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Pupil size directly modulates the feedforward response in human primary visual cortex independently of attention

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ABSTRACT

Controversy revolves around the question of whether psychological factors like attention and emotion can influence the initial feedforward response in primary visual cortex (V1). Although traditionally, the electrophysiological correlate of this response in humans (the C1 component) has been found to be unaltered by psychological influences, a number of recent studies have described attentional and emotional modulations. Yet, research into psychological effects on the feedforward V1 response has neglected possible direct contributions of concomitant pupil-size modulations, which are known to also occur under various conditions of attentional load and emotional state. Here we tested the hypothesis that such pupil-size differences themselves directly affect the feedforward V1 response. We report data from two complementary experiments, in which we used procedures that modulate pupil size without differences in attentional load or emotion while simultaneously recording pupil-size and EEG data. Our results confirm that pupil size indeed directly influences the feedforward V1 response, showing an inverse relationship between pupil size and early V1 activity. While it is unclear in how far this effect represents a functionally-relevant adaptation, it identifies pupil-size differences as an important modulating factor of the feedforward response of V1 and could hence represent a confounding variable in research investigating the neural influence of psychological factors on early visual processing.

Introduction

A classic question in psychology and neuroscience is how early in the processing hierarchy attention can affect sensory responses (Spence, 1999), a question that is also relevant for related processes like the influence of emotion on sensory processing (Vuilleumier, 2005). In humans, the earliest cortical response to visual stimuli arises in V1 after around 60 ms, which is reflected in the C1 component of the human EEG (Jeffreys and Axford, 1972). Traditionally, it has been found that this component is not amenable to modulations by psychological factors like attention (Clark and Hillyard, 1996; Di Russo et al., 2003). Rather, it has been suggested that V1 activity is only modulated late during visual processing, presumably through delayed feedback signals (Boehler et al., 2008; Martinez et al., 1999; Noesselt et al., 2002). Clark and Hillyard (1996), for example, observed attentional enhancements of ERP components that directly follow the C1 (the P1 and N1), but not for the C1 itself. Contrasting with this view, some recent studies have described attentional (Kelly et al., 2008; Rauss et al., 2009, 2012) and emotional C1 modulations (Pourtois et al., 2004; Rossi and Pourtois, 2013; Vanlessen et al., 2014; Zhu and Luo, 2012). For example, Rauss et al. (2009) varied attentional load between task blocks in a discrimination task and demonstrated decreased C1 amplitudes for peripheral task-irrelevant stimuli under increased attentional load. Interestingly, often such modulations were limited to the upper visual field (VF), possibly stemming from the lower spatial resolution of the upper VF, which can hence profit more from attentional enhancements (Pourtois et al., 2008; Rauss et al., 2009). Yet, despite these recent observations, the general notion of attentional and other psychological C1 modulations remains controversial (Ding et al., 2014).

Intriguingly, one possibly important factor has thus far been completely overlooked in this controversy, namely pupil size. Pupil size is known to be modulated by numerous psychological factors, including many of the factors that were recently shown to affect feedforward V1 activity like attentional load and different emotional states (Sirois and Brisson, 2014). This co-occurrence of pupil-size differences with these psychological factors is possibly very relevant since it is conceivable that modulations in V1 activity arise (at least in part) directly from differences in pupil-size rather than from e.g., attentional influences on neural processes in the visual system. Specifically, on a basic level, vision research has shown that pupil size alters the optical properties of the eye (Campbell and Green, 1965), affecting the amount and dispersion of light on the retina and consequently feedforward

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processing of visual information. This suggests that some of the controversy regarding cognitive–affective differences in early visual processing could depend on the size of the pupil at the moment when the C1 is elicited. In this context it is particularly relevant that in the majority of studies reporting psychological C1 effects, the psychological process of interest is engaged some time before a C1-evoking stimulus is presented, leaving enough time for pupil-size changes to occur, and comparisons are often made between trial types that differ in attentional load or emotional state, or even between different experimental blocks, or different participants (e.g., Rauss et al., 2009, 2012; Rossi and Pourtois, 2012; Vanlessen et al., 2014). This overview suggests that it is quite likely that these studies indeed featured different pupil sizes for the different experimental conditions at the moment when the C1 was elicited. Here, we test whether pupil-size variations can directly affect early feedforward visual processing, as indexed by the C1 component.

