Visual evoked potentials to an illusory change in brightness: the Craik–Cornsweet–O'Brien effect

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Can brain electrical activity associated with the Craik–Cornsweet–O'Brien effect (CCOB) be identified in humans? Opposing luminance gradients met in the middle of a square image to create a luminance contrast-defined vertical border. The resulting rectangles on each side of the border were otherwise equiluminant, but appeared to differ in brightness, the CCOB effect. When the contrast gradients were swapped, the participants perceived darker and lighter rectangles trading places. This dynamic CCOB stimulus was reversed 1/s to elicit visual evoked potentials. The CCOB effect was absent in two control conditions. In one, the immediate contrast border, where the gradients met, was replaced by a dark vertical stripe; in the other, the outer segments of both rectangles, where the illusion would otherwise occur, were replaced by dark rectangles, leaving only the contrast-reversing gradients. Visual evoked potential components P1 and N2 were present for the CCOB stimuli, but not the control stimuli. Results are consistent with functional MRI and single unit evidence, suggesting that the brightness of the CCOB effect becomes dissociated from the luminance falling on the eye early in visual processing. These results favor explanations of brightness induction invoking rapid, early amplification of very low spatial-frequency information in the image to approximate natural scenes as opposed to a sluggish brightness adjustment spreading from the contrast border. *NeuroReport* **27:783–786**

NeuroReport 2016, **27**:783–786

Keywords: illusory brightness, O'Brien, visual evoked potentials

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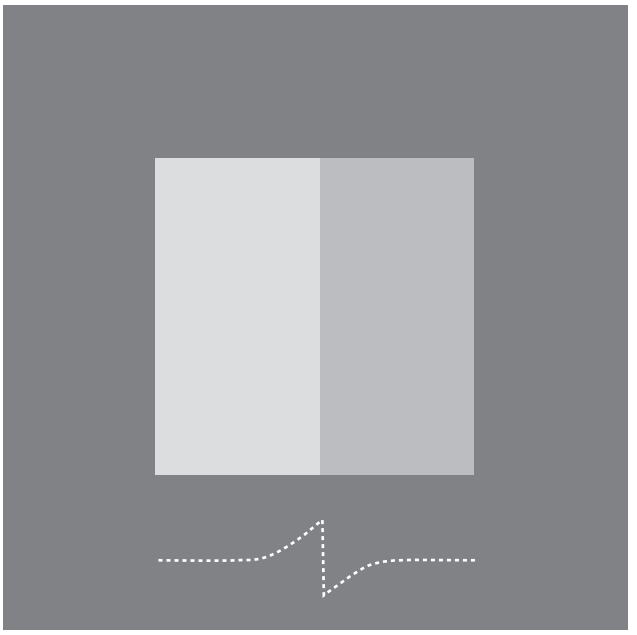
Received 6 April 2016 **accepted** 6 April 2016

Introduction

The visual system organizes light reaching the eyes into a useful rendition of the environment. This involves transformations of the visual information so that it no longer strictly represents the light falling on the eyes. Brightness induction – in which the brightness of part of the visual image is influenced by the luminance of other regions of the visual field – is an important phenomenon in this respect. One instance of brightness induction is the Craik–Cornsweet–O'Brien (CCOB) effect [1–3]. Fig. 1 shows a simple example. Most observers see the right rectangle as darker in comparison with the left rectangle. The actual luminance profile of the image is shown at the bottom. Except for the gradients near the border, the two rectangles are equiluminant. If one covers the border between the rectangles, say with a pencil, the illusion disappears, indicating the importance of the luminance contrast-defined border [5].

Several functional MRI (fMRI) studies in humans have offered conflicting evidence on whether the CCOB illusion is associated only with higher visual cortical areas [6], possibly V1 [7], or even the lateral geniculate nucleus of the thalamus [8]. Single unit recordings from monkeys have shown firing of neurons in V2 to the illusory changes in brightness in a figure with a reversing CCOB border [9].

Fig. 1



The CCOB effect [4]. Reproduced by permission of Brian A. Wandell. CCOB, Craik–Cornsweet–O'Brien effect.

DOI: 10.1097/WNR.0000000000000614

We are aware of no studies of human brain electrical activity associated with CCOB stimuli.

In the present study, we aimed to demonstrate evoked electrical responses in humans to illusory reversals in the brightness of a CCOB stimulus to observe how early in visual processing the CCOB effect emerges, which would have implications for explanations of brightness induction. As shown in Fig. 1, the basic stimulus had a vertical CCOB border creating two rectangles appearing different in brightness. During CCOB presentations, the two border gradients were swapped at a fixed rate so that observers perceived lighter and darker rectangles trading places. Control conditions were run so that the CCOB brain activity could be distinguished from activity associated with the luminance changes in the stimuli.

Methods

Participants

This study was authorized by the university Institutional Review Board for Human Subjects Research (FWA# 00013908). 13 young adult volunteers participated following proper written informed consent.

