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PRACTICAL TOOLS

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A five-channel LED display to investigate UV perception

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Abstract

1. The ability to see ultraviolet (UV) light (<400 nm) may have importance for foraging, communication or navigation in many taxa including insects, crustaceans, fishes, amphibians, reptiles, birds and mammals. Behavioural experiments reveal how vision mediates such behaviour; however, our knowledge of UV perception is constrained by the challenge of creating and calibrating stimuli that reflect or emit UV. Commonly used technologies for displaying visual stimuli—such as computer screens and printers—are designed for human vision and thus are unsuitable for testing UV perception.
2. To overcome this limitation, we designed and constructed a display with five spectral channels with peak wavelengths as follows: red at 629 nm, green at 526 nm, blue at 466 nm, violet at 395 nm and UV at 367 nm. Each pixel of the display consists of five LEDs with a baffle to prevent crosstalk from adjacent pixels and a diffuser to promote uniform colour mixing. The LEDs are driven by high-performance pulse-width-modulated constant-current drivers with a maximum flicker rate of 64 kHz and a maximum frame rate of 6.5 kHz. This method allows colour mixing with wavelengths as low as 350 nm to be calibrated and tested rapidly and concurrently.
3. To demonstrate the utility of this display, we conducted colour detection tests using the anemonefish, *Amphiprion ocellaris*, a species known to have UV-sensitive cones. Fish were able to associate pecking all target colours ('Blue', 'UV-grey' and 'UV') with a food reward, demonstrating for the first time, UV perception in *A. ocellaris*.
4. The RGB-V-UV LED display is a useful device for behavioural tests of colour vision across a broad spectrum (350–650 nm) visible to many animals and can be used to investigate various questions concerning animal perception, including colour discrimination and categorisation. We include design documents and source code so this system can be further developed and modified to investigate other visual behaviours in a variety of taxa.

KEYWORDS

animal behaviour, colour vision, coral reefs, ultraviolet vision, visual ecology

1 | INTRODUCTION

Many animals possess photoreceptors sensitive to wavelengths shorter than 400 nm, or ultraviolet (UV) light, including various insects, crustaceans, fish, amphibians, reptiles, birds and mammals (Hunt et al., 2001; Tovee, 1995). UV vision mediates a variety of behaviours such as predation, foraging, communication, mate selection and navigation (e.g. Bennett et al., 1996; Browman et al., 1994; Hunt et al., 2001; Lisboa et al., 2017). Our understanding of visual perception is largely driven by behavioural experiments to assess the response of animals to calibrated visual stimuli, typically using computer screens or printed paper. However, our knowledge of UV perception is limited because such methods of producing stimuli are designed for human vision and do not controllably emit or reflect UV light.

Previous behavioural studies on UV perception have been mostly limited to UV+ and UV− treatments, relying on spectral filters to block out UV light (Bennett et al., 1996; Smith et al., 2002), barium sulphate (reflectance 300–800 nm) to create UV+ stimuli (Siebeck et al., 2010), or UV-blocking sunscreen to hide UV patterns on animals (e.g. Lisboa et al., 2017). Although these methods allow testing for the presence or absence of UV vision and may reveal aspects of its function, they often lack the ability to control stimulus intensity or are unable to mimic 'complex' colours (also called 'non-spectral'; Stoddard et al., 2020) such as UV-green or UV-yellow. Thus, novel UV-visible stimuli, which can be easily calibrated and controlled, are needed to advance our understanding of UV perception and its ecological significance.

In this study, we introduce a five-channel red-green-blue-violet-ultraviolet (RGB-V-UV) light-emitting diode (LED) display developed specifically for testing animal vision. All of the design documents and computer codes are available at https://github.com/s-bear/UVTV (Powell et al., 2021). Advantages of an LED display include the broad colour space, precise control over chromaticity and brightness, as well as the relative ease and speed of changing the displayed pattern. We demonstrate basic use of the display by conducting a colour detection test with the clownfish *Amphiprion ocellaris* (Cuvier, 1830). We envisage the RGB-V-UV display could be used to assess UV perception in diverse taxa (e.g. fish, reptiles, birds, crustaceans and insects) for various visual tasks.

