



# A customizable, low-cost optomotor apparatus: A powerful tool for behaviourally measuring visual capability

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## Abstract

1. Vision is the dominant sense for many animals, and there is an enormous diversity in visual capabilities. Understanding the visual abilities of a given species can therefore be key for investigating its behaviour and evolution. However, many techniques for quantifying visual capability are expensive, require specialized equipment or are terminal for the animal.
2. Here, we discuss how to measure the optomotor (or optokinetic) response, an innate response that can be elicited without any training in a wide range of taxa, and which is quantifiable, accessible and non-invasive, and provide guidance for carrying out optomotor experiments.
3. We provide instructions for building a customizable, programmable optomotor apparatus using 3D-printed and low-cost materials, discuss experimental design considerations for optomotor assays, including a guide that calculates the dimensions of stimuli of varying spatial frequency, and provide a table summarizing experimental parameters in prior optomotor experiments across a range of species.
4. Ultimately, making this simple technique more accessible will allow more researchers to incorporate measures of visual capability into their work. Additionally, the low cost and ease of construction of our apparatus will allow educators in a variety of settings to include optomotor assays in classroom activities or demonstrations. Although here we focus on using optomotor to measure visual acuity—the ability to perceive detail—the apparatus and stimuli described here can be adapted to measure visual capabilities including spectral, contrast and polarization sensitivity, as well as motion detection, among others.

## KEYWORDS

behavioral assay, optokinetic reflex, spatial resolution, temporal resolution, visual acuity, visual ecology

## 1 | INTRODUCTION

Animal visual capabilities are diverse, meaning it is important to incorporate species-specific measures of visual function into

studies of visually guided behaviour. Such measures are useful for studies of the function, ontogeny or pathologies of visual systems, and for interpreting the results of behavioural assays. However, many methods for quantifying visual capability require specialized,

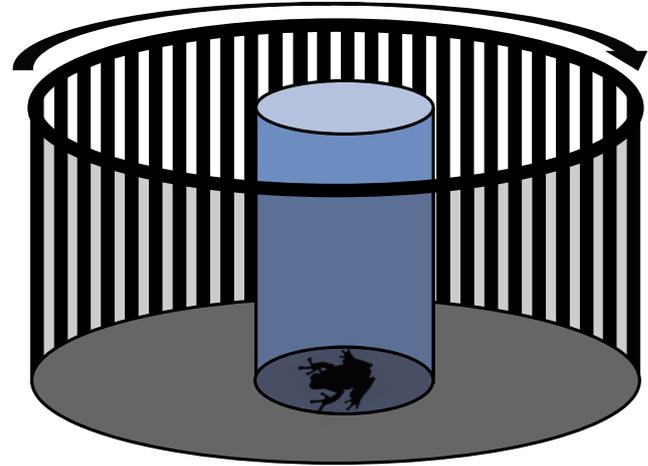
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expensive equipment, involve a dissection of the eye, and/or are terminal for the animal, restricting their use. By contrast, the optomotor response is an established, non-invasive, accessible and inexpensive method of quantifying visual capability that requires no prior training of the animal (see Table 1 for a glossary of terms). Here, we (a) provide instructions for building a customizable, programmable optomotor apparatus using low-cost and 3D-printed materials; (b) discuss design considerations for optomotor experiments; (c) include a guide for creating square-wave stimuli and (d) summarize the experimental parameters used in previous optomotor studies.

The optomotor response is a response to wide-field visual stimulation that can be elicited by placing an animal in a rotating drum surrounded by a stimulus (Figure 1). As the drum rotates, the animal reflexively turns or moves its body, head or eyes (optokinetic or eye nystagmus) to track the rotation (McCann and MacGinitie 1965). The optomotor response is absent if the drum is still, or if the animal cannot detect visual features on which to fixate. Comparing responses to a series of incremental stimuli can therefore be used to determine detection limits. The optomotor response is innate and present in diverse taxa, including mammals (e.g. Abdeljalil et al., 2005; Suthers, 1966), birds (e.g. Goller et al.,



**FIGURE 1** Schematic of optomotor setup. The high-contrast, square-wave stimuli (vertical stripes) rotate around the stationary cylindrical testing arena. Here, viewing distance is fixed by placing the animal inside a second, smaller arena