CCOB stimuli

The 12° square image, mean luminance = 13 cd/m^2, surrounding screen = 3.6 cd/m^2, had a central fixation point at a viewing distance of 80 cm for each 45 s trial. Opposing luminance gradients occupied 3° on either side of the central border, which was either relatively high contrast (18% C at the border) or low contrast (8% C at the border). The luminance of the two halves was identical beyond these gradients. The gradients were reversed at 1/s to elicit visual evoked potentials (VEPs).

Control stimuli

For control 1, the two peripheral, 3° equiluminant sections of the image, where the CCOB illusion would otherwise be experienced, were replaced by dark rectangles (luminance = 2 cd/m^2). The physical changes for the CCOB and control 1 presentations were identical. For control 2, a 1.4° vertical bar covered the border (luminance = 2 cd/m^2), thus eliminating the CCOB illusion, but leaving 77% of the luminance gradients and the periphery of the image visible.

Design

Eight of the 13 volunteers participated in experiment 1, for which there were two trials for each CCOB stimulus (large vs. small contrast gradients). Control 1 was also presented. The remaining five participants were in experiment 2, in which only the small border gradient was presented. Control 2 was also presented. There was one trial per condition.

EEG recordings

Electrode placements were at O_z and 3 cm anterior over the right hemisphere, referenced to the right ear. The two raw electroencephalogram signals were bandpass filtered between 0.01 and 100 Hz and then digitized at 128 samples/s, the video frame rate. Each VEP trial resulted in 45 1-s records (128-sample), which were averaged to yield the VEP waveform.

VEP analysis

The 128 equally spaced voltage measurements across the 1000 ms following each border gradient contrast reversal were averaged across the 45 reversals for each trial. The resulting waveforms were entered into a principal components analysis (PCA) to detect their simpler structure, the temporal regions within the 1000 ms period for which voltages covaried most strongly across conditions and participants. Following an oblique rotation, the temporal locations of the voltages with the largest correlations with each factor – the factor loadings – were identified to interpret the nature of the factor. Each waveform had a factor score on each factor, indexing the extent to which that waveform resembled each factor. The waveforms were then compared between conditions of interest by applying analysis of variance (ANOVA) to their factor scores.

Results

Only one of the 13 participants reported the presence of luminance contrast gradients near the border when the CCOB stimulus was viewed as a stationary image. That is, 12 of 13 simply reported two rectangles differing in brightness.

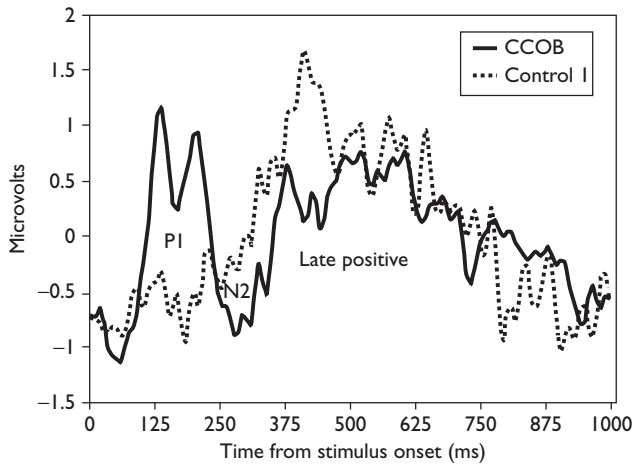
Participants typically reported that the light and dark halves of the figure were switching places for the CCOB stimulus condition. For both the control conditions, all participants reported the presence of luminance gradients and that they changed sides. No participant reported the CCOB effect during either control condition.

Experiment 1

For clarity, gradient (large vs. small contrast), channel (O_z vs. anterior), and trial (1 vs. 2) have been collapsed for Fig. 2, which shows the grand average CCOB and control (periphery eliminated) VEP waveforms. There were no effects of the collapsed variables, as reported below. The CCOB waveform contains a P1 (first positive peak), an N2 (second negative peak), and a late positive component. P1 and N2 appear to be absent for control 1, in which the CCOB illusion was not reported.

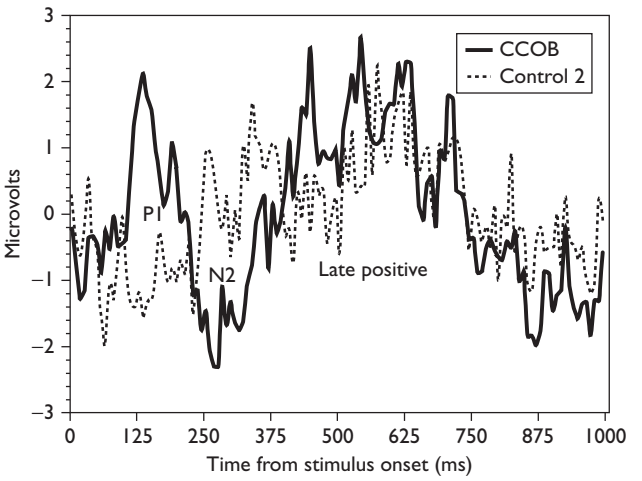
The first three factors (26.4, 19.0, and 8.7% of the total variance) extracted by the PCA were examined. Factor 1 was primarily composed of large loadings within the time period 398–749 ms corresponding to the late positive component (Fig. 2). Factor 2 included large loadings from two time periods – 109 to 172 ms and 203 to 367 ms, the

Fig. 2



CCOB and control 1 VEP waveforms from experiment 1. P1 and N2 components present only for the CCOB stimulus. CCOB, Craik–Cornsweet–O'Brien effect; VEP, visual evoked potential.