2 | MATERIALS AND METHODS

2.1 | The RGB-V-UV display

The system consists of (a) the display panel hosting the LEDs, their drivers and optics and (b) a control module which provides power and a USB interface to the panel, both of which may be housed in (c) a semi- or entirely submersible box for aquatic studies. Each display costs approximately 620 AUD (approximately 430 USD) to manufacture, with a one-time fee of 650 AUD. The entire system is driven via a USB interface to a computer running code to generate and display stimuli to the animals under test.

2.1.1 | Display panel

The display panel consists of a printed circuit board (PCB) with an 8 × 12 array of hexagonal pixels on the front side and their drivers on the back. The pixels have a 5.3 mm centre-to-centre spacing and each contains five LEDs ranging from 367 to 629 nm (Figure 1). The specific LEDs were chosen for their coverage of spectral ranges relevant to various animals, including many teleost fishes, birds, insects and some reptiles (reviewed in Briscoe & Chittka, 2001; Hart & Vorobyev, 2005; Schweikert et al., 2018). To promote uniform colour mixing, a diffuser (0.5 mm PTFE sheet) is mounted 1 cm from the LEDs with a baffle to prevent mixing between pixels (Figure 2).

The LEDs are driven by Texas Instruments TLC5955 pulse-width-modulated (PWM) constant-current sinks at each cathode. The drive current of each LED is adjustable with a resolution better than 1.3 μA and the brightness is set by 16-bit pulse-width modulation (PWM) with a maximum flicker frequency of 64.4 kHz, far exceeding the highest critical fusion frequencies reported for invertebrates (400 Hz; Inger et al., 2014) and vertebrates (145 Hz; Bostrom et al., 2016). As designed, refreshing the display data requires just 154 μs, for a theoretical maximum frame rate of 6.5 kHz. See Figure S1, for example, for patterns and spectra generated by the display. The maximum irradiance of each LED channel producible using our USB powered configuration ranged from 2.53 μW/cm^2 for red to 18.92 μW/cm^2 for UV (Figure S2 for all five channels).

2.1.2 | Control module

The control module consists of a PJRC Teensy 3.2 module. It provides a USB interface to the display in addition to storing configuration data. While convenient, the Teensy 3.2 is limited in speed and can only refresh the display at 4 Hz.

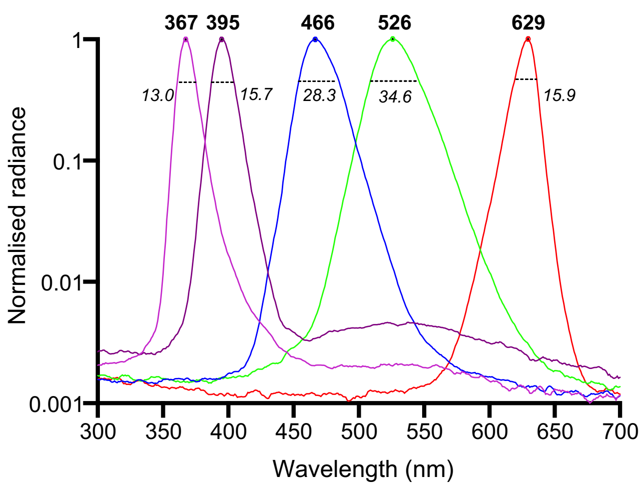

FIGURE 1 Normalised spectral radiance of LEDs as measured with a spectrophotometer. Peak wavelength (**bold**) and the full width at half maximum (FWHM; *italics*) are marked

