Animal-oriented Virtual Environments: illusion, dilation, and discovery

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ABSTRACT

As a research tool, virtual environments hold immense promise for brain scientists. Yet to fully realize this potential in non-human systems, theoretical and conceptual perspectives must be developed. When selectively coupled to nervous systems, virtual environments can help us better understand the functional architecture of animals brains during naturalistic behaviors. While this will no doubt allow us to further our understanding of the neural bases of behavior, there is also an opportunity to uncover the diversity inherent in brain activity and behavior. This is due to two properties of virtual environments: the ability to create sensory illusions, and the ability to dilate space and/or time. These issues will be presented in the context of three types of neurobehavioral phenomena: sensorimotor integration, spatial navigation, and interactivity. For each of these behaviors, a combination of illusory and time dilation examples will be reviewed. Once these applications have been reviewed, implications for improving upon virtual models for inducing the mental phenomena of illusion and time dilation will be considered. To conclude, future directions for this research area will be presented, particularly with relevance to gene-environment interactions.

Introduction

Virtual Environments (VEs) are increasingly being used to uncover the fundamental features of cognition. Areas of investigation include spatial cognition, sensorimotor control, and emotional processing (Bohil, Alicea, and Biocca, 2011). While VEs are an up-and-coming method for studying human cognition, they are increasingly being used in the study of animal cognition as well. VE systems usually consist of a sensory or experiential analogue, such as a series of visual images or tactile stimulations that mimic phenomena encountered in the perceptual world. This allows us not only to faithfully replicate naturalistic conditions for behaviors in the lab, but also explore the limits of the underlying neural systems.

A popular aim in the brain science community is to understand the bases of some cognitive function or disorder (Mar, 2011; Menzel, 2012). By using virtual environments, we wish to control as many environmental variables as possible. Tight control of environmental conditions in an immersive environment should allow us to study the true biological sources of behavioral variation. Removing the environmental vagaries of a behavior may also allow us to induce mental phenomena that can only be simulated in a virtual environment. These include sensory illusions or the dilation of space and/or time. This in turn may allow us to account for the diversity of neural function and behavior under specific conditions. This has been demonstrated in a number of contemporary papers that look at cognitive behaviors including sensorimotor integration, spatial navigation, and interactivity. The papers reviewed here represent the state-of-the-art application of VEs to the naturalistic study of brain activity and behavior. They also serve

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as important clues to more subjective issues that warrant further investigation. Some of these investigations will be done using synthetic analogues, but with broader applicability to many types of animal models.

The Matrix, Inception,........Cognitive Neuroethology?

A number of Hollywood movies of the past few decades have introduced people to the concept of virtual worlds. A common theme among these movies is that the sensory world is deceptive. In “The Matrix”, an analogy of sensory reality was presented as life in a cocoon. Even though the real world had physical and perceptual limits, these limits could be transcended by stepping outside this cocoon. In “Inception”, the dream world provided an opportunity for participants to distort reality and experience these worlds at different time-scales. Increasingly deep levels of sleep were accompanied by a further dilation of reality. A similar analogy has been made between these types of movies and manipulations of hippocampal-dependent memories (see Spiers and Bendor, 2013). In this paper, the perceptual side of fictional mindplay will be explored and hopefully better understood.

With VE systems, we can provide both high-fidelity reconstructions of the real world (a la “The Matrix”) and environments in which typical sensory cues are dilated or otherwise purposefully distorted (a la “Inception”). In this paper, we will explore how virtual environments allow us to uncover features of illusion and time dilation in animals. These effects, seen in a number of contexts and neural systems, can be collectively referred to as the effects of virtuality. The general mechanisms behind this can be further understood using an artificial life model.

There is evidence that these factors are most relevant to animal behavior research, for which naturalistic settings are of primary importance (Zupanc, 2010). Experiments replicating social learning and conspecific interactions using biomimetic robots demonstrate that full replication of sensory cues is not necessary to elicit a response (Krause, Winfield, and Deneubourg, 2011). This may be related to the uncanny valley phenomenon, which conceptually characterizes the way observers perceive too-realistic virtual environment avatars and too-human seeming robots (see Figure 1). So far, the uncanny valley has been observed only in Primates (Penn and Povinelli, 2007; Steckenfinger and Ghanzanfar, 2009). However, the strategic use of VEs to provide stimulus could reveal a similar neural response.