Fig. 3



CCOB and control 2 VEP waveforms from experiment 2. P1 and N2 components present only for the CCOB stimulus. CCOB, Craik–Cornsweet–O'Brien effect; VEP, visual evoked potential.

two sections having opposite signs. Thus, factor 2 corresponds to P1 and N2 (Fig. 2). Factor 3 included loadings scattered across the 1000 ms time period and could not be interpreted.

The extent to which each waveform resembled each factor was indexed by its single factor score for each factor. Three separate three-way ANOVAs (CCOB/control 1 X gradient X channel) were carried out with the factors 1, 2, and 3 factor scores as the dependent variables. There were no significant effects in the factor 1 and factor 3 ANOVAs, or for gradient or channel in the factor 2 ANOVA. For factor 2, the CCOB (mean = 0.134) and control 1 (mean = −0.267) factor scores differed significantly, $F(1, 45) = 9.89$, P value less than 0.01, supporting the association of P1 and N2 with the CCOB illusion.

Experiment 2

Fig. 3 shows the VEP waveforms for the CCOB and control 2 conditions. The CCOB waveform, again, has P1, N2, and late positive components, whereas the control 2 condition lacks P1 and N2.

For the experiment 2 data, points before 90 ms and after 800 ms were excluded from the PCA to obtain a 'clean' factor capturing P1/N2. The first three factors (21.8, 19.3, and 13.6% of the total variance) extracted by the PCA were examined. Factors 2 and 3 contained large loadings scattered across the waveform and could not be interpreted. Factor 1 contained large loadings within the time period 101–226 ms and 258–383 ms, the loadings in the two sections having opposite signs. Thus, factor 1 corresponds to P1 and N2 (Fig. 3). On this factor, factor scores for the CCOB and control 2 waveforms differed significantly (mean difference = 1.164), $F(1, 12) = 12.89$, P value less than 0.005, suggesting that P1 and N2 are associated with the CCOB illusion. No other effects were found in the three ANOVAs.

Discussion

In experiment 1, the P1 and N2 components of the VEP were greater to the CCOB stimulus compared with control 1, in which the outer segments, where the illusion would normally occur, had been replaced. In experiment 2, the same VEP components were smaller compared with the CCOB stimulus in the control condition for which the contrast border was occluded, eliminating the illusion.

The overall results suggest that the evoked activity reported here is associated with the CCOB illusion. Figures 2 and 3 show that the CCOB VEP waveforms diverge from the control waveforms just before 100 ms following border reversal, which is relatively early in cortical processing of the visual input. Evidence from electroencephalogram and fMRI suggests that VEP P1 and N2 components have multiple generators, including V1 and other areas within the occipital lobe [10–12]. Thus, although our results suggest that neural processing associated with a simple CCOB effect can emerge within 100 ms of stimulus presentation, these results cannot be tied to specific generators within the occipital lobe.

When the contrast border was eliminated in control 2, the CCOB illusion was not reported. In macaque, many V2 neurons participating in early visual processing have been shown to reflect 'border ownership' properties [13]. Thus, it appears that the part of the visual image within which a contrast border-defined CCOB brightness adjustment takes place is laid out relatively early in visual processing.

Existing evidence is mixed on the temporal limitations of brightness induction [14–16]. The present results do not support filling-in explanations involving sluggish propagation of luminance information away from the luminance contrast border across many neurons having small receptive fields to fill in large areas to create the CCOB effect [17,18]. Our results are most consistent with low spatial-frequency amplification, or nonlinear gain control, carried out by neural filters tuned to different spatial frequencies and operating in parallel to organize the visual input to the cortex [19,20]. Spatial filtering [21] is a characteristic of the earliest cortical processing of visual information, including area V1 [22]. Our results do not argue against a possible role for higher level visual processes mediating the effects of scene interpretation on the CCOB illusion [23].

The present results do not show that P1 and N2 VEP components represent brain activity that is sufficient for conscious awareness of the CCOB illusion. VEP recordings to CCOB stimuli in a backward masking paradigm combined with systematical psychophysical measurements of the CCOB effect would be interesting in this respect.

Perceptual matches can be obtained between CCOB brightness differences and real luminance differences [17,24]. Neural activity associated with both CCOB brightness and actual luminance has been shown in early cortical visual processing using single unit recordings in monkeys [9] and fMRI in humans [7]. Given that the dynamic CCOB VEP methods used here appear to capture brain activity associated with the CCOB effect, it would be useful to compare VEPs with a CCOB stimulus with responses elicited by perceptually similar real luminance changes to make further inferences on the early cortical activity associated with perceived and physical properties of the visual input.

Acknowledgements

The study was funded by California State University, Bakersfield.

Conflicts of interest

There are no conflicts of interest.

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