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 basis 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 and other potential manipulations will be characterized as the effects of virtuality. These effects and their usefulness for brain science will be understood 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 examples are presented, the implications for improving upon virtual models for more directly inducing the mental phenomena of illusion and time dilation will be considered. To conclude, future directions for integrating this research area into broader biological inquiry will be presented.

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 *et al.*, 2011). While VEs are an up-and-coming method for studying human cognition, they are increasingly also being used in the study of animal cognition. VE systems usually consist of a sensory or experiential analogue. 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 basis of cognitive functions or disorders (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 and the dilation of space and/or time.

Given that these concepts are not immediately intuitive, how do we formally and operationally define sensory illusion and space/time dilation? Our working definition of sensory illusion is focused on a virtual stimulus which can be confused as a real stimulus. The key

property of sensory illusion is perceptual ambiguity, where the virtual stimulus looks nearly real, but is ambiguous enough to create a unique neural response. By contrast, our working definition of space/time dilation involves a virtual stimulus that speeds up or slows down action in a visual reference frame (or sensory event) relative to the natural motion of an object. The definition of natural motion is either intuitive or innate. Intuitive natural motion can be defined as physical objects evaluated by the observer in terms of naive physics (Povinelli, 2003). Innate natural motion can be defined as biological motion, or the movement patterns of organismal bodies as sensed by an observer (Grossman and Blake, 2001). Both of these can be violated through the use of virtual environments, and the neural response can mimic that of sensory illusion.

These phenomena have 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 in animals. They also serve as important clues to more subjective issues that warrant further investigation.

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. With VE models, a similar cocoon can be created inside which the participant can transcend perceptual limits whilst maintaining a highly-faithful representation of the physical world. 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. In this case as well, VE models provide an alternate environment which has a high degree of representational similarity but varying degrees of experiential similarity. 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 applied to animal models..

Why would this be interesting to the study of non-human brain and behavior? 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 the cognitive and neural processing behind 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. By using a model from the human-robot interaction literature (e.g. uncanny valley), we can better generalize the effects of virtuality to cross-species behaviors and neural mechanisms.

Cognitive Neuroethology As An Uncanny Valley

There is evidence that these factors are most relevant to animal behavior research, for which naturalistic settings are of primary importance (Zupanc, 2010). But how much of the environment must be replicated in order for an animal to recognize it as "just like the real thing"? One way this can be characterized is through the uncanny valley phenomenon. The uncanny

2

valley characterizes the manner in which observers perceive too-realistic virtual environment avatars and too-human seeming robots (see Figure 1). Initially (see Figure 1A), the more "real" an object becomes, the more it is associated with its real-world analogue. This phase of the curve is associated with gains in sensory fidelity. The second phase of the curve (see Figure 1B), which consists of two inflection points, is associated with a drop-off in the feeling realness just before a fully "real" emotional response occurs. At this point in the response curve, there is a predicted perceptual decoupling between the highly-realistic representation and the recognition that a robot is human or an object is real. This is an ongoing challenge in the world of human-robot interaction and VE design. However, this technical challenge might also be used to facilitate the "Matrix" and "Inception"-like effect of virtuality mentioned previously.

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 stimuli could reveal a similar neural response in other animals. I propose that the key component that relates the hyper-realism of VE to the uncanny valley effect is not a set of higher-cognitive mechanisms, but rather the information held in perceptual ambiguities. It is these ambiguities and the uncanny valley effect in general that can actually be leveraged to produce the effects of virtuality mentioned previously.

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 (Saygin *et al.*, 2012). Part of this response involves physiological adaptation to motion (Celebrini and Newsome, 1994) as expected of real-world objects. The response to mismatch also involves the associated function of visual motion and theory of mind mechanisms (Gerrans, 2002).This principle of associated function may also allow for perceptual ambiguities to influence 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). Thus, simple ambiguities may be intentionally introduced using virtual environments to trigger controlled departures from the context of reality.