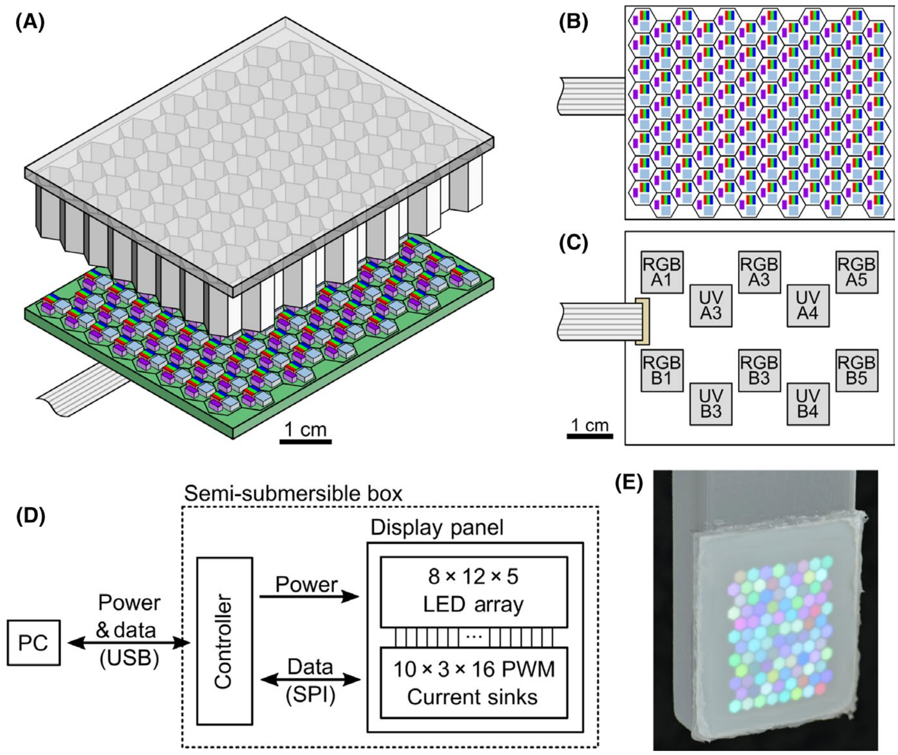

FIGURE 2 (A) A view of the display showing the hexagonal baffle and diffuser for uniform colour mixing. (B) The top of the panel holds the 8 × 12 array of pixels, each with five LEDs. (C) The bottom holds the 10 constant-current LED drivers, each of which powers 48 of the LEDs. (D) Simplified block diagram of the system. (E) LED display in the semi-submersible housing with pixels coloured randomly

2.1.3 | Semi-submersible housing

For aquatic studies, both the display panel and control module can be housed in a semi-submersible box. The box used here was 3D printed from PLA filament and mounted on an aluminium metal frame (Microrax) such that the display was held at a fixed depth. To ensure that the spectrum of the light entering the water is the same as that in air, the PTFE diffuser film was integrated into one wall of the box.

2.2 | Calibration of the display

Visual stimuli generally require calibration in both spectrum and intensity. LEDs typically experience spectral shifts of 2–3 nm over the range of their operating conditions (Manninen & Orreveteläinen, 2007; Schubert, 2006) and may also vary from LED to LED according to their manufacturer, typically by up to 10–20 nm. The LEDs' intensity response is inherently linear under PWM control but may vary in scale. Initially, we set all LEDs in each spectral channel to the same drive current such that each would produce approximately equal photon flux. To correct the intensity variations, we measured each LED's relative intensity by photographing the display at a uniform drive strength with a UV-sensitive camera (Olympus E-PL5, modified by LifePixel). Each LED's drive current was then normalised such that its intensity matched the dimmest of its spectral channel. A second photograph confirms the uniformity, or the procedure may be repeated as necessary (Figure S4). The red LEDs were the least uniform with a standard deviation of 9%, which reduced to 1.6% after two iterations of correction (Table S1). Due to the spatial separation of the LEDs within each pixel, there is additionally a within-pixel spatial variation between the spectral channels that may be discriminable by some animals (Figure S5). The authors were unable to see these variations naturally, but if necessary this may be controlled for by presenting the display at random orientations during behavioural testing.

The spectral uniformity of the display was validated by measuring the spectral irradiance of a random subset (n = 30) of the pixels using a spectrometer (Ocean Optics USB4000) calibrated against a deuterium-halogen lamp (Mikropack DH2000-DUV, calibrated by Ocean Optics). The green LEDs suffered the worst variation here with a standard deviation of 1.30 nm in peak wavelength (Table S2). It is worth noting that for the first display we manufactured, the PTFE diffuser degraded in its ability to scatter red light over the course of a year. Therefore, the diffuser should be checked regularly and replaced if needed.

