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Why do we see what's not there?

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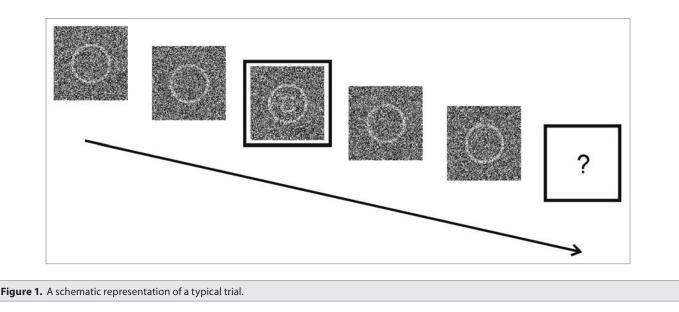
Nonscious perception is not the result of passively processing sensory input, but to large extent of active inference based on previous knowledge. This process of inference does go astray from time to time, and may lead to illusory perception: sometimes people see things that are not there. In a recent study we have shown that this inference may also be influenced by mood. Here we present some additional data, suggesting that illusory percepts are the result of increased top-down processing, which is normally helpful in detecting real stimuli. Finally, we speculate on a possible function of mood-dependent modulation of this top-down processing in social perception in particular.

It is tempting to think of our visual system as a sort of biological video camera, projecting images via the retina onto our mind's eye. This view, however, is clearly oversimplified. Already in the 17th century, now legendary theorists like Descartes, Molyneux, and Berkeley postulated the idea that 'seeing' is not a function of the eyes, but of 'of the soul' (reviewed in ref. 1). It is quite clear nowadays that what we see is not just a function of 'what is out there', but to significant degree influenced by what is going on in our minds. Helmholtz already proposed in the late 19th that vision is an active process, and largely guided by what we already know about the world.²

In the past decade, Helmholtz's idea has seen an enormous boom in theoretical and empirical support in the literature. There is growing consensus that the brain does not passively process the input it receives from the eyes in order to provide us with a visual representation of our environment, but instead continuously generates predictions about what the world should look like. These predictions, based on both memory and expectancy, are subsequently matched with actual visual input. What we are conscious of, is the result of this matching process.3-5 The computational benefits of such a strategy are clear: accurate predictions remove a large portion of redundancy from incoming sensory signals.6 Although the exact neural mechanisms of this predictive process remain somewhat elusive, it is clear that so-called top-down interactions between higher cortical areas, such as the orbitofrontal cortex, and lower-tier visual areas, possibly including the primary visual cortex (V1), play an important role in matching predictions with 'what is out there'.^{3,7}

Top-down modulation of visual processing does obviously affect perception. Expecting a stimulus or being familiar with it lowers detection thresholds, alters its color appearance, and decreases latency of conscious perception.8-10 However, there is ample evidence that the effects of prediction based modulation of visual processing stretch even further: sometimes, expecting a stimulus makes us see one while in fact nothing has been presented at all. Though not completely uncontroversial, there is good evidence that such illusory percepts, too, are the result of topdown modulation of activity in the early visual areas.11-14

Logically, predictive coding models of vision assume that the brain's predictions are purely generated on basis of 'factual knowledge' and statistical inference.⁴ This assumption, however, may be too limited. In a recent study we have demonstrated



that expectancy-induced illusory percepts are strongly modulated by mood. In a challenging face detection task, observers had to detect happy and sad faces embedded in noise. In a significant number of trials in which no face was presented, observers did report a face. Critically, their responses were strongly affected by mood. We manipulated mood of observers by having them listen to music that made them happy or sad. We found that observers were more likely to report illusory happy faces when they were listening to happy music, and vice versa when listening to sad music. The ratio of real happy vs. sad faces was the same for these conditions, however. Therefore, according to strictly expectancy-driven models of predictive coding in vision, mood should not have had an effect. Still, we found that the brain's top-down predictions were 'colored' by the observers' mood.¹⁵

While the computational benefits of using statistical inference in visual processing may be clear, the functional significance of mood-dependent modulations of visual processing is less so. Here, we present some additional electrophysiological data to our recently published work. Moreover, we discuss some recent literature that may shed some light on the question why and how the brain reflects mood in conscious visual perception.