In cases where there is ambiguity in the stimulus (e.g. agents that look real but do not exhibit all of the cues of a real individual), a distinctive neural response related to the mismatch between appearance and motion can be elicited. While this might be directly related to possession of a theory of mind (ToM), it may also be driven by a more general set of neural mechanisms (Changizi, 2011). For example, in humans the ambiguous nature of some virtual stimuli (e.g. agents or complex objects) elicits activity in the bilateral anterior intraparietal sulcus. While this is usually related to prediction error, it can also affect the global state of the action- perception system (Saygin et.al, 2012).

To resolve the issue of equivalent response in non-human animal species, it is worth noting that “The Matrix” is based on cultural features and philosophical notions that suggest the sensory world is itself an illusion (Ahrens et.al, 2012). If this premise holds true for the neural bases of sensation and perception (for an example from Primate vision, see Anderson, Basile,

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and Hampton, 2013), then we should be able to discover the limits of this natural illusion by manipulating the environment and rousing the organism form this illusion. If non-human animals can respond to both rudimentary sensory cues (The Matrix) and phenomena beyond the normal limits of perception (Inception), then the application of VEs to the study of animal cognition and behavior will have much predictive and comparative value.

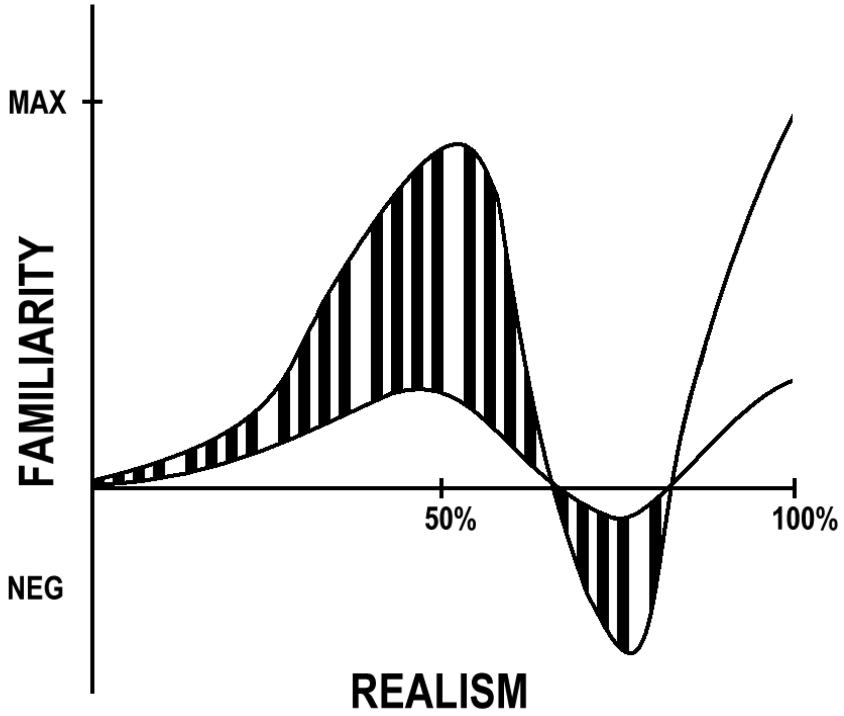

Figure 1. A conceptual demonstration of the uncanny valley, adapted specifically for virtual environments.

Current Examples

To outline the potential of VE system for animal research, we will focus on three areas of contemporary investigation: sensorimotor integration, spatial navigation, and interactivity (see Table 1). All three of these areas have been studied extensively in humans. Furthermore, the first two areas have also been studied extensively in animals, but until recently have not leveraged the advantages of VE technology. These examples utilize a range of experimental apparatus, from simple illusory stimuli and tracking systems to extensive mimicry of sensory cues. The simulation of any one set of environmental stimuli results in the activation of multiple neural circuits and may involve multiple cognitive systems. Yet this diversity of approaches has roughly the same effect: to enable control over the environment and to extend the range of experimentally-observable behaviors. Newly-observed behaviors and neural responses include: semi-realistic neural coding at the cellular level, transferring experience between spatial scales (e.g. beaming), and dynamic changes in distributed population codes. These and other unique findings also allow us to gain an appreciation for the spectrum of neural responses associated with these behaviors in an analytically tractable manner.