**TABLE 1** Glossary of important terms

| Term   | Definition   |
|--|--|
| Visual acuity                                      | The ability of a visual system to resolve static spatial detail  |
| Cycles per degree (cpd)                            | The number of black and white stripe pairs within a single degree of visual angle. As a measure of acuity, the number of black and white stripe pairs that an animal can discriminate in one degree of visual angle                                    |
| Minimum resolvable angle (MRA or $\alpha_{\min}$ ) | Another measure of visual acuity; the angular width of the narrowest black and white stripe pair that can be discerned. When given in degrees, its inverse is cpd  |
| Optomotor response                                 | An innate orienting response evoked by wide-field visual motion  |
| Optokinetic response                               | A combination of slow- and fast-phase eye movements elicited by motion. The slow-phase movements occur as the eyes slowly track a stimulus out of the field of view, and the fast-phase movements occur as the eyes reset to their original position   |
| Nystagmus  | Rapid involuntary movements of the eyes  |
| Square wave  | A periodic wave that varies abruptly in amplitude between two fixed values. In the context of optomotor, square-wave stimuli consist of alternating, vertical black and white stripes of equal width, with abrupt borders between neighbouring stripes |
| Sine wave  | A continuous, periodic wave that involves smooth periodic oscillation. In the context of optomotor, sine-wave stimuli are those in which neighbouring stripes blend together in continuous gradient from white to black                                |

2019), crustaceans (e.g. Caves, Frank, & Johnsen, 2016), insects (e.g. Hassenstein, 1951; Reichardt & Guo, 1986), cephalopods (e.g. Groeger, Cotton, & Williamson, 2005), fish (e.g. Neave, 1984), amphibians (e.g. Manteuffel & Himstedt, 1978) and reptiles (e.g. Lev-Ari, Katz, Lustig, & Katzir, 2017)

Visual acuity, the ability to perceive detail, is an ecologically important visual parameter that can be quantified using the optomotor response. Acuity is highly variable across species, ranging over at least four orders of magnitude and correlating strongly with eye size (Caves et al. 2018). Several morphological and ecological factors, however, can also influence acuity, including eye type (Land and Nilsson 2002); diet type (e.g., Litherland & Collin, 2008; Veilleux & Kirk, 2014) and habitat spatial complexity (e.g., Caves, Sutton, & Johnsen, 2017). Thus, obtaining acuity estimates from species of interest—rather than relying on estimates from related species—is best practice.

Although here we focus on acuity, the apparatus and methods described can be adapted to study spectral sensitivity (by varying stimulus chromatic contrast; e.g. Schaerer & Neumeyer, 1996), contrast sensitivity (by varying achromatic contrast between neighbouring stripes; e.g. Rinner, Rick, & Neuhaus, 2005), motion detection (by rotating low-frequency, high-contrast stimuli at different speeds; e.g. Carvalho, Noltie, & Tillitt, 2002) and polarization sensitivity (by varying the polarization e-vector; e.g. Dacke, Doan, & O'Carroll, 2001). Additionally, the stimuli described here can be used in operant conditioning paradigms that measure acuity, for example training animals to discriminate vertical from horizontal gratings (e.g. Champ, Wallis, Vorobyev, Siebeck, & Marshall, 2014).

## 2 | MATERIALS AND METHODS

Various parameters must be considered when designing optomotor experiments. We discuss these in brief below with respect to our design and provide a full worked example as a supplement.

## 2.1 | Constructing an optomotor apparatus and stimuli

Quantifying acuity using the optomotor response requires (a) a circular 'drum' on which to display stimuli comprising high-contrast vertical stripes of varying spatial frequency; (b) an optomotor apparatus, comprising a rotating platform for the stimuli and a programmable motor to control the speed and direction of rotation and (c) a circular arena which does not rotate, in which to place the animal, and sometimes a restraining device for the animal.

### 2.1.1 | Stimuli

Stimuli can be sine or square waves (Table 1), and there is precedent for the use of either (sine waves: e.g. Haug, Biehlmair, Mueller, & Neuhauss, 2010; Kretschmer, Tariq, Chatila, Wu, & Badea, 2017; square waves: e.g. Caves et al., 2016; Goller et al., 2019; Neave, 1984). Square waves comprise all spatial frequencies up to the wavelength of a given stimulus, whereas sine waves comprise only one spatial frequency; thus, square waves may elicit stronger responses when measuring acuity (see e.g. Maffei & Fiorentini, 1973). Additionally, square-wave stimuli are substantially easier to create using standard printers and paper.

We recommend creating paper stimuli rather than projecting stimuli on screens, because if using a screen one must consider (a) refresh rate, since animals with higher temporal acuity than humans may not perceive motion on a screen as fluid; (b) pixel size, as animals with high acuity may be able to resolve individual pixels; (c) that LCD screens are polarized; (d) that chromatic and luminance information vary with viewing angle, between screens, and to different animal viewers and (e) that monitor edges make it difficult to achieve the appearance of uninterrupted 360° rotation (see Fleishman & Endler [2000] for a relevant discussion of these factors).