Participants (n = 13, 6 males, mean age 20.3 y) were first year students of the bachelor program in Psychology of the University of Groningen. Written

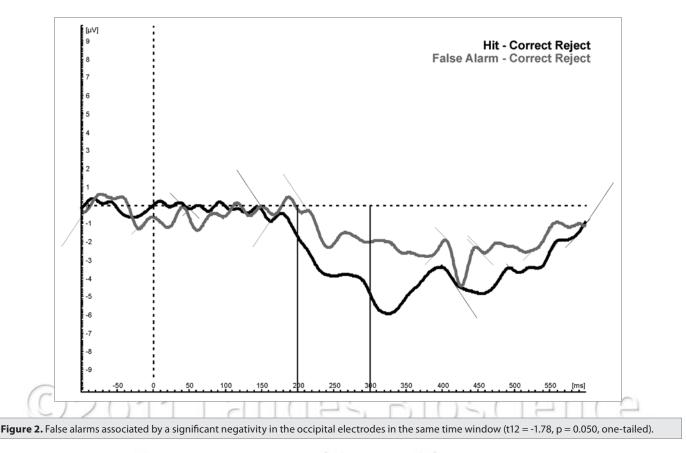
informed consent was obtained from all participants. All participants had normal or corrected-to-normal vision, and reported no neurological or psychiatric problems. This study was approved by local Ethics Committee and conducted according to the Declaration of Helsinki. Visual stimulation was identical to.¹⁵ For a schematic representation of a typical trial, see **Figure 1**.

EEG was recorded using a 32 channel Refa EEG system (TMSi BV, Enschede, The Netherlands), with electrodes positioned according to the 10/20 system. Horizontal and vertical EOG was measured to control for eyeblinks. The EEG signal was digitized and sampled at 500 Hz on a separate acquisition computer. Markers, synchronized with cue onset, were sent with the EEG signal by the stimulation computer to allow for offline segmentation. EEG data was analyzed using Analyzer (Brain Vision Products GmbH, Germany). The raw signal was filtered between 0.5 Hz and 15 Hz, and subsequently corrected for eye movement artifacts. The signal was then segmented into 2,500 ms epochs (1,000 ms pre- and 1,500 ms post cue). Epochs were first baseline-corrected (100 ms baseline), and then checked for artifacts. Segments in which the maximum absolute amplitude exceeded 200 uV were excluded from analysis. Evoked potentials were computed for hits, misses, correct rejects and false alarms. In order to assess neural activity evoked exclusively by perceiving

a face, irrespective of one was presented or not, we subtracted the 'correct reject' activity from the 'hit' and 'false alarm' activity. For statistical analyses, we computed the average activity in the interval from 200–300 ms post stimulus for the two subtraction potentials (hit-correct reject and false alarm-correct reject) in channels O1, O2 and Oz. Activity in this time window in posterior electrodes has been demonstrated to correlate with higher level vision, perceptual integration and visual awareness.¹⁶

In line with our earlier work,15 participants had a false alarm rate of 22% (SD 17%), and a hit rate of 84% (SD 11%). Of all hits, 91% was correctly identified (SD 6%). The evoked potential results show a robust negativity in the posterior electrodes 200-300 ms after stimulus onset for hits vs. correct rejects ($t_{12} = -4.00$, p = 0.001, one-tailed). False alarms, however, were also associated by a significant negativity in the occipital electrodes in the same time window ($t_{12} = -1.78$, p = 0.050, one-tailed) (Fig. 2). Interestingly, overall detection and identification performance were also related to mean VEP amplitude for false alarms: higher performance was related to more negative amplitudes (rho = -0.62, p = 0.012 and rho = -0.50, p = 0.039 respectively).

These results confirm that 'seeing what is not there' is associated with perceptuallike processing. Moreover, since illusory perception is believed to reflect 'pure top-down' processing,¹² the correlation



between illusion-evoked negativity and performance on detection of real stimuli suggests that top-down processing aids in perception of real stimuli.

