Deep layers of primary visual cortex encode postdictive perception

Pieter Barkema, Christoph Koenig, Joost Haarsma, Peter Kok

Department of Imaging Neuroscience, Queen Square Institute of Neurology, University College London, London, UK.

Abstract

Neural representations in primary visual cortex (V1) are not solely determined by bottom-up retinal inputs, but also reflect top-down modulations, where bottom-up and top-down signals are reflected in different cortical layers. Subjective perception is thought to reflect the integration of these signals. Here, we investigated whether this mechanism generalizes to postdictive perception, when later information affects the perception of earlier sensory input. A feedback hypothesis predicts this temporal integration reaches early sensory cortex, while a feedforward hypothesis predicts that this sensory input is integrated downstream. We induced a postdictive visual illusion with sound and hypothesized that multisensory regions would feed back postdictive information into V1. We tested this hypothesis using layer-specific 7T fMRI (N=24), retinotopic mapping and a postdictive illusion paradigm. We validated the illusion and retinal effects and found no evidence for univariate BOLD increase. Using multivariate analysis, however, we found that activity patterns in the deep, but not the middle, layers of V1 reflected the contents of illusory percepts, in line with the feedback hypothesis. Informational connectivity analyses revealed that this information was shared with the Superior Temporal Gyrus, a multisensory hub. These results reveal that perceptual inference in primary visual cortex can be modulated by top-down information arriving after the fact.

Keywords: perception; layer fMRI; postdiction; primary visual cortex; multisensory; retinotopy.

Introduction

Primary visual cortex (V1) is traditionally regarded as a unidirectional hierarchical feature extractor along the ventral stream – combining retinotopic representation into more complex objects and beyond (DiCarlo & Cox, 2007). Perception is, however, more than retinal input as shown by hallucinations, illusions and dreams, for example. Recent evidence suggests V1 also receives non-retinal perceptual information, reflected in the neural activity of deep layers (Kok et al., 2016). It is unclear whether this mechanism extends to postdictive perception, where later information affects earlier sensory input. Does this temporal integration occur downstream of V1, where lagging stimuli catch-up, or does postdiction work through top-down modulation of early sensory regions (Stiles et al., 2022)?

To tackle these questions, we take inspiration from the study by Kok et al. (2016) and combine 7T fMRI and retinotopy with an audio-to-visual postdictive illusion. Based on this study, we hypothesize that primary visual cortex activity reflects multisensory postdictive illusions, supporting a feedback hypothesis of postdictive perception.

Methods

Participants: we recruited 24 participants that were highly susceptible to an audio-to-visual postdictive illusion.

Experiment: we used the Audiovisual Rabbit illusion (AVRI) (Stiles et al., 2018) to induce audio-to-visual postdictive illusions (Figure 1). The participant perceives three flashes from left to right, one by one, paired with sounds, but only the first flash and last flash are real. We used two control conditions where either the second sound was omitted (Congruent Two) or a real flash in the middle was added (Congruent Three). Participants were first asked how many flashes they perceived (two or three) and then how confident they were in their answer from ‘not confident at all’ to ‘very confident’.

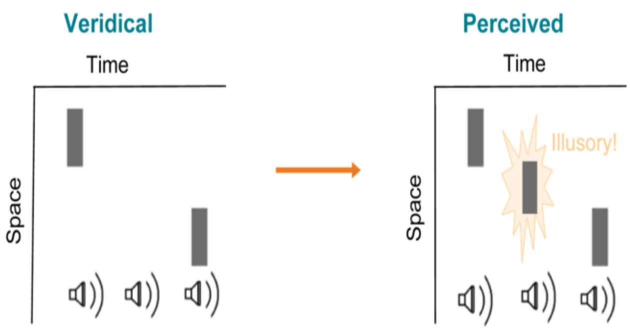

Figure 1: Audiovisual Rabbit Illusion. An audiovisual incongruency induces an illusion that postdictively depends on the last flash-beep pair (adapted from Stiles et al., 2018).

Neuroimaging: we collected 7T fMRI data during the experiment, structural MP2RAGE, and retinotopic mapping data for population receptive field (pRF) mapping analysis (Dumoulin & Wandell, 2008) to evaluate retinotopic specificity.

Multivariate analysis: we test whether neural representations during the illusion were more like the condition when a third flash was actually presented rather than no flash, using correlation analysis.

Results

Behavioural. We screened twenty-four participants for high susceptibility to seeing the illusion with high confidence, while performing well on control conditions. To test whether the illusion succeeded, we compute whether adding a sound to its control leads to significantly more perceived flashes. During the AVRI condition significantly more flashes were perceived than without the second sound ($p<.01$, $t=5.51$).

Neuroimaging. We measured BOLD activity in illusory and control conditions per layer. We found that BOLD amplitude in V1 voxels tuned to the middle flash location reflected retinal input, validating our controls, but we found no evidence to support that BOLD amplitude reflected illusory activity. When applying multivariate analysis, however, we found that voxels in deep layers whose receptive field covered the middle flash encoded the illusory percept ($p=0.03$, $t=2.01$) (Figure 2). Importantly, we do not find this effect in other layers or in other retinotopic locations.

Informational connectivity: We hypothesized that this information might stem from the superior temporal gyrus (Venezia et al., 2017) or hippocampus (Warrington et al., 2025) through top-down connections. We used informational connectivity and found that STG shared significantly more illusory information with V1 deep layers than middle layers ($p=.01$, $t=2.35$), pointing to top-down modulation. This effect was absent for the hippocampus.

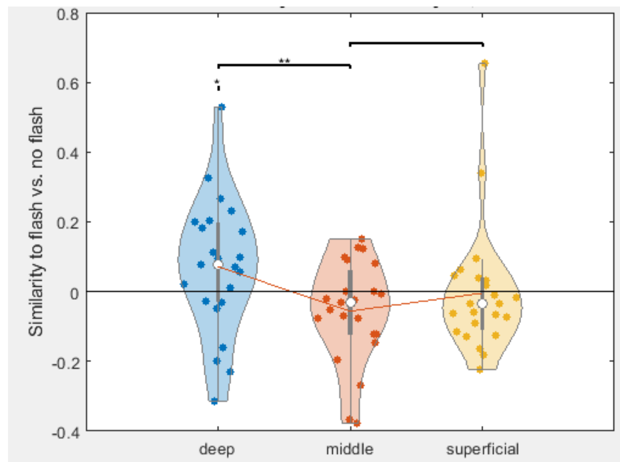

Figure 2: Multivariate analysis per layer. Illusory information was specific to the V1 deep layer and was significantly larger than in V1 middle layer.

Discussion

We investigated whether early sensory cortex plays a role in postdictive perception. We found evidence that primary visual cortex is activated by multisensory postdictive perception through feedback mechanisms. These results also provide support for the notion that the overall amplitude of neural signals is largely driven by retinal input, whereas the *pattern* of activity more closely reflects the contents of subjective perception (Broday-Dvir et al., 2023), likely as a result of integrating bottom-up and top-down signals.

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