3 | BEHAVIOURAL EXPERIMENT

To demonstrate the display's use, we conducted colour detection tests with the anemonefish *Amphiprion ocellaris*, a species with known UV-sensitive cones (λ_{max} = ~386 nm) based on molecular and anatomical analyses (Figure S2; Mitchell et al., 2020) and spatial acuity <5.80 cycles/degree (Stieb et al., 2019). The behavioural experiment was conducted between November 2019 and February 2020 under the approval from The University of Queensland's Animal Ethics Committee (SBS/077/17).

We used 10 female individuals (total length = 3–5 cm) that were housed in individual aquaria (40 × 45 × 22 cm deep) within a

Target colour	LED intensity (% of maximum) Red	Green	Blue	Violet	Ultraviolet
'Blue'	2.40%	2.60%	95.0%	0.011%	0.0079%
'UV-grey'	19.9%	12.8%	5.10%	0.0556%	0.179%
'UV'	0	0	0	0	20%

TABLE 1 Relative LED intensity to produce each target colour. The maximum intensity of the violet and UV LEDs is much greater than the others, hence the smaller coefficients

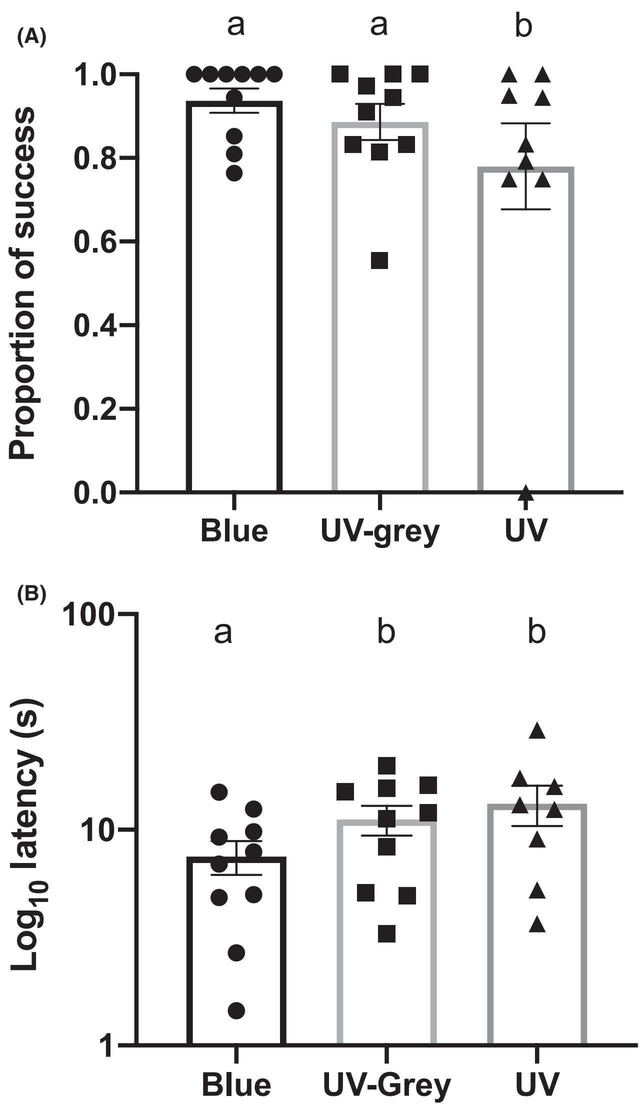

FIGURE 3 (A) Mean proportion of success and (B) latency (s) for fish to find and peck at target pixel displayed on the RGB-V-UV LED display. Error bars show the standard error of the mean. Different letters above bars indicate significant differences between target colours ($p < 0.05$)

recirculating system. Tanks were divided into a testing arena and a starting section by an opaque partition with a sliding door (Figure S4). The LED display in its housing was set 5 cm under the water surface of the testing arena. Due to the poor visual acuity of the fish, we judged it unnecessary to rotate the display between trials.

Fish were trained to approach and peck single-pixel targets of three colours—'Blue', 'UV-grey' and 'UV' (Table 1)—to receive a food reward (see Supporting Information for more details). Each fish completed up to five trials for each of 13 sessions. Each colour was presented between 2 and 24 times (mean ± *SD* = 16.3 ± 6.7) to each fish in a pseudorandomised order. For each trial, we recorded (a) whether the fish successfully pecked the target and (b) the latency (time to detection, s). Trials that exceeded a time limit of 60 s were immediately terminated. A UV-sensitive camera was used by the observer to determine when fish made a correct choice. See Supporting Information for details about statistical analyses.

