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Cortical processing of global form, motion and biological motion under low light levels

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ABSTRACT

Advances in potential treatments for rod and cone dystrophies have increased the need to understand the contributions of rods and cones to higher-level cortical vision. We measured form, motion and biological motion coherence thresholds and EEG steady-state visual evoked potentials (SSVEP) responses under light conditions ranging from photopic to scotopic. Low light increased thresholds for all three kinds of stimuli; however, global form thresholds were relatively more impaired than those for global motion or biological motion. SSVEP responses to coherent global form and motion were reduced in low light, and motion responses showed a shift in topography from the midline to more lateral locations. Contrast sensitivity measures confirmed that basic visual processing was also affected by low light. However, comparison with contrast sensitivity function (CSF) reductions achieved by optical blur indicated that these were insufficient to explain the pattern of results, although the temporal properties of the rod system may also play a role. Overall, mid-level processing in extra-striate areas is differentially affected by light level, in ways that cannot be explained in terms of low-level spatiotemporal sensitivity. A topographical shift in scotopic motion SSVEP responses may reflect either changes to inhibitory feedback mechanisms between V1 and extra-striate regions or a reduction of input to the visual cortex. These results provide insight into how higher-level cortical vision is normally organised in absence of cone input, and provide a basis for comparison with patients with cone dystrophies, before and after treatments aiming to restore cone function.

1. Introduction

The current study investigates the impact of low light conditions on global motion, biological motion, and, for the first time, global (static) form perception. This was achieved using a combination of behavioural psychophysics and steady-state visual evoked potentials (SSVEP) under light intensities ranging from photopic to scotopic levels.

The study aimed to understand the contribution of rods and cones to global form, global motion and biological motion perception. These measures have become increasingly used as indicators of visual function beyond early processing in primary visual cortex. With the advance of new treatments for rod and cone dystrophies, such as gene therapy (Bainbridge et al., 2015; Cideciyan et al., 2008; Jacobson et al., 2012; Komáromy et al., 2010; Sundaram et al., 2014; Zelinger et al., 2015) it is becoming increasingly important to understand how different aspects of visual function, including higher cortical visual functions, are influenced by rod and cone loss. Gaining an understanding of visual function in observers with healthy vision under light conditions designed to activate rods and/or cones will provide important baseline information for comparison with retinal dystrophy patients before and after treatment with new therapies.

Form perception is known to be predominantly processed in ventral stream areas such as V4 (Gallant, Shoup, & Mazer, 2000; Ostwald, Lam, Li, & Kourtzi, 2008; Wilkinson et al., 2000), whilst motion perception is dominated by dorsal stream areas such as MT/V5 and MST (Braddick et al., 2001; Harvey, Braddick, &

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Cowey, 2010; Rees, Friston, & Koch, 2000). This functional segregation allows for differences in the development and potential vulnerabilities of the two pathways to be explored and as a result global form and motion perception have been studied extensively in both typically developing (Atkinson et al., 2004; Braddick, Atkinson, & Wattam-Bell, 2003; Golarai, 2009; Gunn et al., 2002) and atypical populations (Atkinson et al., 1997; Ellemberg, Lewis, Maurer, Brar, & Brent, 2002; Kogan et al., 2004; Lewis et al., 2002; Taylor, Jakobson, Maurer, & Lewis, 2009). The present research, leading up to work with patient populations who developed with atypical visual input, will also allow us to better understand the development of global form, global motion and biological motion perception.

Previous research into visual perception under low light has generally studied early-level visual processing including detection of local motion, visual acuity, stereopsis, flicker fusion and spectral sensitivity (Barlow, 1962; Cavonius & Robbins, 1973; Kellnhofer, Ritschel, Vangorp, Myszkowski, & Seidel, 2014; Kinney, 1958; Livingstone & Hubel, 1994; Mandelbaum & Sloan, 1947; Nygaard & Frumkes, 1985; Riggs, 1965; Teller, 2009; Westheimer, 1965). Research exists into reading under scotopic conditions (Chaparro & Young, 1989, 1993), however research into mid- and high-level vision is relatively sparse.