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Table 1. Comparison of three emerging areas of animal virtual environment research.

	Sensorimotor Integration	**Spatial Navigation**	**Interactivity**
Organism	Zebrafish, *Drosophila*	Mice, Rats, Moths	Rats/Robots/Humans, Monkeys/Robots
Unique behaviors/responses	Semi-realistic neural coding, Dynamic changes in distributed population codes.	Semi-realistic neural coding, Real-time nonlinear plume tracking.	Transfer of experience between spatial scales (beaming).

Sensorimotor Integration

The first featured behavior is sensorimotor integration. An experimental apparatus that is both capable of tightly reproducing the original environment (maintaining integration) and selective distorting it (disrupting integration) is highly useful for understanding the effects of movement disorders and disease. Being able to conduct experiments with this level of environmental control in non-human animals allows for single cell-level contributions to behavioral variation.

Ahrens et.al (2012) have developed an innovative virtual environment for zebrafish that is customized for fish cognition and swimming behavior. Visual scenes are projected onto a screen located underneath the fish's location (petri dish), and consist of square gratings that move along the fish's body from snout to tail. Importantly, the speed of visual cue presentation can be adaptively adjusted relative to swim speed. The Matrix-like quality of this virtual environment is not lost on Gray (2012), who feels that this experiment "reaches up from the page and slaps you across the face". Indeed, to the uninitiated, this seems to a revolutionary approach. Immersion in such a context is sufficient for initiating short-term forms of motor learning. The neural populations responsible for this result are distributed across the brain, including the inferior olive and cerebellum. This is the expected location for motor learning consolidation, which is conserved from fishes to humans.

Zebrafish VE also allows for flexibility in the experimental setup which in turn provides a means to dissect components of the sensorimotor loop in a systematic manner. Engert (2013) has proposed two alternate interaction modes (e.g. experimental preparations) for creating illusory stimuli related to zebrafish swimming behavior. One of these allows for controlled movements and the recording of neural responses to active movement behaviors. The other involves paralyzing the fish and recording the neural activity associated with intended (or fictive) locomotion. In both cases, the contributions of visual stimuli, motion, and the corresponding neural response can be decoupled. While this effect might be explained as an experimental artifact, a similar effect can be produced via robot-fish interaction. In the work of Marras and Porfiri (2012), biological fish were attracted to the locomotion of a robotic fish. Rather than actively decoupling sensory cues, the robot-fish interaction involves replicating the hydrodynamic and other mechanical cues of conspecific swimming behavior. These examples involve elements of an Inception-like dilation of the perceptual world. As we will see in the case of interactivity, neural activity associated with intentional behavior can be both a useful and important indicator of dynamic cognitive responses.

In another set of experiments in insects, virtual environments are used to dilate visual stimuli with regard to motor control. Gray, Pawlowski, and Willis (2002) use the walls of a flight arena to present visual cues that mimic depth and motion to an immobilized insect. In Seelig et.al (2010), a head-fixation task is replicated by having a fly walk on an air-supported ball concurrent with the presentation of visual stimuli. Using this type of VE design, an integrated response was found in horizontal system neurons. Using systems such as these, adaptive behaviors can be initiated in a highly-controlled environment. This not only allows for a range of behavioral regimes to be explored, but multiscale (e.g. cellular and behavioral dynamics) experimental investigations as well.