To resolve the issue of equivalent responses to real and virtual environments 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 basis of sensation and perception (for an example from primate vision, see Andersen *et al.*, 2013), then we should be able to discover the limits of this natural illusion by manipulating the environment and rousing the organism from this illusion. It is important to remember that in this context, Matrix-like illusions are not dependent on the animal reaching some sort of philosophical "realization" that they are in an illusion. Rather, the Matrix-like illusory effect is a metaphor that encapsulates an immersive versus non-immersive experience. Depending on the level of immersion, it may be possible to control not only the sensory cues experienced by the non-human animal, but the entirety of the experience itself. In the Matrix, people are raised and live their entire lives within the context of the Matrix. In this case, the effects of this context are limited to current (e.g. non life-history dependent) experience. However, it also serves as a contrast to perception and action outside of the VE. If non-human

3

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.
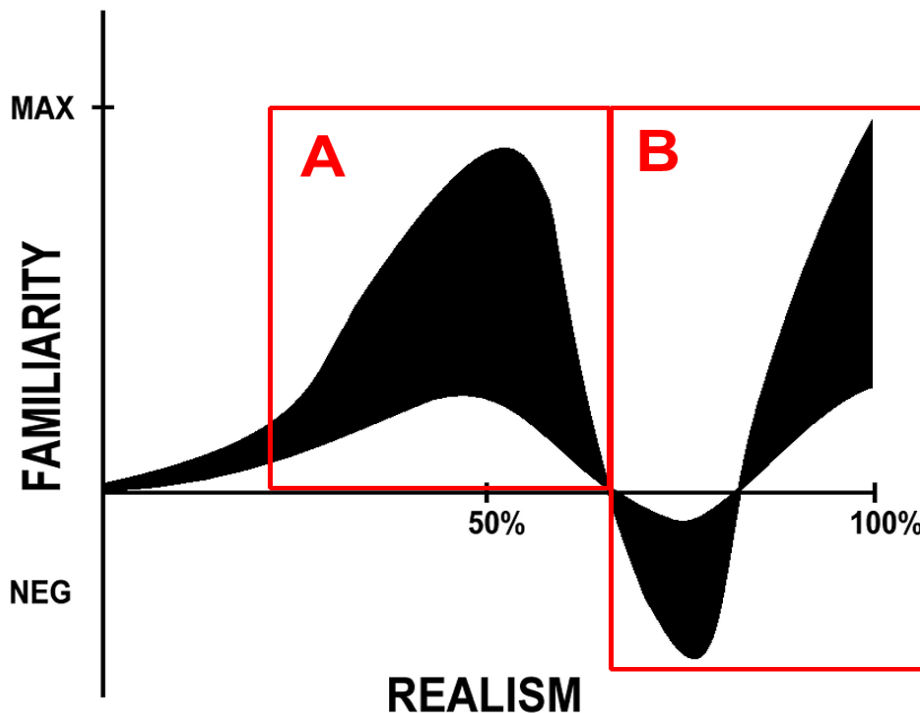
Figure 1. A conceptual demonstration of the uncanny valley, adapted specifically for virtual environments. Familiarity represents the positive or negative emotional valence associated with a given real or conspecific-like representation. Realism represents the fidelity and/or resolution of this representation. A: the first phase of the response curve, B: the second phase of the response curve. Shaded region represents hypothetical individual variation exhibited in the response. Figure adapted from the uncanny valley principle as originally proposed by Mori (1970).

Current Examples

To outline the potential of VE systems for animal research, I 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

4

findings also allow us to gain an appreciation for the spectrum of neural responses associated with these behaviors in an analytically tractable manner.

To better appreciate these examples, recall that the efficaciousness of VE systems is based on more than the ability to generate a series of high-fidelity visual images or tactile stimulations. Part of this unexplained variance has to do with the emotional state and cognitive response (Seyama and Nagayama, 2007) to specific stimuli, as discussed in terms of the uncanny valley. The other component involves the form of virtual intervention. Would it simply be enough to show animal a familiar visual scene, or can experimental outcomes of large effect be elicited by reducing the environment to key features of an experience?

For further clarity, we can turn to two examples of how robotic models have been utilized to study animal behavior. Robotic conspecifics can be used to mimic key mating signals. In this case (Patricelli and Krakauer, 2010), it is not the fidelity of the robot that is important, but rather the quality of the mimicked signal. Robotic approximations of conspecifics can be used to replicate commonly-observed, species-specific behaviors such as ant trail building and rat pup behavior (Akst, 2013). As with the simulation of mating rituals, it is not the details of the behavior and how it is represented in the brain that are important. 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 *et al.*, 2011). These findings suggest that successful simulation and the elicitation of desired behaviors can be reduced to a few key features depending on the cognitive or technological domain.

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 selectively distorting it (disrupting integration) is highly useful for understanding the effects of movement disorders. Being able to conduct experiments with this level of environmental control in non-human animals allows for single cell-level contributions to behavioral variation.

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).