People sometimes see things that are not there, an effect attributed to the fact that sometimes the brain's top-down interpretation of perceptual input takes over the actual percept. Here, we present some additional data to our recent work on mood congruency effects in top-down processing of visual stimuli: we show that illusory perception of schematic faces is associated with a negative evoked potential 200-300 ms after participants were cued a face could appear. Activity in this time window is believed to reflect feedback processing from higher cortical areas back to early visual areas, playing an important role in perceptual interpretation and integration of information into a coherent conscious percept, and in matching the brain's top-down predictions with actual perceptual input.5-7,16

A striking observation in our data are the correlation between amplitude of visual evoked potentials in response to a false alarm, and accuracy in detection and identification of real stimuli. Larger negativities correspond with better detection and identification performance. Because false alarm-evoked negativity may be considered to reflect 'pure' topdown processing,¹² this correlation hints at the possibility that increased top-down processing aids in processing of real stimuli, at the expense of triggering false alarms.

As stated in the introduction, the exact neural mechanisms of matching perceptual input with top-down predictions remain elusive. We may assume, though, that the presumed top-down predictions may be equated with activation of rough visual schemata or stereotypes.^{3,17} Recent studies using a reverse correlation approach have provided support for the idea that such visual stereotypes indeed may exist for facial features, including emotional expressions.¹⁷⁻¹⁹ The data we present here suggests that when detecting faces in noise, activation of such schemata based on prediction (or, in other words, top-down processing) results in superior detection of stimuli, at the cost of an occasional false alarm.

However, our earlier work shows that the observer's mood affects which schema

is activated (a happy or a sad face, for example). This results in the observed increased sensitivity toward stimuli that are mood-congruent.¹⁵ We propose that this mechanism may serve to fine-tune social interactions, and matching our behavior with the emotions of others: when we are in a happy state of mind, our approach of someone who is sad or angry will be different than when we ourselves are in a bad mood as well.

Interestingly, there is some clinical literature backing up this hypothesis. First, in mood disorders, such as depression, facial recognition is impaired: there is an overall bias to interpret facial expressions as overly negative. In other words, neutral faces appear to be sad, for example.²⁰ We theorize that this may be the result of an over-activation of the visual schema for negative facial expression, which subsequently leads to a (mild) distortion in perception of facial expressions.

Another disorder in which there seems to be a link between top-down processing and impairment in face processing is autism. Recent studies have linked autism to anomalies in feedback or top-down processing.² Interestingly, in particular top-down processing of faces seems to be impaired.^{21,22} Although speculative, it is well possible be that this impairment also interferes with matching face processing with one's own emotional state, leading to social-cognitive impairments.

Interestingly, in earlier work on unconscious processing of visual information, we already proposed that complex behavior, in particular social behavior, may be predominantly guided by conscious visual representations. Facial expressions, for example, can be recognized very rapidly, in absence of visual awareness, within an unconscious face processing network. This network, including the amygdala is believed to play a critical role in guiding social-affective behavior.23 However, although this processing within this network maybe fast and independent of awareness, it is also quite crude: we have shown, for example, that the unconscious recognition of emotional expressions tops of at about 70% in a two-alternative forced choice task, whereas conscious recognition is nearly perfect.²⁴ This superior accuracy of conscious visual processing most likely stems from the larger capacity for incorporating spatial detail.25

Given the importance of accurate emotion recognition in social interaction, we have proposed that the brain may prioritize consciously processed information over unconscious information in nonreflexive decision making-a finding we corroborated in a recent electrophysiological study on texture discrimination.¹⁶ The work presented here suggests an additional benefit of recurrent, and thus conscious,²⁶ visual processing: the widespread interactions within the visual processing network allow for the integration of non-sensory information in sensory representations. Such a view fits well with a recently proposed theory by Marciano and Baumeister, who speculate that consciousness serves a special function in facilitating socio-cultural interaction. In particular, they state that consciousness serves to assign meaning and narrative to external events.²⁷ Although this theory primarily applies to conscious thought and not perception, integrating non-sensory elements within a conscious sensory representation would allow for quicker decision making in socio-cultural interactions.¹⁶

Summarizing, our work thus far shows that people sometimes see things that aren't there. These illusory percepts are a 'side-effect' of top-down modulation of visual processing, and may signal to some extent the observer's present affective state. We hypothesize that this mood-dependent modulation of conscious perception may be particularly useful in guiding social interactions.

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