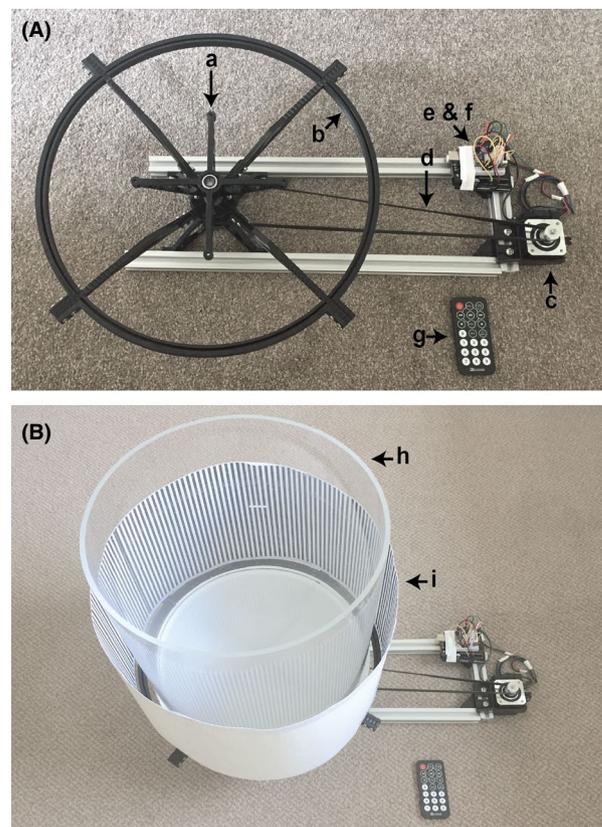
To select spatial frequencies to use in an optomotor experiment, a useful starting point is to estimate a likely acuity value using data from closely related species that have the same eye type and similar eye size and ecology as the species of interest (see recent reviews of acuity in fish [Caves et al. 2017], mammals [Veilleux and Kirk 2014], birds [Martin 2017] and insects [Land 1997]). The units of acuity are cycles per degree (cpd; Table 1), although many studies report minimum resolvable angle (Table 1) using degrees, radians or arc minutes (1/60 of one degree). We suggest reporting acuity in cpd, as the units are unambiguous (cpd is always the inverse of degrees). If reporting MRA, always specify if it is given in radians or degrees.

To assist with creating stimuli, we provide two supplementary files. One calculates the dimensions for cycles of differing spatial frequencies after the user provides the stimulus drum diameter (Cycle Width Calculation Supplement), and the second is a stimulus template. For high-frequency stimuli, printer resolution may give rise to Moiré effects (Figure S3); in the supplemental Worked Example, we discuss how to overcome these visual distortions.

### 2.1.2 | Optomotor apparatus: Motor and platform

A full parts list (Table S1), 3D models, assembly instructions, and microcontroller code are provided at the GitHub repository (<https://github.com/troscianko/optomotor>, <https://doi.org/10.5281/zenodo.3840063>). A construction guide, step-by-step video guide and user forum are available at <http://www.empiricalimaging.com/optomotor/>. Free, open-source software is used throughout, and the Arduino microcontroller and AccelStepper library (v1.59) are open source. All 3D-printed parts were designed in Blender (v2.81) and printed using a Prusa i3 MK3 in ABS plastic. This is a standard fused deposition printer; however, many online services allow uploading of 3D models and delivery via post. The 3D parts are designed to attach to an aluminium base frame made from widely available parts, although alternatives (such as a wooden frame) would be suitable.

Briefly, the apparatus (Figure 2) consists of a drum and arena supported by a central column, which is attached via a pulley to a



**FIGURE 2** Photographs of (A) the 3D-printed and constructed parts of the optomotor apparatus and (B) the arena and stimuli. The central column and support (a) hold the arena in which an animal is placed, and the circular frame (b) supports the stimuli. Rotation of the circular frame is driven by a stepper motor (c) connected to the central column via a pulley (d). The stepper motor is driven by a driver board (e) and Arduino microcontroller (f); Genuino Uno, although many other variants will be suitable). The experimenter can control the equipment remotely using an infrared remote control (g). (B) The central column and support were designed to hold the weight of a 30 cm diameter arena (h; 7 kg when filled with water). Stimuli (i) are supported by the circular frame

stepper motor that is driven by a driver board and microcontroller, allowing the stimuli to rotate. 'Microstepping' allows the setup to achieve 3,200 steps per revolution for smooth control at low drum rotation speeds, and the supplied code allows the remote control buttons to start and stop rotation, change rotation speed or execute specific commands coded by the user.