Spatial Navigation

The second featured behavior is spatial navigation. Spatial navigation is perhaps the best understood of the three featured behaviors due to our extensive knowledge of neural mechanism at both the structural (hippocampus) and single-cell (place and grid cell) levels. Indeed, virtual environments enable the development and confirmation of sophisticated theoretical models of spatial navigation. This is exactly what was done in Holscher et.al (2005) and Harvey et.al (2009). In the Harvey et.al (2009) approach, a mouse is situated atop an air supported-spherical treadmill, and its head is fixed for purposes of *in vivo* measurement. The virtual environment consists of a projection-based visual display. The first-person display features a fisheye-view of a linear track with a reward at the end of the track. This experimental setup resulted in semi-realistic firing patterns for place cells, which encode locations in virtual space. The authors also found three distinct sub-threshold signatures for place fields, which in turn may allow us to confirm theoretical models of neuronal coding (Ekstrom et.al, 2003).

However, it is not clear what the effects of a virtual environment actually are. As the neural response is characterized as semi-realistic by the authors, this suggests virtual environments may not be perceived by the animals as a real world (the virtual representation falling partially into the uncanny valley featured in Figure 1). Alternatively, the possibility exists that virtual worlds simply expose the diversity of responses to highly similar environmental phenomena. In human experiments that focus on the effects of training, subjects are often switched back and forth between virtual and real-world tasks. A similar experimental approach might be used for disentangling the effects of a virtual environment (such as sub-threshold neuronal activations) on an animal. While it is impossible to know which interpretation is correct at this point, future experiments specifically focused on perceptual realism in animals might address this issue more directly.

While traditional spatial navigation experiments require very few Matrix-like or Inception-like manipulations, there is the potential to do experiments in animals where spatial relationships (and perhaps even mental representations of space-time) are warped. The work of Gershow et.al (2012) demonstrates how gradients of airborne cues can be delivered to organisms in a controlled manner using a series of microcontrollers. Some invertebrate species such as moths engage in a form of spatial navigation behavior called plume tracking. Plumes of odorants or other chemicals do not diffuse through their environmental media (e.g. air or water) in a linear fashion, and the information embedded in a plume is made highly nonlinear due to turbulent conditions. By delivering these gradients as highly laminar flows, the diversity and complexity of plume tracking responses can be made tractable.

Interactivity

The third featured behavior is VE-enabled interactivity. Interactivity can be defined as the ability to manipulate and adaptively respond to a wider range of objects and behaviors than would found in a non-virtual context. This is a term I am presenting here for purposes of describing a series of experiments that feature animals interacting with VE systems. This could include computer-generated stimuli or robotic avatars. This can provide either a "Matrix-like" virtual experience (enveloping interactivity) or an "Inception-style" virtual experience (dilation of spatial scale), depending on the application.

Normand et.al (2012) use an ingenious experimental design to study interactivity between rats and humans using a technique called "beaming". In this approach, a rat interacts with a robotic human analogue (ePuck). Humans interact with a telerobotic virtual environment system that maps behavior to ePuck that size-wise is similar to the rat's body. To provide closed-loop feedback, the rat's movements are then tracked and mapped to a human-like avatar in the virtual environment. The beaming approach allows for human interactions to take place at the rat's size scale and vice versa. This also enables inter-species interactions such as the neuroanthropological studies of human-animal interaction featured in (Keil and Downey, 2012). Using beaming in this context might more directly address the existence of ToM within and between species.

Interactivity can also be explored using brain-machine interfaces (BMIs). One pioneer in the area of understanding what non-human primates are thinking when grasping objects is Miguel Nicolelis. In O'Doherty et.al (2011), his group introduces the brain-machine-brain interface, which uses electrophysiological signals from the motor cortex (motion planning) as input to a virtual arm that grasps virtual objects. The additional (e.g. feedback to the brain) component involves stimulation of the sensorimotor cortex that serves as haptic (e.g. touch) feedback. This set of experiments has applications to brain-controlled prosthetic devices. This includes robotic limbs that require close coordination with intentional behaviors, or even devices which record behaviorally-relevant electrical signals in one animal and uses that signal to stimulate the brain of another animal (Pais-Vieira et.al, 2013). This brain-machine-brain interface is currently being realized in application form as the Walk Again project, which aims to enable prosthesis-wearers to engage in activities such as soccer (Yong, 2011).