Whilst our study is primarily concerned with the impact of scotopic and mesopic conditions on mid- and high-level vision, it is also important to consider how far these effects may result from the impact of these conditions on the processing of lower-level mechanisms. Area V1 performs local processing of visual signals, which go on to be integrated for global form and motion processing. Duffy and Hubel (2007) looked at basic receptive field properties of V1 neurons in macaques, including directional selectivity and orientation selectivity, and found that these were maintained in scotopic conditions. This has implications for both global motion and form perception as it suggests that at the local level, perception should be unimpaired. However, other properties of scotopic vision may impact on early visual perception which in turn may affect global processing. For example, visual acuity is known to be reduced in scotopic conditions due to the poor spatial resolution of the rod system. Maximum scotopic acuity is ~0.7 LogMAR as opposed to −0.2 LogMAR in photopic conditions (Riggs, 1965). Reduced acuity may lead to reduced sensitivity to local cues necessary for later integration into global constructs. We have investigated elsewhere (Burton et al., 2015) the effects of reduced acuity and contrast sensitivity on global form and motion processing. Scotopic vision also has relatively sluggish temporal properties, at least in central areas of the visual field, which may have an impact on motion processing (Conner, 1982; Takeuchi & De Valois, 2000).

Studies into coherent motion perception under low light have found it to be generally preserved (Billino, Bremmer, & Gegenfurtner, 2008; Grossman & Blake, 1999). Grossman and Blake (1999) examined coherent motion thresholds under low light using random dot kinematograms (RDK). Translational coherent motion moving at 3.2 deg/s was presented to participants in a 2-interval forced choice task under photopic and scotopic conditions and participants were required to indicate the presence of coherent motion. They reported that coherence thresholds were the same under low light as photopic conditions. Billino et al. (2008) tested detection of translational coherent motion under three light intensities using RDKs. They found that detection thresholds became progressively worse as luminance fell from 98.5 to 0.285 and 0.018 cd/m^2.

Biological motion perception was also investigated in these two studies. Billino et al. (2008), asked participants to detect intact or phase-scrambled biological motion under the three light levels mentioned previously. The motion was embedded within random noise dots and on each trial the proportion of noise dots (i.e. dots' signal to noise ratio) was varied to establish participants' perceptual threshold. Performance revealed a U-shaped result with best performance in photopic conditions, worst performance at mesopic light levels (0.285 cd/m^2) and scotopic performance, at 0.018 cd/m^2, falling between the two. In contrast, Grossman and Blake (1999) found biological motion detection to deteriorate in low light. However, they only tested under the two light levels 3.6 and 0.036 cd/m^2. Testing in darker conditions might have resulted in the U-shaped performance described by Billino et al. (2008).

SSVEPs have not previously been used to study scotopic form and motion perception. However, they have been used in the study of global form and motion development (Hou, Gilmore, Pettet, & Norcia, 2009; Norcia et al., 2005; Palomares, Pettet, Vildavski, Hou, & Norcia, 2009; Wattam-Bell et al., 2010; Weinstein et al., 2012). For example, Wattam-Bell et al. (2010) found distinct difference between infant and adult global form and motion SSVEP topographies. It remains unclear how much these differences reflect immaturities in extra-striate regions, or are a result of lower-level limitations of spatial vision in infancy. Testing under low light conditions will therefore also provide further insight into how global form and motion topography is affected when spatial visual input is reduced.

The current study aimed to build on and extend previous research into visual perception in low light. The light conditions extended over a wider range than those previously used (Billino et al., 2008; Grossman & Blake, 1999) to test vision well into the scotopic range. To obtain a fuller picture of extra-striate processing, we tested perception of coherent form as well as of coherent motion and biological motion. As well as behavioural tests of sensitivity, steady-state EEG measures were used to investigate changes in the amplitudes and cortical distributions of neural responses underlying global form, global motion and biological motion perception under different light levels.

2. Material and methods

2.1. General

2.1.1. Participants

Twenty normally sighted participants (mean age 25.2 years, standard deviation 4.6) completed the experiment within the Faculty of Brain Sciences, Division of Psychology and Language Sciences, University College London. Informed consent was obtained before testing commenced. All work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and experiments were approved by the UCL ethics committee.

2.1.2. Light levels

Four light levels were used in the experiment. This was done in order to assess the relative contribution of rods and cones to perceptual sensitivity and cortical EEG responses. Light levels were achieved using sheets of characterised neutral density filters (Sabre International Ltd, UK) which were placed over the display monitor. There was no other light source in the room besides the display screen.

The four luminance levels were classified as photopic (8.7 cd/m^2), high mesopic (0.8 cd/m^2), low mesopic (2.7×10^{-2} cd/m^2) and scotopic (8.7×10^{-4} cd/m^2). The values here refer to the luminance of the dots/lines making up the stimuli; these were presented against a black background with a 3.24 Log Weber Contrast (LogWC) for each light level. Behavioural tests were completed under the four light conditions whilst EEG tests were