$). This suggests that the AB allowed for greater residual local recurrent processing than masking, replicating the key finding by Fahrenfort and colleagues (2017). Importantly, the present result demonstrates that this effect reflects the difference between the perceptual vs. attentional manipulation rather than differences in behavior, as the masked condition and the AB condition were matched for perceptual performance and metacognition.

The pattern of results of the second peak was notably different. The second decoding peak was impaired by both masking ($F_{1,29}=49.75$, $P<10^{-7}$, $BF_{10}=8.60\times10^4$) and T1-T2 lag ($F_{1,29}=78.48$, $P<10^{-9}$, $BF_{10}=4.32\times10^5$), and the matched conditions (masked and AB condition) did not differ significantly from each other ($t_{29}=0.21$, $P=0.837$, $BF_{01}=5.04$) (**Fig. 2C**, “Illusory triangle: 375-475 ms”). Furthermore, another rm ANOVA comparing the first and second decoding peak between the matched conditions (masked/AB) revealed a significant interaction, reflecting a larger difference between the AB and the masked condition in the first than in the second decoding peak ($F_{1,29}=31.53$, $P<10^{-5}$, $BF_{10}=1693.17$). The pattern of behavioral results, both for perceptual performance and metacognitive sensitivity, closely resembled the second decoding peak: sensitivity in all three metrics dropped from the no-manipulations condition to the masked and AB

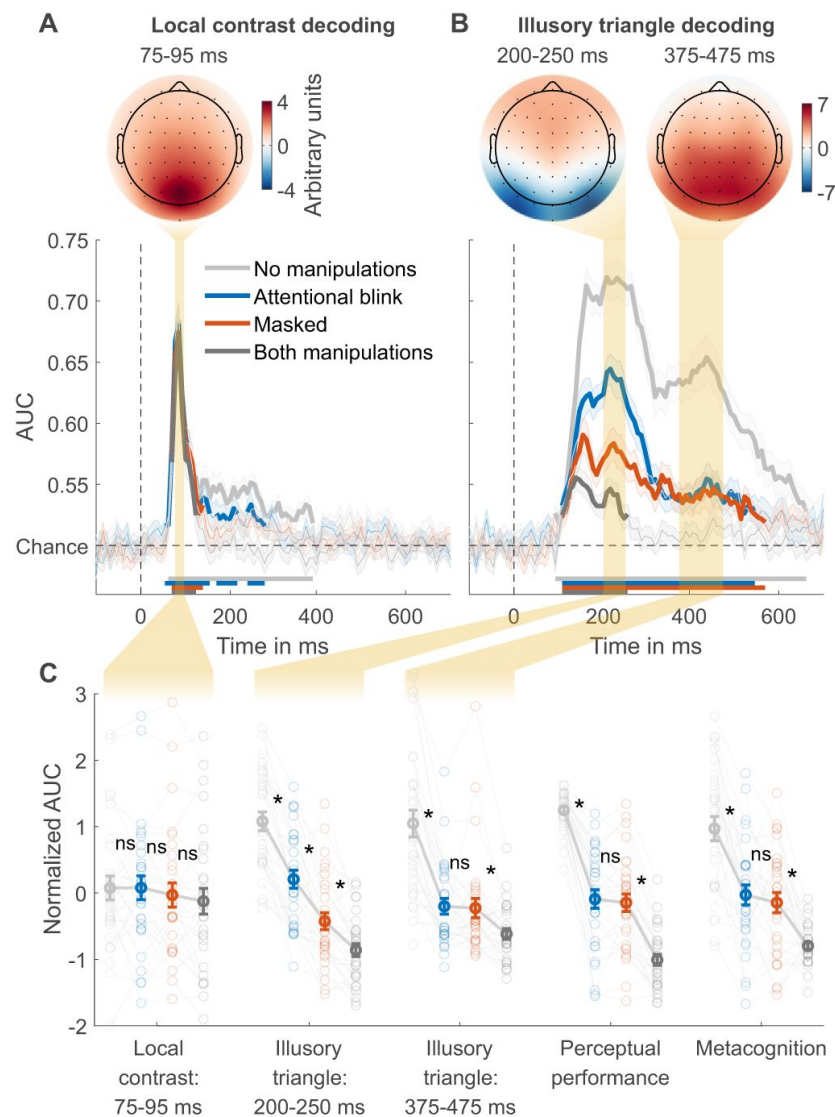


Figure 2.

Local contrast and illusory triangle decoding using first targets as training data.

(A) Local contrast decoding. (B) Illusory Kanizsa triangle decoding. For both features, covariance/class separability maps reflecting underlying neural sources are shown. Below these maps: mean decoding performance, area under the receiver operating characteristic curve (AUC), over time $\pm$ standard error of the mean (SEM). Thick lines differ from chance: $P < 0.05$, cluster-based permutation test. (C) Normalized (Z-scored) AUC for every measure: mean decoding time windows and two types of behavior. Each measure is Z-scored separately. Perceptual performance refers to participants' ability to detect the Kanizsa illusion. Metacognition refers to participants' ability to evaluate their own performance using confidence judgments. See Figure S3 for the same analyses but then for off-diagonal decoding profiles. Error bars are mean $\pm$ SEM. Individual data points are plotted using low contrast. Ns is not significant ($P \geq 0.166$, $BF_{01} \geq 2.07$). * $P \leq 0.002$.

conditions, while sensitivity did not differ significantly between these performance-matched conditions (**Fig. 2C**). Two additional rm ANOVAs with the factors measure (behavior, second EEG decoding peak) and condition (no-manipulations, masked, AB; We excluded the both-manipulations condition from this analysis due to scale restrictions: in this condition, EEG decoding at the second peak was at chance, while behavioral performance was above chance, leaving more room for behavior to drop from the masked and AB condition) for perceptual performance and metacognitive sensitivity revealed no significant interaction (performance: $F_{2,58}=0.27$, $P=0.762$, $BF_{01}=8.47$; metacognition: $F_{2,58}=0.54$, $P=0.586$, $BF_{01}=6.04$). This similarity between behavior and EEG decoding replicates the findings of [Fahrenfort and colleagues \(2017\)](#) who also found a striking similarity between late Kanizsa decoding (at 406 ms) and behavioral Kanizsa detection. These results indicate that global recurrent processing at these later points in time reflected conscious access to the Kanizsa illusion.

Additional rm ANOVAs comparing the effect of the consciousness manipulations on local contrast decoding with their effects on the first and second illusion decoding peak showed that, compared to contrast decoding, both manipulations had stronger effects on the first illusion decoding peak (masking: $F_{1,29}=99.35$, $P<10^{-10}$, $BF_{10}=1.73\times 10^8$; AB: $F_{1,29}=38.95$, $P<10^{-6}$, $BF_{10}=1.43\times 10^4$) and on the second illusion decoding peak (masking: $F_{1,29}=22.25$, $P<10^{-4}$, $BF_{10}=477.25$; AB: $F_{1,29}=49.60$, $P<10^{-7}$, $BF_{10}=3.59\times 10^4$). In the light of evidence showing that unconscious processing is susceptible to conscious top-down influences ([Kentridge et al., 2004](#); [Kiefer & Brendel, 2006](#); [Naccache et al., 2002](#)), we ran control analyses showing that early local contrast decoding was not improved by rendering contrast task-relevant (see [Supplementary Information](#) and **Fig. S5**), indicating that these differences between illusion and contrast decoding did not reflect differences in task-relevance. This suggests that masking and the AB specifically influenced local and global recurrent processing respectively, while early feedforward processing was less affected.

While the findings presented so far used the T1 data to train the classifiers, we replicated all key findings when training the classifiers on an independent training set where individual stimuli were presented in isolation (**Fig. 3A**, results in the [Supplementary Information](#) and **Fig. S6**).

Distinguishing collinearity and illusion-specific processing

The performance matched masked and AB condition differed only in the first illusion decoding peak, our putative marker of local recurrent processing, which was markedly more impaired in the masked than in the AB condition. Next, we determined whether this effect reflected relatively preserved processing of collinearity or of the Kanizsa illusion during attentional impairment specifically. In our target stimulus, collinearity was present when the Pac-Man stimuli aligned, inducing the illusory Kanizsa triangle. Notably, collinearity was also present when the line segments of the “two-legged white circles” of the stimulus aligned, forming the non-illusory triangle. Note that the line segments making up the triangle were equally long, and the spaces between them equally large, for the illusory and non-illusory triangles. The addition of this element of collinearity to our stimuli was a key difference to the study by [Fahrenfort and colleagues \(2017\)](#), allowing us to compare non-illusory triangle decoding to illusory triangle decoding in order to distinguish between collinearity and illusion-specific processing.

However, in the main RSVP task the illusory triangle was task-relevant, while non-illusory triangles were always task-irrelevant. To equate the effect of task-relevance in the comparison, classifiers were trained on an independent training set in which each relevant stimulus feature was task-relevant. Specifically, in different experimental blocks participants focused either on local contrast, the non-illusory triangle, or the illusory triangle (**Fig. 3A**). We trained a classifier to distinguish between the presence and absence of the task-relevant non-illusory triangle (collinearity-only) and the same was done for the task-relevant illusory triangle (collinearity-plus-illusion). Then, both classifiers were used to decode the presence vs. absence of the illusory

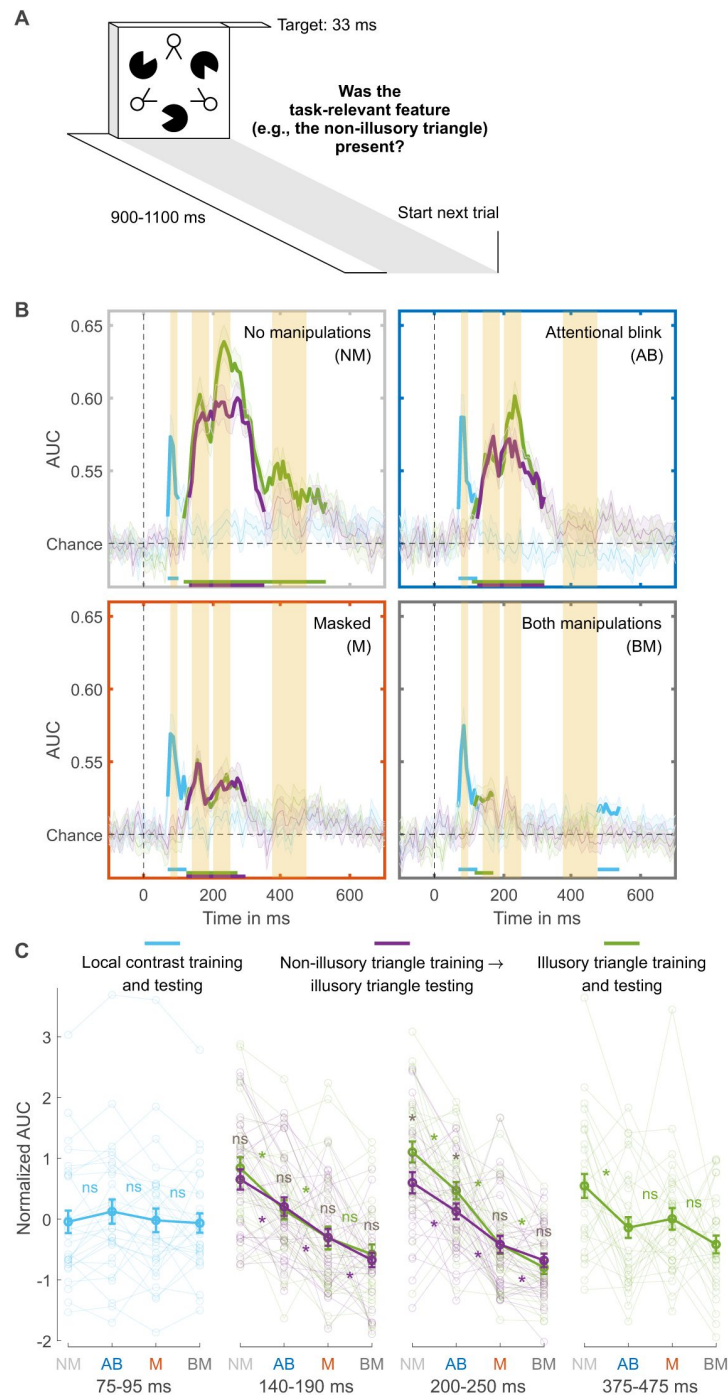


Figure 3.