Illusion and Time Dilation: a virtual model perspective

While a skeptic might view this literature review as an empirical curiosity, there may be other ways to understand the phenomena of illusion and dilation independently of our three previous examples. Virtual models rely on two assumptions about the generalized animal response to virtuality supported by the previous experiments we have just reviewed. One assumption is that these effects are rooted in symbolic and adaptable representations of the sensory world. While there is scant evidence of higher-level representation in non-human animals, basic representational systems such as numerosity have been observed in animals ranging from fish (Agrillo, Piffer, and Bisazza, 2011) to macaques (Roitman, Brannon, and Platt, 2007).

Another assumption is that these representations may be subject to fictive conditioning. Fictive conditioning, which could be considered a form of associative learning, involves the acquisition of a learned response due to a stimulus that mimics what is actually being learned. One example of this is the supernumary hand illusion in humans (Guterstam, Petkova, and Ehrsson, 2011). In this phenomenon, information from one sense (vision) compensates for the lack of information from another sense (touch) to establish a stable (but fictive) association between the body and a third (prosthetic) arm. Yet despite such assumptions, there is an opportunity for systems neuroscientists to better understand the nuances and limits of function for various pathways and processes.

Returning to the issue of realism in VE, it is worth mentioning the notion of animals possessing a ToM is controversial. In any case, animals likely do not suspend disbelief in the same way humans do. Eliciting responses consistent with the uncanny valley effect might be possible when animals interact with VE. For example, it has been found that bodily awareness exists and can be manipulated in monkeys (Maravita and Iriki, 2004). It may even be that VE systems might aid or even enable complex cognitive responses. The extent to which this is true will partially determine the future potential of using VE in animal contexts.

Key features of a virtual architecture for illusion

To build a virtual representation for illusion, we must ask three questions. The first involves the sensory systems that are engaged by the environment. Since behaving animals engage the environment in a naturalistic fashion, considering the connections between higher-level cognition (e.g. attention) and psychophysiological phenomena (e.g. microsaccades) might be useful in selectively manipulating the input. (Otero-Millan, Mackinik, and Martinez-Conde, 2012). In immersive contexts, however, the selective decoupling of vision from touch/proprioception and even audition is very important.

The virtual environment also engages components of the neural substrate. While the sensory systems are engaged during interactions with virtual environments, areas related to multisensory integration and memory consolidation are also engaged. This is particularly true for long-lived illusions that are more than the by-product of visual aftereffects. As a result of this neural and sensory engagement, we should expect certain behavioral dynamics that correspond with those exhibited in the natural world. This is a consequence of behaviors being engaged in context. Ideally, an illusion should produce a behavioral response to the illusion that is similar or identical to the same stimulus in the natural world. More likely (and more common with less immersive stimuli) is a behavioral shift that does not mimic the real world. This can be due to a lack of realism in the virtual stimuli, but may also be due to a lack of contextual cues.

This expected inverted U response is based on the idea that once a virtual environment reaches a certain level of realness, the brain can no longer distinguish between real and virtual stimuli. In the case of highly immersive environments, there may be an augmented effect on cognitive processes such as attention and memory (Ragan, Sowndararajan, Kopper, and Bowman, 2010). Yet much like in the case of the uncanny valley, there is a regime where the brain treats virtual stimuli very differently from their physical world counterparts. Figure 2, Frame A shows the theoretical relationship between a continuous measure of immersion and task performance.