Of 416 trials, 360 were successful in that the fish found and pecked at the target. Fish were able to detect all three colours; however, fish were less successful in detecting pure UV compared to UV-grey ($z = 2.97$, $n = 416$, $p = 0.011$) and blue ($z = 3.60$, $n = 416$, $p = 0.001$; Figure 3A). Mean latency was also significantly lower for blue compared to pure UV ($z = 3.70$, $n = 360$, $p < 0.001$) and UV-grey ($z = 2.70$, $n = 360$, $p = 0.018$; Figure 3B).

4 | DISCUSSION

We have provided the design, manufacturing documents and computer codes for an RGB-V-UV LED display for conducting behavioural tests of colour vision in a controlled and efficient manner. Our method has an advantage over other tests of colour vision because it allows a broad spectrum of colours (as short as 367 nm) at varying intensities to be easily produced, making it feasible to investigate colour perception throughout the UV-visible colour space. Our study is not the first to use UV LEDs to test UV perception (e.g. Bok et al., 2018; Stoddard et al., 2020); however, it is one of the first pixelated UV LED display that has the capabilities to show both mixed spectra and potentially moving images (also see Kócsi et al., 2020).

Additionally, we presented a limited behavioural study, demonstrating that *A. ocellaris* can detect pure UV and UV-grey colours. Interestingly, the pure UV stimulus had a significantly lower success rate and higher latency than the UV-grey and the blue stimuli. This detection study is a precursor to a more comprehensive colour discrimination study using Ishihara-style stimuli, where the targets are presented against a background with the same luminance (Cheney et al., 2019; Santiago et al., 2020). Using this approach with our RGB-V-UV LED display could provide valuable information on UV discrimination thresholds in a variety of UV-sensitive animals for which only non-UV discrimination thresholds have been assessed such as the honeybee *Apis mellifera* (Vorobyev et al., 2001), domestic chicks *Gallus gallus* (Olsson et al., 2015), the guppy *Poecilia reticulata*

(Sibeaux et al., 2019) and a cichlid *Metriaclima benetos* (Escobar-Camacho et al., 2019).

Other visual experiments previously done in visible wavelengths could be expanded on by applying our RGB-V-UV LED display including tests for comparing the importance of different wavelengths for navigation (e.g. Franzke et al., 2020), colour perception in twilight and nocturnal conditions (e.g. Kelber et al., 2002), chromatic versus achromatic cues in object segregation (Mitchell et al., 2017), sensory bias (e.g. Cheney et al., 2013), UV colour categorisation (e.g. Jones et al., 2001), colour generalisation (e.g. Baddeley et al., 2007) and luminance vision (e.g. Miquilini et al., 2017; Berg et al., 2020). Our display could be used as a spatial visual stimulator (e.g. Franke et al., 2019); however the low spatial resolution could be a limiting factor. With some modification, specifically increasing the panel size and using a higher-speed controller, it would be feasible to use our design to present moving stimuli (i.e. video), such as random-dot kinematograms which have been used to test motion perception in primates (e.g. Britten et al., 1992) and mice (Marques et al., 2018). Our RGB-V-UV display offers a flexible new platform for conducting a wide variety of behavioural tests of UV perception with a relative ease and efficiency not previously possible.

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CONFLICTS OF INTEREST

The authors declare no competing interests.

AUTHORS' CONTRIBUTIONS

K.L.C., S.B.P., F.C., J.M. and L.J.M. conceived the study and together with A.M.P. designed the experiments; S.B.P. designed, assembled and programmed the LED display with conceptual input from J.M.; L.J.M. and S.B.P. calibrated the LED display; A.M.P. and L.J.M. conducted the behavioural experiments; A.M.P. and K.L.C. analysed the experimental data; S.B.P., L.J.M., A.M.P. and K.L.C. wrote the initial manuscript. All authors reviewed and approved the final version of the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Behavioural data are available from the University of Queensland library at https://doi.org/10.14264/3e1e21e (Powell et al., 2021). Manufacturing documents and computer codes are available on GitHub at https://zenodo.org/record/4420371 (Powell & Mutantnemo, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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