Separating collinearity and illusion-specific processes using the independent training dataset.

(A) Trial design used for obtaining the independent training dataset. (B) Illusory triangle decoding, after training classifiers on the independent training set on either the non-illusory (collinearity-only, purple lines) or illusory triangle (collinearity-plus-illusion, green lines). For comparison, training and testing on local contrast is shown in light blue. Mean decoding performance, area under the receiver operating characteristic curve (AUC), over time $\pm$ standard error of the mean (SEM) is shown. Thick lines differ from chance: $P < 0.05$, cluster-based permutation test. The highlighted time windows are 75-95, 140-190, 200-250, and 375-475 ms, corresponding to separate panels in (C), which shows normalized (Z-scored) mean AUC for every time window. Each window is Z-scored separately. Error bars are mean $\pm$ SEM. Individual data points are plotted using low contrast. Ns is not significant ($P \geq 0.084$, $BF_{01} \geq 1.26$). * $P \leq 0.048$.

triangle in the main RSVP task (cross-task-decoding approach), which ensured that both training and testing were always performed on task-relevant stimuli. By comparing Kanizsa decoding performance in the RSVP task based on the collinearity-only classifier with decoding performance based on the collinearity-plus-illusion classifier, we effectively subtracted out the contribution of collinearity processing to illusion decoding, thereby isolating illusion-specific processing.

Preserved collinearity and illusion-specific processing during the attentional blink

To determine a time window for (the start of) collinearity-only processing, we first trained and tested classifiers to distinguish present vs. absent non-illusory triangles (training and testing on non-illusory triangles only). We trained two classifiers, one on the T1 in the RSVP task and one on the independent training set ([Fig. S2](#)) and tested their performance in decoding the non-illusory triangle in the T2 data, where this non-illusory triangle was always task-irrelevant. The results of both classifiers converged, and these analyses revealed a peak in decoding accuracy at ~164 ms (yielding a collinearity-only time window between 140–190 ms), right before the 200–250 ms time window of the first illusion decoding peak ([Fig. S2B](#)). This 140–190 ms collinearity-only time window was also evident when classifiers were used to categorize the presence vs. absence of the Kanizsa illusion ([Fig. S2C](#), first time window), as well as in previous research ([Fahrenfort et al., 2017](#)), suggesting that collinearity processing also contributes to Kanizsa decoding.

We examined how decoding the presence vs. absence of the Kanizsa illusion in the RSVP task was affected by the consciousness manipulations, while training classifiers either on the illusory (collinearity-plus-illusion) or non-illusory (collinearity-only) triangle from the independent training set (as described above). [Figure 3B](#) shows the decoding accuracies of these analyses across the entire time window (purple and green lines). Follow-up analyses were performed using the 140–190 ms collinearity-only window (see the previous paragraph). An rm ANOVA with the factors masking (present/absent), T1–T2 lag (short/long), and training set (illusory/non-illusory triangle) revealed that both masking and the short T1–T2 lag impaired decoding accuracy (masking: $F_{1,29}=58.95$, $P<10^{-7}$, $BF_{10}=8.22\times 10^5$; T1–T2 lag: $F_{1,29}=24.90$, $P<10^{-4}$, $BF_{10}=776.00$). Furthermore, paired t-tests comparing the matched conditions (masked vs. AB condition) confirmed that decoding accuracy was more impaired in the masked than AB condition, both when training was done on the illusory ($t_{29}=2.26$, $P=0.031$, $BF_{01}=0.58$) and non-illusory triangle ($t_{29}=2.78$, $P=0.009$, $BF_{01}=0.21$; [Fig. 3C](#), “140–190 ms”). Focusing on the performance matched conditions and the role of the training set, an rm ANOVA with the factors condition (masked/AB) and training set (illusory/non-illusory triangle) on T2 illusory triangle decoding revealed no significant effect of training set ($F_{1,29}=0.09$, $P=0.766$, $BF_{01}=4.22$), i.e., no evidence for illusion-specific processing, and no significant interaction ($F_{1,29}=0.04$, $P=0.837$, $BF_{01}=3.74$). This demonstrates that neural processing in the 140–190 ms window indeed reflected collinearity-only rather than illusion-specific processing.

The marker for illusion-specific processing emerged later, namely in the 200–250 ms time window that encompassed the first illusion decoding peak reported above. As can be seen in [Figure 3B](#), when no consciousness manipulations were applied (unmasked, long T1–T2 lag), there was significant illusion-specific processing, i.e., T2 illusory triangle decoding was better after training a classifier on the Kanizsa illusion (collinearity-plus-illusion, green line) than after training a classifier on the non-illusory triangle (collinearity-only, purple line) ($t_{29}=4.22$, $P<0.001$, $BF_{10}=128.47$). Turning to the performance matched conditions, an rm ANOVA with the factors condition (masked/AB) and training set (illusory/non-illusory triangle) on T2 illusory triangle decoding yielded a significant effect of condition ($F_{1,29}=16.59$, $P<0.001$, $BF_{10}=90.73$), with overall better decoding for the AB than for the masked condition, and importantly, a significant interaction ($F_{1,29}=4.65$, $P=0.039$, $BF_{10}=2.19$). [Figure 3B](#) shows that decoding after training on illusory triangles (collinearity-plus-illusion) was better than after training on non-illusory triangles (collinearity-only) for the AB ($t_{29}=2.51$, $P=0.018$, $BF_{10}=2.78$, [Fig. 3B](#), top right) but not for the

masked condition ($t_{29}=-0.02$, $P=0.982$, $BF_{01}=5.14$, **Fig. 3B**, bottom left). Thus, while illusion-specific processing was evident in the AB condition, it was fully abolished in the masked condition. Illusion-specific processing was not even affected by the AB, as an rm ANOVA with the factors condition (no manipulations/AB) and training set (illusory/non-illusory triangle) revealed no significant interaction ($F_{1,29}=1.33$, $P=0.259$, $BF_{01}=2.30$). The classifier trained on non-illusory triangles (collinearity-only) also performed better during the AB than during the masked condition ($t_{29}=2.85$, $P=0.008$, $BF_{10}=5.43$ **Fig. 3C**, “200-250 ms”, purple line), hence both collinearity-only and illusion-specific processing were most strongly impaired by masking. Control analyses presented in the **Supplementary information (Fig. S7)** demonstrate that cross-feature-decoding can indeed isolate illusion-specific processes and does not reflect other, e.g., task- or attention-related, processes (for further control analyses testing the effect of task-relevance on local contrast processing, see **Supplementary Information** and **Fig. S5**).

Finally, we focused on the late 375–475 ms window, encompassing the second illusion decoding peak, which was directly linked to behavioral performance (see above, **Fig. 3B**, last time window). Similarly, as above, illusory triangle decoding was now based on training the decoder on the illusory triangles from the independent training set. Replicating our main analysis, classifier performance was impaired by both masking ($F_{1,29}=6.01$, $P=0.020$, $BF_{10}=2.37$) and T1-T2 lag ($F_{1,29}=10.10$, $P=0.004$, $BF_{10}=10.12$), with no significant differences between the two performance matched conditions ($t_{29}=-0.63$, $P=0.531$, $BF_{01}=4.27$) (**Fig. 3C**, “375-475 ms”).

Discussion

We demonstrate that perceptual and attentional manipulations, despite similarly impairing conscious access, exhibit distinct neural profiles in the brain. To investigate this difference, we decoded different visual features targeting distinct stages of visual processing from human EEG activity, while carefully matching a masked condition and an attentional blink (AB) condition in perceptual and metacognitive performance. Therefore, any observed neural difference between the masked and the AB condition could be unequivocally attributed to differences between attentional and perceptual manipulations of conscious access. While decoding of local contrast was barely affected by the two consciousness manipulations, early (200–250 ms, occipital) decoding of the illusory Kanizsa triangle was markedly more impaired in the masked than in the AB condition (Fahrenfort et al., 2017), even though behavior was matched. By contrast, later (375–475 ms, centroparietal) illusion decoding was similarly impaired by masking and by the AB, closely resembling their matched effects on behavior.

Furthermore, we differentiated between collinearity-only and illusion-specific processing and found that both processes were more strongly impaired by masking than by the AB. Notably, illusion-specific processing was unaffected by the AB, but completely abolished by masking.

Decoding of these different stimulus features at different points in time, together with their topography, may be regarded as markers of distinct neural processes. Based on neurophysiology and previous neuroimaging studies, the early decoding peak for local contrast decoding (75–95 ms after target stimulus onset) likely reflects feedforward processing (Fahrenfort et al., 2007, 2017; Kandel et al., 2000; Lamme & Roelfsema, 2000). The first illusion decoding peak (200–250 ms) may be regarded as a marker of local recurrent processing, while the second illusion decoding peak (375–475 ms) likely reflects global recurrent processing (Fahrenfort et al., 2017). Thus, our findings suggest that both perceptual and attentional impairments leave feedforward processing largely intact and similarly impair global recurrent processing, while local recurrent processing is markedly more impaired by perceptual than by attentional impairments.

This pattern of results is consistent with a previous study that used EEG to decode Kanizsa-like illusory surfaces during masking and the AB (Fahrenfort et al., 2017). However, the present study also revealed some effects where Fahrenfort and colleagues (2017) failed to obtain statistical significance, likely reflecting the present study's considerably larger sample size and greater statistical power. For example, in the present study the marker for feedforward processing was weakly but significantly impaired by masking, and the marker for local recurrency was significantly impaired not only by masking but also by the AB, although to a lesser extent. Most importantly, however, we replicated the key findings that local recurrent processing was more strongly impaired by masking than by the AB, and that global recurrent processing was similarly impaired by masking and the AB and closely linked to task performance, reflecting conscious access. Crucially, having matched the key conditions behaviorally, the present finding of greater local recurrency during the AB can now unequivocally be attributed to the attentional vs. perceptual manipulation of consciousness.