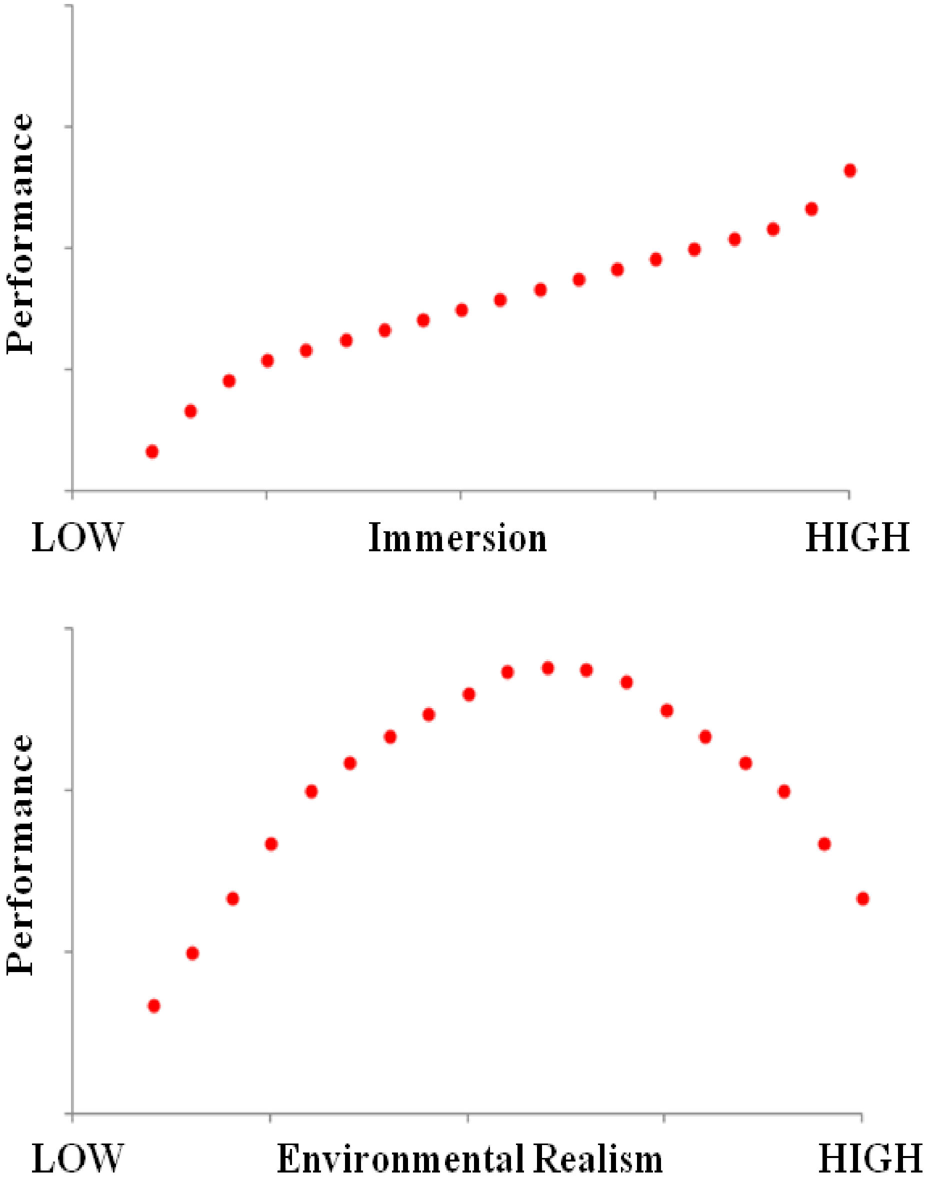

Figure 2. Two expected relationships related to time dilation (A) and illusion (B). In both cases, a positive linear relationship between the degree of realism and immersion is assumed.

Key features of a virtual architecture for time dilation

Similar questions to those that define illusory experiences in animals can also be asked in the context of time dilation. Depending on the degree of immersion, there are a range of sensory systems that could be engaged during time dilation. In mammals, this might include the auditory and the vestibular systems working in concert to register the flow of events. Unlike illusion, multisensory integration must not be disrupted over long periods of time.

The neural substrates of time dilation involve structures related to learning and memory, spatial cognition, and time-keeping. In mammals, these include the hippocampus and cerebellum. In cases where time-dilation is successfully achieved, we should expect enhanced activity in these regions. Time-dilation should lead to unique behavioral dynamics, very different from those expected from illusion. Highly-immersive environments should produce sped-up or slowed-down responses that are consistent with the type of dilation employed. The outcome of time-dilation is a learning effect that may reconstitute neural synchrony (Axmachera et.al, 2006). Figure 2, Frame B shows the theoretical relationship between the degree of environmental realism and task performance.

