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Research article

Cross-species 3D virtual reality toolbox for visual and cognitive experiments

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HIGHLIGHTS

- This toolbox adds VR capability to any pre-existing data acquisition framework.
- Cross-species usage, from rodents to humans, is supported.
- Possible paradigms range from simple search to complex contextual learning.
- Can be paired with eye tracking and electrophysiological recording.
- Minimizes implementation costs and doesn't require specific hardware.

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ABSTRACT

Background: Although simplified visual stimuli, such as dots or gratings presented on homogeneous backgrounds, provide strict control over the stimulus parameters during visual experiments, they fail to approximate visual stimulation in natural conditions. Adoption of virtual reality (VR) in neuroscience research has been proposed to circumvent this problem, by combining strict control of experimental variables and behavioral monitoring within complex and realistic environments.
New method: We have created a VR toolbox that maximizes experimental flexibility while minimizing implementation costs. A free VR engine (Unreal 3) has been customized to interface with any control software via text commands, allowing seamless introduction into pre-existing laboratory data acquisition frameworks. Furthermore, control functions are provided for the two most common programming languages used in visual neuroscience: Matlab and Python.
Results: The toolbox offers milliseconds time resolution necessary for electrophysiological recordings and is flexible enough to support cross-species usage across a wide range of paradigms.
Comparison with existing methods: Unlike previously proposed VR solutions whose implementation is complex and time-consuming, our toolbox requires minimal customization or technical expertise to interface with pre-existing data acquisition frameworks as it relies on already familiar programming environments. Moreover, as it is compatible with a variety of display and input devices, identical VR testing paradigms can be used across species, from rodents to humans.
Conclusions: This toolbox facilitates the addition of VR capabilities to any laboratory without perturbing pre-existing data acquisition frameworks, or requiring any major hardware changes.

1. Introduction

In visual neuroscience, researchers have long faced the challenge of conducting ecologically valid measurements of experimental variables while maintaining strict experimental control over visual displays. For example, most visual experiments in both human and non-human primates have used simplified stimuli (e.g., bars, dots or gratings) on homogeneous backgrounds, raising the

Abbreviations: NTP, network time protocol; OOP, object oriented programming; TCP, transmission control protocol; UDK, unreal development kit.

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question of whether their results could be directly extrapolated to more naturalistic viewing conditions (Bohil et al., 2011; Nishimoto and Gallant, 2011). Indeed, under normal viewing conditions the retina is bombarded by a multitude of background signals and visual receptive fields seldom contain a single stationary stimulus. Although challenging, some studies have shown that it is possible to decipher basic neuronal properties (e.g., receptive field and tuning) from more naturalistic stimuli, using sophisticated analysis methods (Nishimoto and Gallant, 2011). However, ecological validity might still be undermined by the nature of the visual stimuli, often limited to passive viewing of static pictures or movies, whose relevance to the subject's natural behavior is unclear. Thus, recording and interpreting physiological signals in naturalistic environments remains a challenge for visual neuroscientists.

Modern virtual reality (VR) technology may provide a solution to this problem. It allows researchers to design and therefore strictly control dynamic, realistic and immersive environments, while closely monitoring behavioral and physiological responses during testing (Loomis et al., 1999; Bohil et al., 2011). VR technology has indeed been preferred over real stimuli to generate intuitive sensorimotor responses across multiple species, from insects to humans, as its advantages range far beyond precise experimental control (Bohil et al., 2011). Firstly, subjects are kept sufficiently static during VR navigation to enable electrophysiological or imaging experiments. Secondly, VR environments can be created, scaled and manipulated by researchers in a manner that is almost impossible in physically constrained real-world testing environments. Thirdly, VR experiments are more engaging for subjects, compared to passive viewing, as they require complex and ecologically valid behavioral responses to multisensory stimulation (e.g., approaching a virtual food source or escaping from a virtual predator). Finally, VR environments circumvent many ethical limitations by preventing injuries in "hazardous" tasks (Tarr and Warren, 2002; Slater et al., 2006; Mueller et al., 2012).