Furthermore, the addition of line segments forming a non-illusory triangle to the stimulus employed in the present study allowed us to distinguish between collinearity and illusion-specific processing. Although the present EEG decoding measures cannot provide direct evidence for feedback vs. lateral processes, based on neurophysiological evidence that collinearity processing primarily relies on lateral connections (Bosking et al., 1997; Gilbert & Wiesel, 1979; Li, 1998; Liang et al., 2017; K. E. Schmidt et al., 1997; Stettler et al., 2002), while processing of the Kanizsa illusion involves both lateral and feedback connections (Halgren et al., 2003; Kok et al., 2016; Kok & de Lange, 2014; Lee & Nguyen, 2001; Pak et al., 2020; Wokke et al., 2013), the comparison of collinearity-only to illusion-specific processing may provide insight into the components of local recurrent processing: lateral and feedback connections (Lamme et al., 1998; Roelfsema, 2006). It should be noted that not all neurophysiological evidence unequivocally links processing of collinearity and of the Kanizsa illusion to lateral and feedback processing, respectively (Angelucci et al., 2002; Bair et al., 2003; Chen et al., 2014), so that overlap in decoding the illusory and non-illusory triangle may reflect other mechanisms, for example feedback processes representing the triangular shapes as well. However, following our reasoning, the decoding results suggest that lateral processing occurred earlier (140–190 ms after target stimulus onset) than illusion-specific feedback processing (200–250 ms), in line with animal research (Angelucci & Bressloff, 2006; Lamme et al., 1998; Roelfsema, 2006).

Both lateral and feedback processing were more strongly affected by masking than by the AB, indicating that the “attentional blindness” stage of the four-stage model of consciousness (Fig. 1A) involves both lateral and feedback connections. Furthermore, masking had a stronger effect on illusion-specific feedback processing than on lateral processing. Notably, illusion-specific feedback processes were unaffected by the AB, but completely abolished by masking. As current theories do not distinguish between the roles of lateral vs. feedback connections for consciousness, the present findings may enrich empirical and theoretical work on perceptual vs. attentional mechanisms of consciousness (Block, 2005; Dehaene et al., 2006; Hatamimajoumerd et al., 2022; Lamme, 2010; Pitts et al., 2018; Sergent & Dehaene, 2004), clearly distinguishing the neural profiles of each processing stage of the influential four-stage model of conscious experience (Fig. 1A). Along with the distinct temporal and spatial EEG decoding patterns associated with lateral and feedback processing, our findings suggest a processing sequence from feedforward processing to local recurrent interactions encompassing lateral-to-feedback connections, ultimately leading to global recurrency and conscious report.

Our results suggest that, compared to masking, the AB left local recurrent processing intact, while feedforward processing did not differ between the two manipulations. Local recurrent processing plays a critical role in perceptual integration, facilitating the organization of fragmented sensory information, such as lines, surfaces, and objects, into a coherent whole (Roelfsema, 2023). Our EEG decoding results support this notion, demonstrating that the AB allows for greater processing of collinearity and the illusion specifically within a time window spanning 140 to 250 ms after

stimulus onset, likely reflecting sparing of local recurrent processes in visual cortex (Fahrenfort et al., 2017 [↗](#); Kok et al., 2016 [↗](#)). This aligns with established models of the AB phenomenon, in which the AB reflects a late post-perceptual central bottleneck characterized by limited attentional capacity (Shapiro et al., 1997 [↗](#)), so that sensory information presented during the AB can nevertheless undergo extensive processing, allowing for perceptual integration, possibly even leading up to semantic analysis (Luck et al., 1996 [↗](#)). Clearly, these findings do not imply that unconscious high-level (e.g., semantic) processing can only occur during inattention, nor do they necessarily generalize to other forms of inattention. Indeed, while the AB represents a prime example of late attentional filtering, other ways of inducing inattention or distraction (e.g., by manipulating spatial attention) may filter information earlier in the processing hierarchy (e.g., Luck & Hillyard, 1994 [↗](#) vs. Vogel et al., 1998 [↗](#)).

Preserved local recurrent processing during the AB is also consistent with classic load theory (Lavie & Dalton, 2014 [↗](#)), where increasing perceptual load (Lavie & de Fockert, 2003 [↗](#)) more strongly reduces distractor processing than increasing cognitive load (e.g., by engaging working memory, as in our AB condition). According to this theory, perceptual and attentional manipulations serve as early and late filters for incoming sensory information, respectively, resulting in more extensive processing under inattention. Indeed, one of the few neuroimaging studies that included both manipulations found that only perceptual but not cognitive (working memory) load decreased fMRI activity in the parahippocampal place area in response to distractor scenes (Yi et al., 2004 [↗](#)), although not all neuroimaging evidence is consistent with a stronger effect of perceptual than cognitive load (Brockhoff et al., 2022 [↗](#)).

Furthermore, previous research has shown that the impact of inattention vs. masking can depend on the neural architecture required for the task at hand. For example, processes related to the detection of conflicting response tendencies, a hallmark of cognitive control and strongly associated with the prefrontal cortex (Ridderinkhof et al., 2004 [↗](#)), are more susceptible to inattention, which reduces the depth of stimulus processing (Nuiten et al., 2021 [↗](#)) than to masking, restricting recurrent interactions, but allowing for deep feedforward processing (all the way up to prefrontal cortex) (Jiang et al., 2018 [↗](#); van Gaal et al., 2008 [↗](#)). Such deep feedforward processing can be sufficient for unconscious high-level processing, as indicated by a rich literature demonstrating high-level (e.g., semantic) processing during masking (Kouider & Dehaene, 2007 [↗](#); Van den Bussche et al., 2009 [↗](#); van Gaal & Lamme, 2012 [↗](#)). Thus, rather than enabling deep unconscious processing, preserved local recurrency during inattention may afford other processing advantages linked to its proposed role in perceptual integration (Lamme, 2020 [↗](#)), such as integration of stimulus elements over space or time.

Having delineated these distinct stages of feedforward, lateral, feedback and global recurrent processing, one important avenue for future research is to distinguish between unconscious and conscious perceptual processes at these stages. Having opted to equate performance across manipulations in our study, behavioral performance was above chance level for both consciousness manipulations. Follow-up research investigating perceptual integration of fully unconscious stimuli could address ongoing debates between influential theories of consciousness (Cogitate Consortium et al., 2023 [↗](#); Mudrik et al., 2014 [↗](#)). The global neuronal workspace theory suggests a durable, yet unconscious processing stage (referred to as “preconscious”), where the input is not globally available, and amplification through top-down attention is required for conscious access and report (Dehaene et al., 2006 [↗](#)). In contrast, others have argued that already local recurrent interactions reflect subjective phenomenal experience (Block, 2005 [↗](#); Lamme, 2010 [↗](#)). Moreover, markers like the P300 and ours for global recurrent processing may reflect functions not directly related to conscious experience, like report or decision-making (Alilović et al., 2023 [↗](#); Canales-Johnson et al., 2023 [↗](#); Pitts et al., 2018 [↗](#)). Another way forward therefore consists in combining no-report paradigms (Sergent et al., 2021 [↗](#); Tsuchiya et al., 2015 [↗](#)) with our EEG markers to examine whether local or global recurrent processing more accurately reflects consciousness in the absence of report.

Methods

Participants

Thirty-three participants took part in the first two sessions (independent EEG training set and practice). Three of them met the practice session's pre-established criteria for exclusion (see "Procedure"). The remaining 30 participants (22 ± 3 years old, 10 men, 2 left-handed) took part in the final (main experimental) session. They all had normal or corrected-to-normal vision. The study was approved by the local ethics committee. Participants gave informed consent and received research credits or 15 euros per hour.

Stimuli

The target stimulus set had a 2 (illusory Kanizsa triangle: present/absent) $\times$ 2 (non-illusory triangle: present/absent) $\times$ 2 (rotation: present/absent) design, resulting in eight stimuli (**Fig. 1B**). Three aligned Pac-Man elements induced the Kanizsa illusion. The non-illusory triangle was present when the stimuli's three other elements (the "two-legged white circles") were aligned. The controls for both the illusory and non-illusory triangle were created by rotating their elements by 90 degrees. Differences in local contrast were created by rotating the entire stimulus by 180 degrees. The targets spanned 7.5 degrees by 8.3 degrees of visual angle. The shortest distance between the edges of the three Pac-Man stimuli as well as between the edges of the three aligned two-legged white circles was 2.8 degrees of visual angle. Although neuronal responses to collinearity in primary visual cortex are most robust when this distance is smaller (Kapadia et al., 1995, 2000), longer-range lateral connections between neurons with similar orientation selectivity can span distances corresponding to visual angles considerably greater than 2.8 degrees (Bosking et al., 1997; Stettler et al., 2002).

The distractor stimulus set was the same as the target stimulus set, with two exceptions. First, the distractors were red instead of black. Second, the distractors' six elements were rotated by 180 degrees relative to the targets', so neither the illusory nor non-illusory triangle was ever present in the distractors. Masks consisted of six differently shaped elements, all capable of covering the targets' elements. Six masks were created by rotating the original mask five times by 60 degrees. They spanned 8.5 degrees by 9.1 degrees of visual angle. The fixation cross, which was always present, was adapted from Thaler et al. (2013).

Procedure

The experiment consisted of three separate sessions conducted on different days: a three-hour session to collect EEG data for the independent training set, a 1.5-hour practice session, and a three-hour experimental session. Tasks were programmed in Presentation software (Neurobehavioral Systems) and displayed on a 23-inch, 60 Hz, 1920 $\times$ 1080 pixels monitor. On each trial of the experimental session, participants were shown two targets (T1 and T2) within a rapid serial visual presentation (RSVP) of distractors (**Fig. 1C**). The targets and distractors had a stimulus onset asynchrony of 100 ms. T2 and distractors were presented for 17 ms each. To improve the decoding analyses' training dataset, T1 was presented for 67 ms. The longer presentation duration facilitated attending to T1, which should result in greater deployment of attentional resources and thereby increase the size of the AB. T1 was preceded by five distractors and T2 was followed by six distractors.

T2 visibility was manipulated in two ways, using a perceptual and an attentional manipulation (**Fig. 1A**). The perceptual manipulation consisted in masking T2 with three masks, each presented for 17 ms with an interstimulus interval of 0 ms. The three masks were selected randomly, but all differed from each other. Half of the T2s were masked; for the other half, no

masks were presented (unmasked condition). The attentional manipulation consisted in shortening the T1–T2 lag from a long interval of eight distractors (900 ms) to a short interval of one or two distractors (200 or 300 ms). Half the trials had a long lag, the other half had a short lag. The short lag duration was determined for each participant individually during the training session. Short lags were expected to result in an AB. Participants were instructed to fixate on the fixation cross. After the RSVP, they indicated for each target whether it contained the Kanizsa illusion or not. For T2, participants simultaneously reported their confidence in their response: low, medium, or high, resulting in six response options. To get accurate ratings, participants first responded to T2 and then to T1. Response screens lasted until the response. In short, the experimental session had an 8 (T1 stimulus conditions) $\times$ 8 (T2 stimulus conditions) $\times$ 2 (masked/unmasked) $\times$ 2 (short/long T1–T2 lag) task design, resulting in 256 conditions. Each condition was presented four times, totaling 1024 trials.