A Vision For the Future

While there are many unknowns in terms of how animals respond to their environment, not to mention the diversity inherent in animal brains and sensory systems, we can nevertheless selectively manipulate these variables using virtual environments. In the broader scheme of animal cognition, parallels with human cognition can be drawn in for no other reason than to illustrate potential cognitive mechanisms that might be involved in producing the effects observed across a range of experiments. While these effects constitute a relatively unexplored component of animal behavior, they may lead to new discoveries in animal cognition and perhaps in the genetic substrates of conserved animal behaviors.

Elicitation of these behavioral effects is dependent on the configuration of the virtual environment itself. Unlike natural environments, virtual environments are highly stereotyped and goes not include much of the noise associated with biological realism (Dennett, 2013). Nevertheless, environmental realism can be high, and findings in human experiments suggest that this is not an epiphenomenon (Bohil, Alicea, and Biocca, 2011). In addition, virtual environments are highly flexible and provide an experimental test bed for exploring the potential richness of animal perceptual, cognitive, and social behavior. Since there are a range of possible design configurations for animal research-oriented VE systems, many of which can tailored to scientific question and organism of interest, the possibilities for further application and future research are exhaustive. Furthermore, costs can be minimized through clever design features. This may enable moderately high-throughput and semi-portable behavioral assays. This ultimately provides the experimentalist with a highly-controllable, selectively enriched (Nithianantharajah and Hannan, 2006), and customizable environment.

The benefit of this might be considered in terms of gene-environment interactions (see Figure 3). With the rapid adoption and increasing affordability of next-generation sequencing technologies, it is now possible to target assays of a genome in combination with genome-wide association (GWAS) studies to uncover the genetic components of a trait. What is still a mystery are the interactions between genes, behavior, and environment. Gene sequencing combined with robust environmental control can elucidate some of these interactions, while also providing insights into the ultimate processing limits of functionally-distinct neural systems.

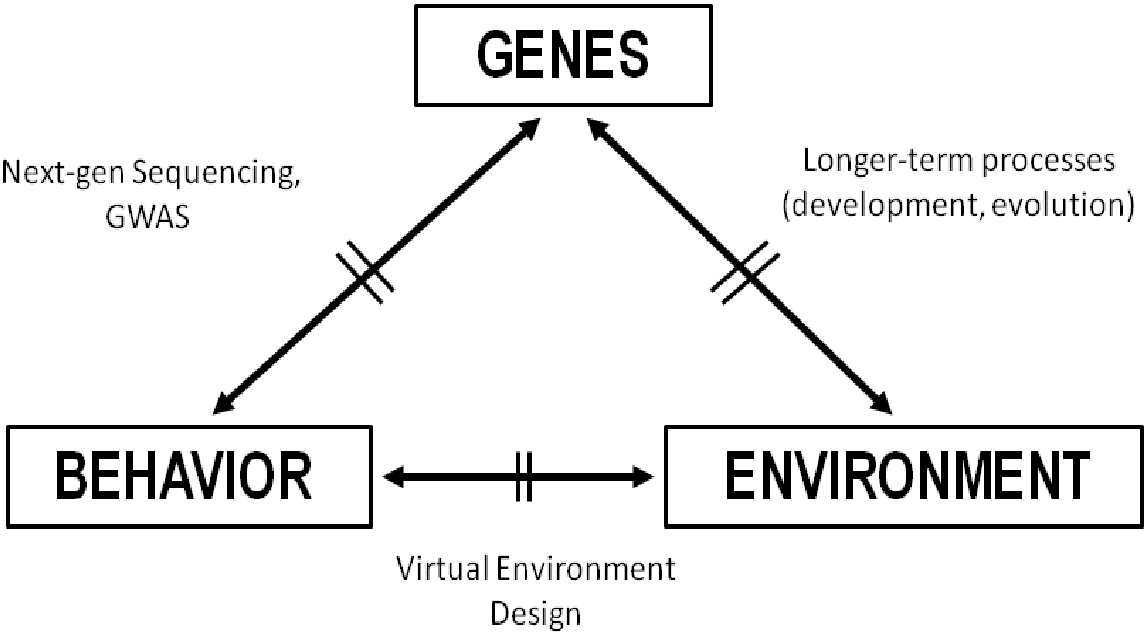

Figure 3. The role of VE in the milieu of interactions (genes, behavior, and environment) that define an organism's world.

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