To address this question, we simultaneously recorded EEG and pupil-size data of human observers in two complementary experiments that modulated pupil size in a fashion devoid of differences in stimulation luminance, attentional load, emotional state, or effort allocation. In Experiment 1, participants covertly attended to a white or a black disk, which were simultaneously presented in the left and right VF (Fig. 1a). Covert attention to these disks modulates pupil size, despite the display being physically identical (Binda et al., 2013; see also Mathot et al., 2013). In Experiment 2 we presented visual illusion stimuli that elicit an illusory brightness perception despite equal overall physical luminance (Fig. 2a; Laeng and Endestad, 2012). Importantly, in both experiments, there was enough time for the pupil to dilate or

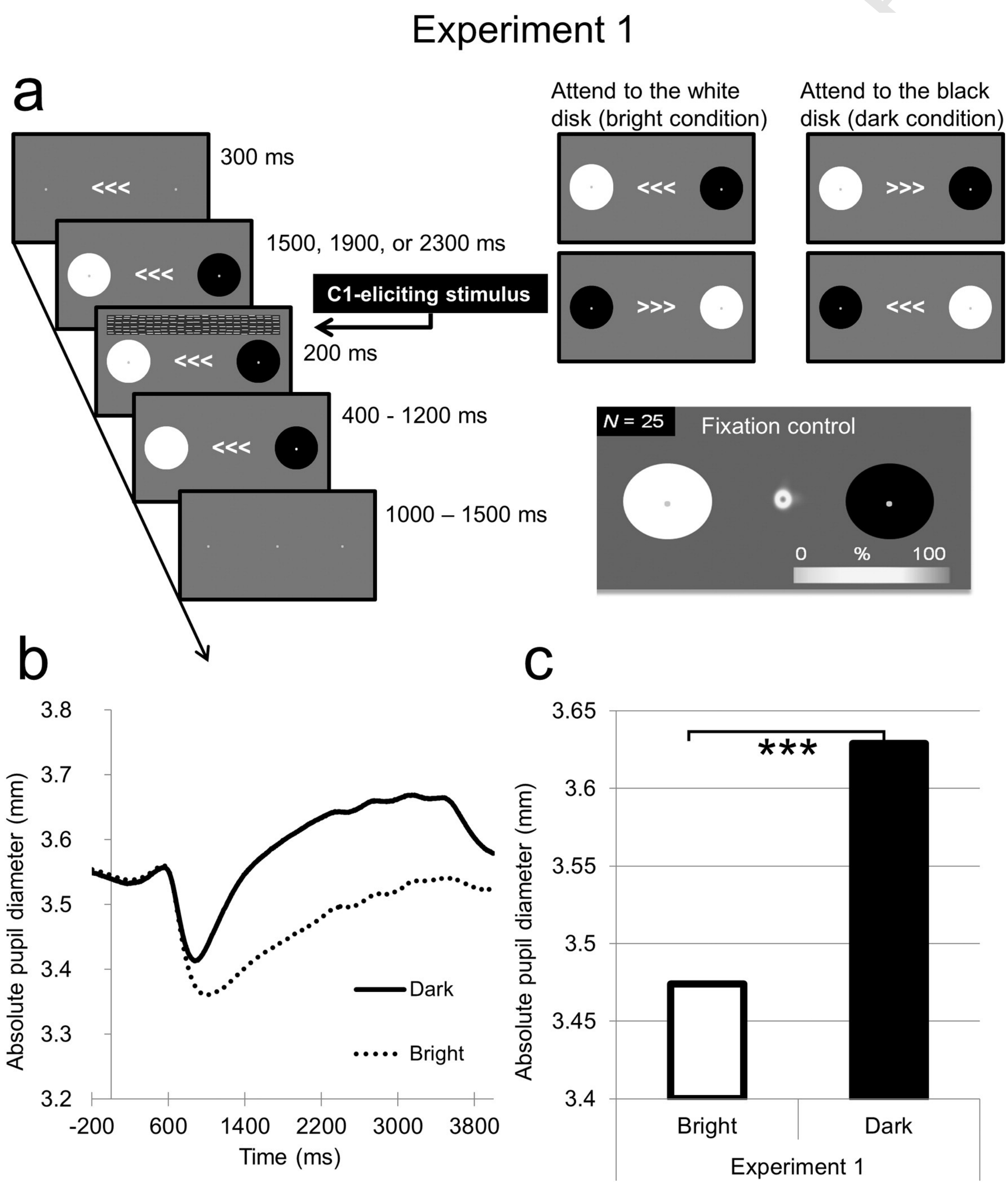

Fig. 1. Experiment 1. (a) Trial examples specifying durations of the different events. Note that C1-eliciting stimuli were presented in the upper VF and lower VF in different trials (upper VF in this example). Pupil size was modulated by orienting participants' attention covertly to the white or black disk. (b) Time course of absolute pupil size change. (c) Pupil-size averages quantified around the moment of C1 stimulation as used in the statistical analysis (*$p < .05$, ***$p < .001$).