The experimental session was preceded by the practice session, in which participants were familiarized with the task. To proceed to the experimental session, participants had to score above 80% correct for both T1 and unmasked, long lag T2. One participant was excluded for failing to achieve this. The training session was also used to determine for each participant the duration of the short lag (200 or 300 ms T1–T2 interval) that induced the largest AB (lowest T2 accuracy) and that was used in the subsequent experimental session. Two participants were excluded due to their AB size falling below the predetermined criterion. Specifically, their T2 accuracy at both short lags did not exhibit a decrease of more than 5% compared to long lags.

One of the main goals of this study was to match perceptual performance between the perceptual and the attentional manipulation. We did this in two ways. First, during the training session, the matching was done by staircasing mask contrast using the weighted up-down method (Kaernbach, 1991 [↗](#)). Contrast levels ranged from 0 (black) to 255 (white). Mask contrast started at level 220. Each correct response made the task more difficult: masks got darker by downward step size S_{down} . Each incorrect response made the task easier: masks got lighter by upward step size S_{up} . Step sizes were determined by $S_{\text{up}} \times p = S_{\text{down}} \times (1 - p)$, where p is the accuracy at short lags. The smallest step size was always nine contrast levels. A reversal is making a mistake after a correct response, or vice versa. The staircase ended after 25 reversals. The mask contrast with which the experimental session started was the average contrast level of the last 20 reversals. Second, during the experimental session, after every 32 masked trials, mask contrast could be updated in accordance with our goal to match accuracy over participants, while also matching accuracy within participants as well as possible.

To ensure that confidence ratings for these matched conditions (masked, long lag and unmasked, short lag) were not influenced by participants anchoring their confidence ratings to the very easy and very difficult unmatched conditions (no and both manipulations, respectively), one type of block only contained the matched conditions, while the other block type contained the two remaining, unmatched conditions (masked, short lag and unmasked, long lag). To ensure every confidence rating would have enough trials for creating receiver operating characteristic curves, participants were instructed to distribute their responses evenly over all ratings within a block. Participants received feedback about the distribution of their responses. The mask contrasts from a performance matched block were used in the subsequent non-performance matched block to ensure that masking remained orthogonal to the AB manipulation. The experimental session therefore always started with a performance matched block.

We wanted to compare illusory triangle decoding to non-illusory triangle decoding. However, during the experimental session, the non-illusory triangle was never task-relevant, only the illusory one was. During the independent EEG classification training session, we therefore made each visual feature, one after the other, task-relevant. A target was presented for 33 ms every 900–1100 ms (**Fig. 3A** [↗](#)). Participants had to fixate on the fixation cross and indicate whether the

current task-relevant feature was absent or present. For each feature, each target was presented 64 times, totaling 512 trials. The order of the task-relevant features was counterbalanced over participants. For all sessions, response button mapping was counterbalanced within tasks.

Behavioral analysis

To quantify perceptual performance, we constructed receiver operating characteristic (ROC) curves by plotting objective hit rates against objective false alarm rates. We used the six response options to get five inflection points (Green & Swets, 1966 [\[1\]](#)). We also quantified metacognitive sensitivity: the ability to know whether you were right or wrong. Performance is high when you are confident in objectively correct responses and not confident in objectively incorrect responses. We again constructed ROC curves, now by plotting the rate of high-confidence correct responses (subjective hit rates) against the rate of high-confidence incorrect responses (subjective false alarm rates). We used the three confidence ratings to get two inflection points. To ensure that T1 was attended, trials with incorrect T1 responses were excluded. Frequentist and Bayesian repeated measures ANOVAs and t-tests were used to test the differences between experimental conditions. Bayesian statistics were calculated in JASP (JASP Team, 2024 [\[2\]](#)) with default prior scales (Cauchy distribution, scale 0.707).

EEG recording and preprocessing

EEG was recorded at 1024 Hz using a 64 channel ActiveTwo system (BioSemi). Four electrooculographic (EOG) electrodes measured horizontal and vertical eye movements. The data were analyzed with MATLAB (MathWorks). For most of the preprocessing steps, EEGLAB was used (Delorme & Makeig, 2004 [\[3\]](#)). The data were re-referenced to the earlobes. Poor channels were interpolated. High-pass filtering can cause artifacts in decoding analyses; we therefore removed slow drifts using trial-masked robust detrending (van Driel et al., 2021 [\[4\]](#)). Each target was epoched from -250 to 1000 ms relative to target onset. To improve the results from the independent component analysis (ICA), baseline correction was applied using the whole epoch as baseline (Groppe et al., 2009 [\[5\]](#)). ICA was used to remove blinks. Blink components were removed manually. Baseline correction was applied, now using a -250 to 0 ms window relative to target onset. Trials with values outside of a -300 to 300 microvolts range were removed. We used an adapted version of FieldTrip's `ft_artifact_zvalue` function to detect and remove trials with muscle artifacts (Oostenveld et al., 2011 [\[6\]](#)). As in the behavioral analyses, trials with incorrect T1 responses were excluded. Finally, the data were downsampled to 128 Hz.

Multivariate pattern analyses

We decoded the different visual features (local contrast, non-illusory triangle, and illusory Kanizsa triangle, respectively; **Fig. 1B** [\[7\]](#)) using the Amsterdam Decoding and Modeling (ADAM) toolbox (Fahrenfort et al., 2018 [\[8\]](#)). For each participant and each visual feature, a linear discriminant classifier was trained on the T1 data and tested on each condition of the T2 data. The classifier was trained to discriminate between the feature's (e.g., the illusory triangle's) absence and presence based on the preprocessed EEG activity across all electrodes. AUC was again used as the performance measure. This procedure was executed for every time sample in a trial, yielding classification performance over time. For the time samples from -100 to 700 ms relative to target onset, we used a two-sided t-test to evaluate whether classifier performance differed from chance. We used cluster-based permutation testing (1000 iterations at a threshold of 0.05) to correct for multiple comparisons (Maris & Oostenveld, 2007 [\[9\]](#)). To obtain topographic maps showing the neural sources of the classifier performance, we multiplied the classifier weights with the data covariance matrix, yielding covariance/class separability maps (Haufe et al., 2014 [\[10\]](#)).

In the decoding analyses described in the results, we applied “diagonal decoding”: classifiers were tested on the same time sample they were trained on. We did the same analyses again, now by applying “off-diagonal decoding”: classifiers trained on a particular time point are tested on all

time points (King & Dehaene, 2014 [↗](#)). Off-diagonal decoding allowed us to explore whether patterns of activity during the time windows of interest were stable over time (Fig. S3 [↗](#)), which is especially interesting for illusion decoding. For the illusory triangle, classifiers were trained on the 200-250 ms window and then averaged, and then decoding AUC was plotted from -100 to 700 ms off-diagonally. Note that for this analysis, late off-diagonal decoding (e.g., in the 375-475 ms time-window shown in panel C) is thought to reflect (longer-lasting) local recurrent interactions as well (Alilović et al., 2023 [↗](#)). A similar off-diagonal analysis was done for the local contrast trained on the 75-95 ms time-window.

To distinguish between collinearity-only and illusion-specific processing, we trained classifiers on independent data based on collinearity-only (the non-illusory triangle was task-relevant) or collinearity-plus-illusion (the illusory triangle was task-relevant) and then decoded the Kanizsa illusion in T2s of the main RSVP task. The rationale for this analysis is that collinearity is present both when the Pac-Man stimuli align to form the illusory Kanizsa triangle and when the two-legged white circles align to form a non-illusory triangle, but only in the case of the Kanizsa triangle do participants experience an illusion. The comparison of T2 illusion decoding between the classifiers trained on the illusion and on collinearity-only in the training set may therefore isolate illusion-specific (likely involving feedback processing) from basic collinearity processing (likely involving lateral connections; Fig. 3 [↗](#)). In the **Supplementary information (Fig. S6)** [↗](#), we compare the independent training set to the training set used for the main analyses, the T1 data from the RSVP task.

As described in the **Supplementary information** [↗](#) as well, a tenfold cross-validation scheme was applied to the data from the independent training set to decode local contrast. Individual participants' data were split into ten equal-sized folds after randomizing the task's trial order. A classifier was then trained on nine folds and tested on the tenth one, ensuring independence of the training and testing sets. This procedure was repeated until each fold served as the test set once. Classifier performance, AUC, was averaged across all ten iterations (Fig. S5 [↗](#)).

As in the behavioral analyses, frequentist and Bayesian repeated measures ANOVAs and t-tests were used to test the differences between experimental conditions.

Data availability

All code and data related to this paper are available at https://uvaauas.figshare.com/projects/Perceptual_versus_attentional_impairments_of_conscious_access_Distinct_neural_mechanisms_despite_equal_task_performance/230501 [↗](#).

Additional files

Supplementary information [↗](#)

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Reviewer #1 (Public review):

Summary:

In this work, Noorman and colleagues test the predictions of the "four-stage model" of consciousness by combining psychophysics and scalp EEG in humans. The study relies on an elegant experimental design to investigate the respective impact of attentional and perceptual blindness on visual processing.

The study is very well summarised, the text is clear and the methods seem sound. Overall, a very solid piece of work. I haven't identified any major weaknesses. Below I raise a few questions of interpretation that may possibly be the subject of a revision of the text.

(1) The perceptual performance on Fig1D appears to show huge variation across participants, with some participants at chance levels and others with performance > 90% in the attentional blink and/or masked conditions. This seems to reveal that the procedure to match performance across participants was not very successful. Could this impact the results? The authors highlight the fact that they did not resort to post-selection or exclusion of participants, but at the same time do not discuss this equally important point.

(2) In the analysis on collinearity and illusion-specific processing, the authors conclude that the absence of a significant effect of training set demonstrates collinearity-only processing. I don't think that this conclusion is warranted: as the illusory and non-illusory share the same shape, so more elaborate object processing could also be occurring. Please discuss.

(3) Discussion, lines 426-429: It is stated that the results align with the notion that processes of perceptual segmentation and organization represent the mechanism of conscious experience. My interpretation of the results is that they show the contrary: for the same visibility level in the attentional blind or masking conditions, these processes can be implicated or not, which suggests a role during unconscious processing instead.

(4) The two paradigms developed here could be used jointly to highlight non-idiosyncratic NCCs, i.e. EEG markers of visibility or confidence that generalise regardless of the method used. Have the authors attempted to train the classifier on one method and apply it to another (e.g. AB to masking and vice versa)? What perceptual level is assumed to transfer?

(4) How can the results be integrated with the attentional literature showing that attentional filters can be applied early in the processing hierarchy?