### 2.1.3 | Experimental arena

The experimental arena is a non-rotating cylinder where the animal is placed during trials. The arena should be transparent and allow the subject to see the stimuli with the minimum of visual distortion. Extruded clear acrylic (PMMA) tube is widely available and ideal for this purpose, and has the added advantage of a low refractive index, thus causing minimal visual distortion when submerged underwater for testing aquatic species. The arena dimensions will depend on the species of interest (see Table S2), but importantly, the angular width of the stripes will change with distance between viewer and stimulus. Thus, it is preferable where possible to employ a restraint or second, smaller arena (Figure 1; Table S2) that restricts movement towards or away from the stimulus. Alternatively, it is possible to video record trials and calculate angular widths in real time as the animal moves around the arena. The setup shown here can accommodate stimuli up to 35 cm in diameter, although the design can be scaled up by increasing the drum size (simply using a larger base), and/or by scaling up the wheel 3D-printed components. Additional weight can be accommodated by printing the base bracket with thicker walls, or in solid plastic.

## 2.2 | Additional experimental considerations

Acuity estimates from optomotor assays should agree with anatomical estimates 'whenever the experimental conditions have been selected carefully enough' (Wehner 1981). We discuss those experimental conditions here.

### 2.2.1 | Acclimation to optomotor apparatus and light environment

First, acuity is generally lower in dimmer light (e.g. Abdeljalil et al., 2005; Caves et al., 2016; Groeger et al., 2005; but see Rahmann et al., 1979; Vestal, 1973). Thus, experimental light levels should be bright enough to ensure normal visual functioning for the study organism (unless one is purposely manipulating light levels, e.g. Abdeljalil et al., 2005). Light adaptation state can also affect the optomotor response. For example, mice allowed 10 min to acclimate to experimental lighting displayed robust, reproducible optomotor responses (Abdeljalil et al. 2005), but mice adapted for only 30 s showed inconsistent, weak optomotor responses (Thaung et al. 2002). Additionally, animals that are stressed from being moved into an optomotor arena could

display weak optomotor responses, so at the very least acclimation time should be sufficient to reduce stress in the focal animal.

The use of thermally stable (non-flickering) light sources such as arc lamps or LEDs powered via voltage regulators is highly recommended, as flickering light sources may elicit temporal aliasing artefacts (e.g. causing an optomotor response in the opposite direction as the drum). LEDs that run straight from mains (i.e. wired in series without the use of a low-voltage ballast) and fluorescent tube lights should be avoided because they flash at various temporal frequencies.

### 2.2.2 | Stimulus rotation speed

Rotating the stimulus too fast will conflate acuity with motion detection. It is highly recommended that preliminary trials identify the lowest practical speed which elicits a strong, reproducible response at a range of spatial frequencies. See Table S2 for a table of rotation speeds in published studies that examine the optomotor response across a diversity of taxa.

### 2.2.3 | Criteria for positive optomotor response

Generally, an optomotor response can be classed as positive if one or more of the following criteria are met: (a) smooth tracking of stimulus rotation by the body, head or eyes; (b) changing tracking direction with changes in the direction of stimulus rotation and (c) stopping movement when the stimulus stops rotating. Preliminary trials will help determine what criteria constitute a positive response in a given species. Usually, each stimulus is presented multiple times in different directions of rotation. Some species exhibit latency (30 s or more, e.g. chameleons, Lev-Ari et al., 2017) to begin responding to stimuli, and the optomotor response can be prone to habituation, so the length and number of trials over which an animal maintains a robust response will vary with the species in question.

## 3 | CONCLUDING REMARKS

The optomotor response provides an accessible way to probe visual function in a variety of organisms. Although care should be taken in extrapolating from the results of an optomotor assay to more complex behaviours such as feeding, schooling or signalling, quantifying acuity will allow for a more thorough understanding of a given species' ecology and behaviour and will contribute invaluable data to our understanding of broader trends in acuity across species.

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## AUTHORS' CONTRIBUTIONS

E.M.C., J.T. and L.A.K. formulated the ideas; J.T. developed 3D-printed parts, wiring diagrams and code; E.M.C. tested the optomotor apparatus; E.M.C. wrote the manuscript; J.T. and L.A.K. edited the manuscript and provided feedback.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.13449>.

## DATA AVAILABILITY STATEMENT

A full parts list, 3D models, assembly instructions and microcontroller code are provided under Creative Commons license at the GitHub repository (<https://github.com/troscianko/optomotor>), and are archived through Zenodo <https://doi.org/10.5281/zenodo.3840063> (Troscianko, 2020) and as supplementary material. Construction guide, video guide, user forum and future updates are provided here: <http://www.empiricalimaging.com/optomotor/>.

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#### SUPPORTING INFORMATION

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

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