Although most drawbacks of early VR solutions (i.e., poor image quality and low level of details) have been addressed through technological advances, the resulting increase in systems' complexity and in the expertise required for their implementation have forced most laboratories to design inflexible and singularly purposed systems (Loomis et al., 1999; Bohil et al., 2011; Mueller et al., 2012; Jangraw et al., 2014). For example, laboratories interested only in monitoring behavioral responses during navigation or foraging often lack the temporal precision and/or resolution required for electrophysiological experiments (Caplan et al., 2003; Astur et al., 2004; Newman et al., 2007; Weidemann et al., 2009; Doeller et al., 2010). Additionally, previous systems have been designed in a species-specific manner by either using fixed input/output devices (e.g., gamepad or trackball) or written cues (Hölscher et al., 2005; Harvey et al., 2009; Aronov and Tank, 2014; Slobounov et al., 2015). Although many existing VR platforms are customizable to fit one's desired paradigm, they often require a two-tier architecture (i.e., one computer for the VR engine and a second computer running experimental control software). This entails learning each tier's specific script library, sometimes under multiple programming languages (Mueller et al., 2012; Jangraw et al., 2014), which greatly increases implementation cost in both time and resources. While many commercial applications have been proposed to overcome these issues (e.g., Vizard, WorldViz, USA; Eon Reality, USA), their high cost may hinder their widespread use. Furthermore, as is often the case with third-party solutions, most of commercial applications use proprietary control software and require specific input/output computer peripheral devices, which could render their implementation in an pre-existing experimental pipeline problematic (Mueller et al., 2012; Jangraw et al., 2014).

Here we aimed to create a freely available VR solution that combines professional grade graphics, high flexibility and cross-species support, which could be implemented in any existing laboratory's data acquisition framework. To achieve this, we applied the architecture proposed by Adobbati et al. (2001) and Carpin et al. (2007): remotely controlling a VR engine via simple text commands sent over a dedicated network connection. Since most programming environments implement the transmission control protocol (TCP) for network data transfer, virtually any programming language can be used to control the virtual environment (VE). Furthermore, as experimenters are most likely to select control software with which they are already acquainted, they are only required to familiarize themselves with the VR engine, greatly reducing implementation costs. As examples, we provide fully functional control script libraries based on the two most common platforms in neuroscience research: Matlab (Psychophysics Toolbox: Brainard, 1997; MonkeyLogic: Asaad et al., 2012) and Python (PsychoPy: Peirce, 2007; Vision egg: Straw, 2008). These libraries were designed to interact with the freely available Unreal Engine 3 development kit (UDK, May 2012 release; Epic Games, USA). Although UDK was specifically designed for commercial video game creation, it has been used in countless virtual applications, from static architectural design to dynamic physics simulation (e.g., driving, fire propagation). This broad range of possible applications showcases its high flexibility and ease of use, two required characteristics in any VR engines.

2. Materials and methods

2.1. General architecture

The proposed VR system completely segregates the experimenter and subject during the experimental procedures via a two-tier architecture (Fig. 1). Indeed, as information is bi-directionally exchanged between the UDK computer and the control computer, both subject and experimenter interact with their own distinct interface. The separate interfaces allow the experimenter to instantaneously modify the task parameters, while preventing input device conflicts (e.g., multiple computer mice) and preserving the subject's experience. Moreover, the available computational resources on the control computer can allow experimenters to monitor the subject's behavior by displaying position, gaze or current state information in real-time. Although it is possible to run VR experiments on a single computer, we strongly recommend to avoid non-VR operations on the UDK computer in order to optimize display quality, to prevent frame loss and maximize temporal precision. This is especially important for electrophysiological experiments where the control computer must integrate inputs (e.g., eye tracker and VR engine) and synchronize output signals (e.g., electrophysiological recording equipment and reward system) to properly guide task flow. While these procedures might not be sufficiently computationally demanding to affect display quality in purely behavioral studies, the high computing power required to render high-quality 3D environments at higher refresh rates (i.e., >100 Hz) might alter the proper timing of data recording and output signals. Lastly, as this toolbox is aimed at facilitating the addition of VR capabilities to any pre-existing visual neuroscience data acquisition framework, the simple introduction of the VR computer, while preserving the current experimental computer and its pre-existing interface with external hardware (e.g., eye tracker, electrophysiological recording system and reward system) greatly reduces implementation costs. The UDK computer and the TCP control scripts thus replace the display adapter of the previous system.

The experimental cascade begins with the subject interfacing with the UDK computer (Fig. 1, gold rectangle; 8 core 3.4 GHz Windows 7 PC with 16 GB of RAM and 2 GB of dedicated video memory) through its appropriate input device. As this framework was developed to be species independent, subjects could be rodent, monkey,