Comments on revisions:

I'm very pleased with the responses to my previous comments, and congratulate the authors on this excellent piece of work.

<https://doi.org/10.7554/eLife.97900.2.sa3>

Reviewer #2 (Public review):

Summary:

This is a very elegant and important EEG study that unifies within a single set of behaviorally equated experimental conditions conscious access (and therefore also conscious access failures) during visual masking and attentional blink (AB) paradigms in humans. By a systematic and clever use of multivariate pattern classifiers across conditions, they could dissect, confirm, and extend a key distinction (initially framed within the GNWT framework) between 'subliminal' and 'pre-conscious' unconscious levels of processing. In particular, the authors could provide strong evidence to distinguish here within the same paradigm these two levels of unconscious processing that precede conscious access : (i) an early (< 80ms) bottom-up and local (in brain) stage of perceptual processing ('local contrast processing') that was preserved in both unconscious conditions, (ii) a later stage and more integrated

processing (200-250ms) that was impaired by masking but preserved during AB. On the basis of preexisting studies and theoretical arguments, they suggest that this later stage could correspond to lateral and local recurrent feedback processes. Then, the late conscious access stage appeared as a P3b-like event.

Strengths:

The methodology and analyses are strong and valid. This work adds an important piece in the current scientific debate about levels of unconscious processing and specificities of conscious access in relation to feed-forward, lateral, and late brain-scale top-down recurrent processing.

Comments on revisions:

I congratulate the authors for the quality of their revised ms. They convincingly addressed each of the issues raised in my previous review.

<https://doi.org/10.7554/eLife.97900.2.sa2>

Reviewer #3 (Public review):

Summary:

This work aims to investigate how perceptual and attentional processes affect conscious access in humans. By using multivariate decoding analysis of electroencephalography (EEG) data, the authors explored the neural temporal dynamics of visual processing across different levels of complexity (local contrast, collinearity, and illusory perception). This is achieved by comparing the decidability of an illusory percept in matched conditions of perceptual (i.e., degrading the strength of sensory input using visual masking) and attentional impairment (i.e., impairing top-down attention using attentional blink, AB). The decoding results reveal three distinct temporal responses associated with the three levels of visual processing. Interestingly, the early stage of local contrast processing remains unaffected by both masking and AB. However, the later stage of collinearity and illusory percept processing are impaired by the perceptual manipulation but remained unaffected by the attentional manipulation. These findings contribute to the understanding of the unique neural dynamics of perceptual and attentional functions and how they interact with the different stages of conscious access.

Strengths:

The study investigates perceptual and attentional impairments across multiple levels of visual processing in a single experiment. Local contrast, collinearity, and illusory perception were manipulated using different configurations of the same visual stimuli. This clever design allows for the investigation of different levels of visual processing under similar low-level conditions.

Moreover, behavioural performance was matched between perceptual and attentional manipulations. One of the main problems when comparing perceptual and attentional manipulations on conscious access is that they tend to impact performance at different levels, with perceptual manipulations like masking producing larger effects. The study utilizes a staircasing procedure to find the optimal contrast of the mask stimuli to produce a performance impairment to the illusory perception comparable to the attentional condition, both in terms of perceptual performance (i.e., indicating whether the target contained the Kanizsa illusion) and metacognition (i.e., confidence in the response).

The results show a clear dissociation between the three levels of visual processing in terms of temporal dynamics. Local contrast was represented at an early stage (~80 ms), while

collinearity and illusory perception were associated with later stages (~200-250 ms). Furthermore, the results provide clear evidence in support of a dissociation between the effects of perceptual and attentional processes on conscious access: while the former affected both neuronal correlates of collinearity and illusory perception, the latter did not have any effect on the processing of the more complex visual features involved in the illusion perception.

Weaknesses:

The design of the study and the results presented are very similar to those in Fahrenfort et al. (2017), reducing its novelty. Similar to the current study, Fahrenfort et al. (2017) tested the idea that if both masking and AB impact perceptual integration, they should affect the neural markers of perceptual integration in a similar way. They found that behavioural performance (hit/false alarm rate) was affected by both masking and AB, even though only the latter was significant in the unmasked condition. In contrast, an early classification peak was exclusively affected by masking. A later classification peak mirrored the behavioural findings, with classification performance impacted by both masking and AB.

The interpretation of the results primarily relies on the recurrent processing theory of consciousness (Lamme, 2020), which lead to the assumption that local contrast and illusory perception reflect feedforward and (lateral and feedback) recurrent connections, respectively. It should be mentioned, however, that this theoretical prediction is not directly tested in the study. Moreover, the evidence for the dissociation between illusion and collinearity in terms of lateral and feedback connections seems at least limited. For instance, Kok et al. (2016) found that, whereas bottom-up stimulation activated all cortical layers, feedback activity induced by illusory figures led to a selective activation of the deep layers. Lee & Nguyen (2001), instead, found that V1 neurons respond to illusory contours of the Kanizsa figures, particularly in the superficial layers. Although both studies reference feedback connections, neither provides clear evidence for the involvement of lateral connections.

The evidence in favour of primarily lateral connections driving collinearity seems mixed as well. On one hand, Liang et al. (2017) showed that feedback and lateral connections closely interact to mediate image grouping and segmentation. On the other hand, Stettler et al. (2002) showed that, whereas the intrinsic connections link similarly oriented domains in V1, V2 to V1 feedback displays no such specificity. Additionally, the other studies cited in the manuscript focused solely on lateral connections without examining feedback pathways, making it challenging to draw definitive conclusions.

Comments on revisions:

The authors have thoroughly addressed all my comments and provided comprehensive responses to each point raised.

<https://doi.org/10.7554/eLife.97900.2.sa1>

Author response:

The following is the authors' response to the original reviews.

Reviewer #1 (Public Review):

Summary:

In this work, Noorman and colleagues test the predictions of the "four-stage model" of consciousness by combining psychophysics and scalp EEG in humans. The study relies on

an elegant experimental design to investigate the respective impact of attentional and perceptual blindness on visual processing.

The study is very well summarised, the text is clear and the methods seem sound. Overall, a very solid piece of work. I haven't identified any major weaknesses. Below I raise a few questions of interpretation that may possibly be the subject of a revision of the text.

We thank the reviewer for their positive assessment of our work and for their extremely helpful and constructive comments that helped to significantly improve the quality of our manuscript.

(1) The perceptual performance on Fig1D appears to show huge variation across participants, with some participants at chance levels and others with performance > 90% in the attentional blink and/or masked conditions. This seems to reveal that the procedure to match performance across participants was not very successful. Could this impact the results? The authors highlight the fact that they did not resort to postselection or exclusion of participants, but at the same time do not discuss this equally important point.

Performance was indeed highly variable between observers, as is commonly found in attentional-blink (AB) and masking studies. For some observers, the AB pushes performance almost to chance level, whereas for others it has almost no effect. A similar effect can be seen in masking. We did our best to match accuracy over participants, while also matching accuracy within participants as well as possible, adjusting mask contrast manually during the experimental session. Naturally, those that are strongly affected by masking need not be the same participants as those that are strongly affected by the AB, given the fact that they rely on different mechanisms (which is also one of the main points of the manuscript). To answer the research question, what mattered most was that at the group-level, performance was well matched between the two key conditions. As all our statistical inferences, both for behavior and EEG decoding, rest on this group level. We do not think that variability at the individual/subject level detracts from this general approach.

In the Results, we added that our goal was to match performance across participants:

“Importantly, mask contrast in the masked condition was adjusted using a staircasing procedure to match performance in the AB condition, ensuring comparable perceptual performance in the masked and the AB condition across participants (see Methods for more details).”

In the Methods, we added:

“Second, during the experimental session, after every 32 masked trials, mask contrast could be manually updated in accordance with our goal to match accuracy over participants, while also matching accuracy within participants as well as possible.”

(2) In the analysis on collinearity and illusion-specific processing, the authors conclude that the absence of a significant effect of training set demonstrates collinearity-only processing. I don't think that this conclusion is warranted: as the illusory and nonillusory share the same shape, so more elaborate object processing could also be occurring. Please discuss.

We agree with this qualification of our interpretation, and included the reviewer's account as an alternative explanation in the Discussion section:

“It should be noted that not all neurophysiological evidence unequivocally links processing of collinearity and of the Kanizsa illusion to lateral and feedback processing, respectively

(Angelucci et al., 2002; Bair et al., 2003; Chen et al., 2014), so that overlap in decoding the illusory and non-illusory triangle may reflect other mechanisms, for example feedback processes representing the triangular shapes as well.”

(3) Discussion, lines 426-429: It is stated that the results align with the notion that processes of perceptual segmentation and organization represent the mechanism of conscious experience. My interpretation of the results is that they show the contrary: for the same visibility level in the attentional blind or masking conditions, these processes can be implicated or not, which suggests a role during unconscious processing instead.

We agree with the reviewer that the interpretation of this result depends on the definition of consciousness that one adheres to. If one takes report as the leading metric for consciousness (=conscious access), one can indeed conclude that perceptual segmentation/organization can also occur unconsciously. However, if the processing that results in the qualitative nature of an image (rather than whether it is reported) is taken as leading – such as the processing that results in the formation of an illusory percept – (=phenomenal) the conclusion can be quite different. This speaks to the still ongoing debate regarding the existence of phenomenal vs access consciousness, and the literature on no-report paradigms amongst others (see last paragraph of the discussion). Because the current data do not speak directly to this debate, we decided to remove the sentence about “conscious experience”, and edited this part of the manuscript (also addressing a comment about preserved unconscious processing during masking by Reviewer 2) by limiting the interpretation of unconscious processing to those aspects that are uncontroversial:

“Such deep feedforward processing can be sufficient for unconscious high-level processing, as indicated by a rich literature demonstrating high-level (e.g., semantic) processing during masking (Kouider & Dehaene, 2007; Van den Bussche et al., 2009; van Gaal & Lamme, 2012). Thus, rather than enabling deep unconscious processing, preserved local recurrency during inattention may afford other processing advantages linked to its proposed role in perceptual integration (Lamme, 2020), such as integration of stimulus elements over space or time.”

(4) The two paradigms developed here could be used jointly to highlight nonidiosyncratic NCCs, i.e. EEG markers of visibility or confidence that generalise regardless of the method used. Have the authors attempted to train the classifier on one method and apply it to another (e.g. AB to masking and vice versa)? What perceptual level is assumed to transfer?

To avoid issues with post-hoc selection of (visible vs. invisible) trials (discussed in the Introduction), we did not divide our trials into conscious and unconscious trials, and thus did not attempt to reveal NCCs, or NCCs generalizing across the two paradigms. Note also that this approach alone would not resolve the debate regarding the ‘true’ NCC as it hinges on the operational definition of consciousness one adheres to; also see our response to the previous point the reviewer raised. Our main analysis revealed that the illusory triangle could be decoded with above-chance accuracy during both masking and the AB over extended periods of time with similar topographies (Fig. 2B), so that significant cross-decoding would be expected over roughly the same extended period of time (except for the heightened 200-250 ms peak). However, as our focus was on differences between the two manipulations and because we did not use post-hoc sorting of trials, we did not add these analyses.

(5) How can the results be integrated with the attentional literature showing that attentional filters can be applied early in the processing hierarchy?

Compared to certain manipulations of spatial attention, the AB phenomenon is generally considered to represent an instance of “late” attentional filtering. In the Discussion section

we included a paragraph on classic load theory, where early and late filtering depend on perceptual and attentional load. Just preceding this paragraph, we added this:

“Clearly, these findings do not imply that unconscious high-level (e.g., semantic) processing can only occur during inattention, nor do they necessarily generalize to other forms of inattention. Indeed, while the AB represents a prime example of late attentional filtering, other ways of inducing inattention or distraction (e.g., by manipulating spatial attention) may filter information earlier in the processing hierarchy (e.g., Luck & Hillyard, 1994 vs. Vogel et al., 1998).”

Reviewer #2 (Public Review):

Summary:

This is a very elegant and important EEG study that unifies within a single set of behaviorally equated experimental conditions conscious access (and therefore also conscious access failures) during visual masking and attentional blink (AB) paradigms in humans. By a systematic and clever use of multivariate pattern classifiers across conditions, they could dissect, confirm, and extend a key distinction (initially framed within the GNWT framework) between 'subliminal' and 'pre-conscious' unconscious levels of processing. In particular, the authors could provide strong evidence to distinguish here within the same paradigm these two levels of unconscious processing that precede conscious access : (i) an early (< 80ms) bottom-up and local (in brain) stage of perceptual processing ('local contrast processing') that was preserved in both unconscious conditions, (ii) a later stage and more integrated processing (200-250ms) that was impaired by masking but preserved during AB. On the basis of preexisting studies and theoretical arguments, they suggest that this later stage could correspond to lateral and local recurrent feedback processes. Then, the late conscious access stage appeared as a P3b-like event.

Strengths:

The methodology and analyses are strong and valid. This work adds an important piece in the current scientific debate about levels of unconscious processing and specificities of conscious access in relation to feed-forward, lateral, and late brain-scale top-down recurrent processing.

Weaknesses:

- The authors could improve clarity of the rich set of decoding analyses across conditions.*
- They could also enrich their Introduction and Discussion sections by taking into account the importance of conscious influences on some unconscious cognitive processes (revision of traditional concept of 'automaticity'), that may introduce some complexity in Results interpretation*
- They should discuss the rich literature reporting high-level unconscious processing in masking paradigms (culminating in semantic processing of digits, words or even small group of words, and pictures) in the light of their proposal (deeper unconscious processing during AB than during masking).*

We thank the reviewer for their positive assessment of our study and for their insightful comments and helpful suggestions that helped to significantly strengthen our paper. We provide a more detailed point-by-point response in the “recommendations for the authors” section below. In brief, we followed the reviewer’s suggestions and revised the Results/Discussion to include references to influences on unconscious processes and expanded our discussion of unconscious effects during masking vs. AB.

Reviewer #3 (Public Review):

Summary:

This work aims to investigate how perceptual and attentional processes affect conscious access in humans. By using multivariate decoding analysis of electroencephalography (EEG) data, the authors explored the neural temporal dynamics of visual processing across different levels of complexity (local contrast, collinearity, and illusory perception). This is achieved by comparing the decidability of an illusory percept in matched conditions of perceptual (i.e., degrading the strength of sensory input using visual masking) and attentional impairment (i.e., impairing topdown attention using attentional blink, AB). The decoding results reveal three distinct temporal responses associated with the three levels of visual processing. Interestingly, the early stage of local contrast processing remains unaffected by both masking and AB. However, the later stage of collinearity and illusory percept processing are impaired by the perceptual manipulation but remain unaffected by the attentional manipulation. These findings contribute to the understanding of the unique neural dynamics of perceptual and attentional functions and how they interact with the different stages of conscious access.

Strengths:

The study investigates perceptual and attentional impairments across multiple levels of visual processing in a single experiment. Local contrast, collinearity, and illusory perception were manipulated using different configurations of the same visual stimuli. This clever design allows for the investigation of different levels of visual processing under similar low-level conditions.

Moreover, behavioural performance was matched between perceptual and attentional manipulations. One of the main problems when comparing perceptual and attentional manipulations on conscious access is that they tend to impact performance at different levels, with perceptual manipulations like masking producing larger effects. The study utilizes a staircasing procedure to find the optimal contrast of the mask stimuli to produce a performance impairment to the illusory perception comparable to the attentional condition, both in terms of perceptual performance (i.e., indicating whether the target contained the Kanizsa illusion) and metacognition (i.e., confidence in the response).

The results show a clear dissociation between the three levels of visual processing in terms of temporal dynamics. Local contrast was represented at an early stage (~80 ms), while collinearity and illusory perception were associated with later stages (~200-250 ms). Furthermore, the results provide clear evidence in support of a dissociation between the effects of perceptual and attentional processes on conscious access: while the former affected both neuronal correlates of collinearity and illusory perception, the latter did not have any effect on the processing of the more complex visual features involved in the illusion perception.

Weaknesses:

The design of the study and the results presented are very similar to those in Fahrenfort et al. (2017), reducing its novelty. Similar to the current study, Fahrenfort et al. (2017) tested the idea that if both masking and AB impact perceptual integration, they should affect the neural markers of perceptual integration in a similar way. They found that behavioural performance (hit/false alarm rate) was affected by both masking and AB, even though only the latter was significant in the unmasked condition. An early classification peak was instead only affected by masking. However, a late classification

peak showed a pattern similar to the behavioural results, with classification affected by both masking and AB.

The interpretation of the results mainly centres on the theoretical framework of the recurrent processing theory of consciousness (Lamme, 2020), which lead to the assumption that local contrast, collinearity, and the illusory perception reflect feedforward, local recurrent, and global recurrent connections, respectively. It should be mentioned, however, that this theoretical prediction is not directly tested in the study. Moreover, the evidence for the dissociation between illusion and collinearity in terms of lateral and feedback connections seems at least limited. For instance, Kok et al. (2016) found that, whereas bottom-up stimulation activated all cortical layers, feedback activity induced by illusory figures led to a selective activation of the deep layers. Lee & Nguyen (2001), instead, found that V1 neurons respond to illusory contours of the Kanizsa figures, particularly in the superficial layers. They all mention feedback connections, but none seem to point to lateral connections.

Moreover, the evidence in favour of primarily lateral connections driving collinearity seems mixed as well. On one hand, Liang et al. (2017) showed that feedback and lateral connections closely interact to mediate image grouping and segmentation. On the other hand, Stettler et al. (2002) showed that, whereas the intrinsic connections link similarly oriented domains in V1, V2 to V1 feedback displays no such specificity. Furthermore, the other studies mentioned in the manuscript did not investigate feedback connections but only lateral ones, making it difficult to draw any clear conclusions.

We thank the reviewer for their careful review and positive assessment of our study, as well as for their constructive criticism and helpful suggestions. We provide a more detailed point-by-point response in the “recommendations for the authors” section below. In brief, we addressed the reviewer’s comments and suggestions by better relating our study to Fahrenfort et al.’s (2017) paper and by highlighting the limitations inherent in linking our findings to distinct neural mechanisms (in particular, to lateral vs. feedback connections).

Recommendations for the authors:

Reviewer #1 (Recommendations For The Authors):

- *Methods: it states that "The distance between the three Pac-Man stimuli as well as between the three aligned two-legged white circles was 2.8 degrees of visual angle". It is unclear what this distance refers to. Is it the shortest distance between the edges of the objects?*

It is indeed the shortest distance between the edges of the objects. This is now included in the Methods.

- *Methods: It's unclear to me if the mask updating procedure during the experimental session was based on detection rate or on the perceptual performance index reported on Fig1D. Please clarify.*

It was based on accuracy calculated over 32 trials. We have included this information in the Methods.

- *Methods and Results: I did not understand why the described procedure used to ensure that confidence ratings are not contaminated by differences in perceptual performance was necessary. To me, it just seems to make the "no manipulations" and "both manipulations" less comparable to the other 2 conditions.*

To calculate accurate estimates of metacognitive sensitivity for the two matched conditions, we wanted participants to make use of the full confidence scale (asking them to distribute their responses evenly over all ratings within a block). By mixing all conditions in the same block, we would have run the risk of participants anchoring their confidence ratings to the unmatched very easy and very difficult conditions (no and both manipulations condition). We made this point explicit in the Results section and in the Methods section:

“To ensure that the distribution of confidence ratings in the performancematched masked and AB condition was not influenced by participants anchoring their confidence ratings to the unmatched very easy and very difficult conditions (no and both manipulations condition, respectively), the masked and AB condition were presented in the same experimental block, while the other block type included the no and both manipulations condition.”

“To ensure that confidence ratings for these matched conditions (masked, long lag and unmasked, short lag) were not influenced by participants anchoring their confidence ratings to the very easy and very difficult unmatched conditions (no and both manipulations, respectively), one type of block only contained the matched conditions, while the other block type contained the two remaining, unmatched conditions (masked, short lag and unmasked, long lag).”

| - *Methods: what priors were used for Bayesian analyses?*

Bayesian statistics were calculated in JASP (JASP Team, 2024) with default prior scales (Cauchy distribution, scale 0.707). This is now added to the Methods.

| - *Results, line 162: It states that classifiers were applied on "raw EEG activity" but the Methods specify preprocessing steps. "Preprocessed EEG activity" seems more appropriate.*

We changed the term to “preprocessed EEG activity” in the Methods and to “(minimally) preprocessed EEG activity (see Methods)” in the Results, respectively.

| - *Results, line 173: The effect of masking on local contrast decoding is reported as "marginal". If the alpha is set at 0.05, it seems that this effect is significant and should not be reported as marginal.*

We changed the wording from “marginal” to “small but significant.”

| - *Fig1: The fixation cross is not displayed.*

Because adding the fixation cross would have made the figure of the trial design look crowded and less clear, we decided to exclude it from this schematic trial representation. We are now stating this also in the legend of figure 1.

| - *Fig 3A: In the upper left panel, isn't there a missing significant effect of the "local contrast training and testing" condition in the first window? If not, this condition seems oddly underpowered compared to the other two conditions.*

Thanks for the catch! The highlighting in bold and the significance bar were indeed lacking for this condition in the upper left panel (blue line). We corrected the figure in our revision.

| - *Supplementary text and Fig S6: It is unclear to me why the two control analyses (the black lines vs. the green and purple lines) are pooled together in the same figure. They*

seem to test for different, non-comparable contrasts (they share neither training nor testing sets), and I find it confusing to find them on the same figure.

We agree that this may be confusing, and deleted the results from one control analysis from the figure (black line, i.e., training on contrast, testing on illusion), as the reviewer correctly pointed out that it displayed a non-comparable analysis. Given that this control analysis did not reveal any significant decoding, we now report its results only in the Supplementary text.

- Fig S6: I think the title of the legend should say testing on the non-illusory triangle instead of testing on the illusory triangle to match the supplementary text.

This was a typo – thank you! Corrected.

Reviewer #2 (Recommendations For The Authors):

Issue #1: One key asymmetry between the three levels of T2 attributes (i.e.: local contrast; non-illusory triangle; illusory Kanisza triangle) is related to the top-down conscious posture driven by the task that was exclusively focusing on the last attribute (illusory Kanisza triangle). Therefore, any difference in EEG decoding performance across these three levels could also depend to this asymmetry. For instance, if participants were engaged to report local contrast or non-illusory triangle, one could wonder if decoding performance could differ from the one used here. This potential confound was addressed by the authors by using decoders trained in different datasets in which the main task was to report one the two other attributes. They could then test how classifiers trained on the task-related attribute behave on the main dataset. However, this part of the study is crucial but not 100% clear, and the links with the results of these control experiments are not fully explicit. Could the author better clarify this important point (see also Issue #1 and #3).

The reviewer raises an important point, alluding to potential differences between decoded features regarding task relevance. There are two separate sets of analyses where task relevance may have been a factor, our main analyses comparing illusion to contrast decoding, and our comparison of collinearity vs. illusion-specific processing.

In our main analysis, we are indeed reporting decoding of a task-relevant feature (illusion) and of a task-irrelevant feature (local contrast, i.e., rotation of the Pac-Man inducers). Note, however, that the Pac-Man inducers were always task-relevant, as they needed to be processed to perceive illusory triangles, so that local contrast decoding was based on task-relevant stimulus elements, even though participants did not respond to local contrast differences in the main experiment. However, we also ran control analyses testing the effect of task-relevance on local contrast decoding in our independent training data set and in another (independent) study, where local contrast was, in separate experimental blocks, task-relevant or task-irrelevant. The results are reported in the Supplementary Text and in Figure S5. In brief, task-relevance did not improve early (70–95 ms) decoding of local contrast. We are thus confident that the comparison of local contrast to illusion decoding in our main analysis was not substantially affected by differences in task relevance. In our previous manuscript version, we referred to these control analyses only in the collinearity-vs-illusion section of the Results. In our revision, we added the following in the Results section comparing illusion to contrast decoding:

“In the light of evidence showing that unconscious processing is susceptible to conscious top-down influences (Kentridge et al., 2004; Kiefer & Brendel, 2006; Naccache et al., 2002), we ran control analyses showing that early local contrast decoding was not improved by rendering contrast task-relevant (see Supplementary Information and Fig. S5), indicating that these

differences between illusion and contrast decoding did not reflect differences in task-relevance.”

In addition to our main analysis, there is the concern that our comparison of collinearity vs. illusion-specific processing may have been affected by differences in task-relevance between the stimuli inducing the non-illusory triangle (the “two-legged white circles”, collinearity-only) and the stimuli inducing the Kanizsa illusion (the PacMan inducers, collinearity-plus-illusion). We would like to emphasize that in our main analysis classifiers were always used to decode T2 illusion presence vs. absence (collinearity-plus-illusion), and never to decode T2 collinearity-only. To distinguish collinearity-only from collinearity-plus-illusion processing, we only varied the training data (training classifiers on collinearity-only or collinearity-plus-illusion), using the independent training data set, where collinearity-only and collinearity-plus-illusion (and rotation) were task-relevant (in separate blocks). As discussed in the Supplementary Information, for this analysis approach to be valid, collinearity-only processing should be similar for the illusory and the non-illusory triangle, and this is what control analyses demonstrated (Fig. S7). In any case, general task-relevance was equated for the collinearity-only and the collinearity-plus-illusion classifiers.

Finally, in supplementary Figure 6 we also show that our main results reported in Figure 2 (discussed at the top of this response) were very similar when the classifiers were trained on the independent localizer dataset in which each stimulus feature could be task-relevant.

Together, for the reasons described above, we believe that differences in EEG decoding performance across these three stimulus levels did are unlikely to depend also depend on a “task-relevance” asymmetry.

Issue #2: Following on my previous point the authors should better mention the concept of conscious influences on unconscious processing that led to a full revision of the notion of automaticity in cognitive science [1 , 2 , 3 , 4]. For instance, the discovery that conscious endogenous temporal and spatial attention modulate unconscious subliminal processing paved the way to this revision. This concept raises the importance of Issue#1: equating performance on the main task across AB and masking is not enough to guarantee that differences of neural processing of the unattended attributes of T2 (i.e.: task-unrelated attributes) are not, in part, due to this asymmetry rather than to a systematic difference of unconscious processing strengtsh [5 , 6-8]. Obviously, the reported differences for real-triangle decoding between AB and masking cannot be totally explained by such a factor (because this is a task-unrelated attribute for both AB and masking conditions), but still this issue should be better introduced, addressed, clarified (Issue #1 and #3) and discussed.

We would like to refer to our response to the previous point: Control analyses for local contrast decoding showed that task relevance had no influence on our marker for feedforward processing. Most importantly, as outlined above, we did not perform real-triangle decoding – all our decoding analyses focused on comparing collinearity-only vs. collinearity-plus-illusion were run on the task-relevant T2 illusion (decoding its presence vs. absence). The key difference was solely the training set, where the collinearity-only classifier was trained on the (task-relevant) real triangle and the collinearity-plus-illusion classifier was trained on the (task-relevant) Kanizsa triangle. Thus, overall task relevance was controlled in these analyses.

In our revision, we are now also citing the studies proposed by the reviewer, when discussing the control analyses testing for an effect of task-relevance on local contrast decoding:

“In the light of evidence showing that unconscious processing is susceptible to conscious top-down influences (Kentridge et al., 2004; Kiefer & Brendel, 2006; Naccache et al., 2002), we ran control analyses showing that early local contrast decoding was not improved by rendering

contrast task-relevant (see Supplementary Information and Fig. S5), indicating that these differences between illusion and contrast decoding did not reflect differences in task-relevance.”

Issue #3: In terms of clarity, I would suggest the authors to add a synthetic figure providing an overall view of all pairs of intra and cross-conditions decoding analyses and mentioning main task for training and testing sets for each analysis (see my previous and related points). Indeed, at one point, the reader can get lost and this would not only strengthen accessibility to the detailed picture of results, but also pinpoint the limits of the work (see previous point).

We understand the point the reviewer is raising and acknowledge that some of our analyses, in particular those using different training and testing sets, may be difficult to grasp. But given the variety of different analyses using different training and testing sets, different temporal windows, as well as different stimulus features, it was not possible to design an intuitive synthetic figure summarizing the key results. We hope that the added text in the Results and Discussion section will be sufficient to guide the reader through our set of analyses.

In our revision, we are now more clearly highlighting that, in addition to presenting the key results in our main text that were based on training classifiers on the T1 data, “we replicated all key findings when training the classifiers on an independent training set where individual stimuli were presented in isolation (Fig. 3A, results in the Supplementary Information and Fig. S6).” For this, we added a schematic showing the procedure of the independent training set to Figure 3, more clearly pointing the reader to the use of a separate training data set.

Issue #4: In the light of these findings the authors should discuss more thoroughly the question of unconscious high-level representations in masking versus AB: in particular, a longstanding issue relates to unconscious semantic processing of words, numbers or pictures. According to their findings, they tend to suggest that semantic processing should be more enabled in AB than in masking. However, a rich literature provided a substantial number of results (including results from the last authors Simon Van Gaal) that tend to support the notion of unconscious semantic processing in subliminal processing (see in particular: [9 , 10 , 11 , 12 , 13]). So, and as mentioned by the authors, while there is evidence for semantic processing during AB they should better discuss how they would explain unconscious semantic subliminal processing. While a possibility could be to question the unconscious attribute of several subliminal results, the same argument also holds for AB studies. Another possible track of discussion would be to differentiate AB and subliminal perception in terms of strength and durability of the corresponding unconscious representations, but not necessarily in terms of cognitive richness. Indeed, one may discuss that semantic processing of stimuli that do not need complex spatial integration (e.g.: words or digits as compared to illusory Kanisza tested here) can still be observed under subliminal conditions.

We thank the reviewer for pointing us to this shortcoming of our previous Discussion. Note that our data does not directly speak to the question of high-level unconscious representations in masking vs AB, because such conclusions would hinge on the operational definition of consciousness one adheres to (also see response to Reviewer 1). Nevertheless, we do follow the reviewer’s suggestions and added the following in the Discussion (also addressing a point about other forms of attention raised by Reviewer 1):

“Clearly, these findings do not imply that unconscious high-level (e.g., semantic) processing can only occur during inattention, nor do they necessarily generalize to other forms of inattention. Indeed, while the AB represents a prime example of late attentional filtering, other ways of inducing inattention or distraction (e.g., by manipulating spatial attention) may

filter information earlier in the processing hierarchy (e.g., Luck & Hillyard, 1994 vs. Vogel et al., 1998).”

And, in a following paragraph in the Discussion:

“Such deep feedforward processing can be sufficient for unconscious high-level processing, as indicated by a rich literature demonstrating high-level (e.g., semantic) processing during masking (Kouider & Dehaene, 2007; Van den Bussche et al., 2009; van Gaal & Lamme, 2012). Thus, rather than enabling high-level unconscious processing, preserved local recurrency during inattention may afford other processing advantages linked to its proposed role in perceptual integration (Lamme, 2020), such as integration of stimulus elements over space or time.

Reviewer #3 (Recommendations For The Authors):

(1) The objective of Fahrenfort et al., 2017 seems very similar to that of the current study. What are the main differences between the two studies? Moreover, Fahrenfort et al., 2017 conducted similar decoding analyses to those performed in the current study.

Which results were replicated in the current study, and which ones are novel? Highlighting these differences in the manuscript would be beneficial.

We now provide a more comprehensive coverage of the study by Fahrenfort et al., 2017. In the Introduction, we added a brief summary of the key findings, highlighting that this study’s findings could have reflected differences in task performance rather than differences between masking and AB:

“For example, Fahrenfort and colleagues (2017) found that illusory surfaces could be decoded from electroencephalogram (EEG) data during the AB but not during masking. This was taken as evidence that local recurrent interactions, supporting perceptual integration, were preserved during inattention but fully abolished by masking. However, masking had a much stronger behavioral effect than the AB, effectively reducing task performance to chance level. Indeed, a control experiment using weaker masking, which resulted in behavioral performance well above chance similar to the main experiment’s AB condition, revealed some evidence for preserved local recurrent interactions also during masking. However, these conditions were tested in separate experiments with small samples, precluding a direct comparison of perceptual vs. attentional blindness at matched levels of behavioral performance. To test ...”

In the Results, we are now also highlighting this key advancement by directly referencing the previous study:

“Thus, whereas in previous studies task performance was considerably higher during the AB than during masking (e.g., Fahrenfort et al., 2017), in the present study the masked and the AB condition were matched in both measures of conscious access.” When reporting the EEG decoding results in the Results section, we continuously cite the Fahrenfort et al. (2017) study to highlight similarities in the study’s findings. We also added a few sentences explicitly relating the key findings of the two studies:

“This suggests that the AB allowed for greater local recurrent processing than masking, replicating the key finding by Fahrenfort and colleagues (2017). Importantly, the present result demonstrates that this effect reflects the difference between the perceptual vs. attentional manipulation rather than differences in behavior, as the masked and the AB condition were matched for perceptual performance and metacognition.”

“This similarity between behavior and EEG decoding replicates the findings of Fahrenfort and colleagues (2017) who also found a striking similarity between late Kanizsa decoding (at

406 ms) and behavioral Kanizsa detection. These results indicate that global recurrent processing at these later points in time reflected conscious access to the Kanizsa illusion.”

We also more clearly highlighted where our study goes beyond Fahrenfort et al.’s (2017), e.g., in the Results:

“The addition of this element of collinearity to our stimuli was a key difference to the study by Fahrenfort and colleagues (2017), allowing us to compare non-illusory triangle decoding to illusory triangle decoding in order to distinguish between collinearity and illusion-specific processing.”

And in the Discussion:

“Furthermore, the addition of line segments forming a non-illusory triangle to the stimulus employed in the present study allowed us to distinguish between collinearity and illusion-specific processing.”

Also, in the Discussion, we added a paragraph “summarizing which results were replicated in the current study, and which ones are novel”, as suggested by the reviewer:

“This pattern of results is consistent with a previous study that used EEG to decode Kanizsa-like illusory surfaces during masking and the AB (Fahrenfort et al., 2017). However, the present study also revealed some effects where Fahrenfort and colleagues (2017) failed to obtain statistical significance, likely reflecting the present study’s considerably larger sample size and greater statistical power. For example, in the present study the marker for feedforward processing was weakly but significantly impaired by masking, and the marker for local recurrency was significantly impaired not only by masking but also by the AB, although to a lesser extent. Most importantly, however, we replicated the key findings that local recurrent processing was more strongly impaired by masking than by the AB, and that global recurrent processing was similarly impaired by masking and the AB and closely linked to task performance, reflecting conscious access. Crucially, having matched the key conditions behaviorally, the present finding of greater local recurrency during the AB can now unequivocally be attributed to the attentional vs. perceptual manipulation of consciousness.”

Finally, we changed the title to “Distinct neural mechanisms underlying perceptual and attentional impairments of conscious access despite equal task performance” to highlight one of the crucial differences between the Fahrenfort et al., study and this study, namely the fact that we equalized task performance between the two critical conditions (AB and masking).

(2) It is not clear from the text the link between the current study and the literature on the role of lateral and feedback connections in consciousness (Lamme, 2020). A better explanation is needed.

To our knowledge, consciousness theories such as recurrent processing theory by Lamme make currently no distinction between the role of lateral and feedback connections for consciousness. The principled distinction lies between unconscious feedforward processing and phenomenally conscious or “preconscious” local recurrent processing, where local recurrency refers to both lateral (or horizontal) and feedback connections. We added a sentence in the Discussion:

“As current theories do not distinguish between the roles of lateral vs. feedback connections for consciousness, the present findings may enrich empirical and theoretical work on perceptual vs. attentional mechanisms of consciousness ...”

(3) When training on T1 and testing on T2, EEG data showed an early peak in local contrast classification at 75-95 ms over posterior electrodes. The authors stated that this

modulation was only marginally affected by masking (and not at all by AB); however, the main effect of masking is significant. Why was this effect interpreted as nonrelevant?

Following this and Reviewer 1's comment, we changed the wording from "marginal" to "weak but significant." We considered this effect "weak" and of lesser relevance, because its Bayes factor indicated that the alternative hypothesis was only 1.31 times more likely than the null hypothesis of no effect, representing only "anecdotal" evidence, which is in sharp contrast to the robust effects of the consciousness manipulations on illusion decoding reported later. Furthermore, later ANOVAs comparing the effect of masking on contrast vs. illusion decoding revealed much stronger effects on illusion decoding than on contrast decoding ($BFs > 3.59 \times 10^4$).

(4) The decoding analysis on the illusory percept yielded two separate peaks of decoding, one from 200 to 250 ms and another from 275 to 475 ms. The early component was localized occipitally and interpreted as local sensory processing, while the late peak was described as a marker for global recurrent processing. This latter peak was localized in the parietal cortex and associated with the P300. Can the authors show the topography of the P300 evoked response obtained from the current study as a comparison? Moreover, source reconstruction analysis would probably provide a better understanding of the cortical localization of the two peaks.

Figure S4 now shows the P300 from electrode Pz, demonstrating a stronger positivity between 375 and 475 ms when the illusory triangle was present than when it was absent. We did not run a source reconstruction analysis.

(5) The authors mention that the behavioural results closely resembled the pattern of the second decoding peak results. However, they did not show any evidence for this relationship. For instance, is there a correlation between the two measures across or within participants? Does this relationship differ between the illusion report and the confidence rating?

This relationship became evident from simply eyeballing the results figures: Both in behavior and EEG decoding performance dropped from the both-manipulations condition to the AB and masked conditions, while these conditions did not differ significantly. Following a similar observation of a close similarity between behavior and the second/late illusion decoding peak in the study by Fahrenfort et al. (2017), we adopted their analysis approach and ran two additional ANOVAs, adding "measure" (behavior vs. EEG) as a factor. For this analysis, we dropped the both-manipulations condition due to scale restrictions (as noted in footnote 1: "We excluded the bothmanipulations condition from this analysis due to scale restrictions: in this condition, EEG decoding at the second peak was at chance, while behavioral performance was above chance, leaving more room for behavior to drop from the masked and AB condition."). The analysis revealed that there were no interactions with condition:

"The pattern of behavioral results, both for perceptual performance and metacognitive sensitivity, closely resembled the second decoding peak: sensitivity in all three metrics dropped from the no-manipulations condition to the masked and AB conditions, while sensitivity did not differ significantly between these performancematched conditions (Fig. 2C). Two additional rm ANOVAs with the factors measure (behavior, second EEG decoding peak) and condition (no-manipulations, masked, AB)¹ for perceptual performance and metacognitive sensitivity revealed no significant interaction (performance: $F_{2,58}=0.27$, $P=0.762$, $BF_{01}=8.47$; metacognition: $F_{2,58}/_{sub}=0.54$, $P=0.586$, $BF_{2,58}=6.04$). This similarity between behavior and EEG decoding replicates the findings of Fahrenfort and colleagues (2017) who also found a striking similarity between late Kanizsa decoding (at 406 ms) and behavioral Kanizsa detection. These results indicate that global recurrent processing at these later points in time reflected conscious access to the Kanizsa illusion."

(6) The marker for illusion-specific processing emerged later (200-250 ms), with the nonmanipulation decoding performing better after training on the illusion than the nonillusory triangle. This difference emerged only in the AB condition, and it was fully abolished by masking. The authors confirmed that the illusion-specific processing was not affected by the AB manipulations by running a rm ANOVA which did not result in a significant interaction between condition and training set. However, unlike the other non-significant results, a Bayes Factor is missing here.

We added Bayes factors to all (significant and non-significant) rm ANOVAs.

(7) The same analysis yielded a second illusion decoding peak at 375-475 ms. This effect was impaired by both masking and AB, with no significant differences between the two conditions. The authors stated that this result was directly linked to behavioural performance. However, it is not clear to me what they mean (see point 5).

We added analyses comparing behavior and EEG decoding directly (see our response to point 5).

(8) The introduction starts by stating that perceptual and attentional processes differently affect consciousness access. This differentiation has been studied thoroughly in the consciousness literature, with a focus on how attention differs from consciousness (e.g., Koch & Tsuchiya, TiCS, 2007; Pitts, Lutsyshyna & Hillyard, Phil. Trans. Roy. Soc. B Biol. Sci., 2018). The authors stated that "these findings confirm and enrich empirical and theoretical work on perceptual vs. attentional mechanisms of consciousness clearly distinguishing and specifying the neural profiles of each processing stage of the influential four-stage model of conscious experience". I found it surprising that this aspect was not discussed further. What was the state of the art before this study was conducted? What are the mentioned neural profiles? How did the current results enrich the literature on this topic?

We would like to point out that our study is not primarily concerned with the conceptual distinction between consciousness and attention, which has been the central focus of e.g., Koch and Tsuchiya (2007). While this literature was concerned with ways to dissociate consciousness and attention, we tacitly assumed that attention and consciousness are now generally considered as different constructs. Our study is thus not dealing with dissociations between attention and consciousness, nor with the distinction between phenomenal consciousness and conscious access, but is concerned with different ways of impairing conscious access (defined as the ability to report about a stimulus), either via perceptual or via attentional manipulations. For the state of the art before the study was conducted, we would like to refer to the motivation of our study in the Introduction, e.g., previous studies' difficulties in unequivocally linking greater local recurrency during attentional than perceptual blindness to the consciousness manipulation, given performance confounds (we expanded this Introduction section). We also expanded a paragraph in the discussion to remind the reader of the neural profiles of the 4-stage model and to highlight the novelty of our findings related to the distinction between lateral and feedback processes:

"As current theories do not distinguish between the roles of lateral vs. feedback connections for consciousness, the present findings may enrich empirical and theoretical work on perceptual vs. attentional mechanisms of consciousness (Block, 2005; Dehaene et al., 2006; Hatamimajoumerd et al., 2022; Lamme, 2010; Pitts et al., 2018; Sergent & Dehaene, 2004), clearly distinguishing the neural profiles of each processing stage of the influential four-stage model of conscious experience (Fig. 1A). Along with the distinct temporal and spatial EEG decoding patterns associated with lateral and feedback processing, our findings suggest a

processing sequence from feedforward processing to local recurrent interactions encompassing lateral-to-feedback connections, ultimately leading to global recurrency and conscious report.”

(9) When stating that this is the first study in which behavioural measures of conscious perception were matched between the attentional blink and masking, it would be beneficial to highlight the main differences between the current study and the one from Fahrenfort et al., 2017, with which the current study shares many similarities in the experimental design (see point 1).

We would like to refer the reviewer to our response to point 1), where we detail how we expanded the discussion of similarities and differences between our present study and Fahrenfort et al. (2017).

(10) The discussion emphasizes how the current study "suggests a processing sequence from feedforward processing to local recurrent interactions encompassing lateral-to-feedback connections, ultimately leading to global recurrency and conscious report". For transparency, it is though important to highlight that one limit of the current study is that it does not provide direct evidence for the specified types of connections (see point 6).

We added a qualification in the Discussion section:

“Although the present EEG decoding measures cannot provide direct evidence for feedback vs. lateral processes, based on neurophysiological evidence, ...”

Furthermore, we added this qualification in the Discussion section:

“It should be noted that the not all neurophysiological evidence unequivocally links processing of collinearity and of the Kanizsa illusion to lateral and feedback processing, respectively (Angelucci et al., 2002; Bair et al., 2003; Chen et al., 2014), so that overlap in decoding the illusory and non-illusory triangle may reflect other mechanisms, for example feedback processing as well.”

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<https://doi.org/10.7554/eLife.97900.2.sa0>