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

5

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. Immersion in such a context is sufficient for initiating short-term forms of motor learning (Gray, 2012). The neural populations responsible for motor learning 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. In this case, possible illusory stimuli include (but may not be limited to) oscillating visual gratings and animations that are inconsistent with an organism's perception of self-motion (Lappe *et al.*, 1999). These type of illusions presented in an experimental setup allows for direct measurement of movement and the recording of neural responses to active behavior. 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 through an inconsistency between an organism's self-motion and the surrounding environment.

While this effect might be explained as an experimental artifact, robot-fish interaction studies might help us further appreciate the role of conspecific-like self-motion cues in regulating how perception and action are coupled and decoupled. 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. While the coupling or decoupling of self-motion and behavior may be context-dependent in nature, VE and robotic studies have shown (in an almost accidental fashion) how true to context stimuli must be to elicit the proper neural responses. 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 *et al.*(2002) use the walls of a flight arena to present visual cues that mimic depth and motion to an immobilized insect. This was done in a specialized arena which is shown and discussed in Gray et.al (2002) and Seelig *et al.* (2010). 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

6

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 VE actually are. As the neural response is characterized as semi-realistic by the authors, this suggests VE 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 can be switched back and forth between virtual and real-world tasks (Rose *et al.*, 2000). Ideally, the virtual condition should provide gains in expertise that are transferrable to the real world analogue task. 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 more directly address this issue.

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 motor responses associated with plume tracking 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 temporal or 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

7

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 the neural mechanisms underlying grasping in non-human primates 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 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). 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).

Illusion, Time Dilation, and Virtual Models

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 just reviewed. One assumption is that these responses 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 *et al.*, 2011) to macaques (Roitman *et al.*, 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 via one sense that compensates for a lack of stimulus in another sense. One example of this is the supernumerary hand illusion in humans (Guterstam *et al.*, 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 noting that whether or not non-human animals possess a bona-fide ToM is controversial. However, eliciting species-specific responses to virtual stimuli consistent with the uncanny valley effect should be quite possible. To explain how this might occur, we can turn to the work of Maravita and Iriki (2004). In this study, experimenters trained a monkey to use a physical rake to retrieve objects from the environment.

8

Electrophysiological and behavioral evidence post-training suggests that the rake had become incorporated into the animal's body schema (Macaluso and Maravita, 2010), as the tool itself becomes an extension of the arm. This incorporation of objects is consistent with the Uncanny Valley model, and serves as a link between affect and cognition (Lewis and Lloyd, 2010).

In extending the Uncanny Valley model to virtual environments, it is generally true that objects become more real as their fidelity increases. However, as they are incorporated into the body schema, they become less emotionally salient as real objects. This dropoff is not observed for physical objects (Carlson *et al.*, 2010), but is predicted to occur for virtual objects even of high fidelity. Finally, once the individual is fully immersed in the VE and becomes acclimated to the use of the virtual object, the virtual object then becomes fully consistent with the body's self-representation and sensory representation of the surrounding environment. In this sense, the virtual becomes real. 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

A virtual representation for illusion follows three sets of observations.. 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 *et al.*, 2012). In immersive contexts, 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 after effects. 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 animal 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 *et al.*, 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 2A shows the theoretical relationship between a continuous measure of immersion and task performance. The general variable called performance (see Figure 2) indicates a potential measure of goal-oriented behavior (e.g. swimming orientation, target accuracy) relative to a real-world control.

In the cases of dilation and illusion, Figure 2 illustrates what should generally be expected in a VE system applied to a given animal species. The predictions for dilation (Figure

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2A) show a roughly linear relationship between the degree of immersion and performance. In this case, immersion can be defined as the degree of exposure an organism has to a VE system. Generally, the degree of immersion increases with the level of performance. A secondary prediction is for this tendency to tail off towards very high and very low levels of immersion, as immediate distinctions between the real and virtual worlds become impossible.

By contrast, the predictions for illusion (Figure 2B) involve an inverted U-shaped relationship between performance and environmental realism. As the amount of environmental realism increases from very low resolution simulation of the environment (e.g. 2-bit visual scenes), performance likewise increases. Yet for very high resolution simulations (where multiple sensory modalities are simulated at very-high fidelity), performance drops off. This is predicted on the basis of the Uncanny Valley effect, which can interfere with perception and action.

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 visual and vestibular systems working in concert to register the location and position of the organism's body in the environment (Fetsch *et al.*, 2012). Unlike illusion, multisensory integration must not be disrupted over long periods of time.
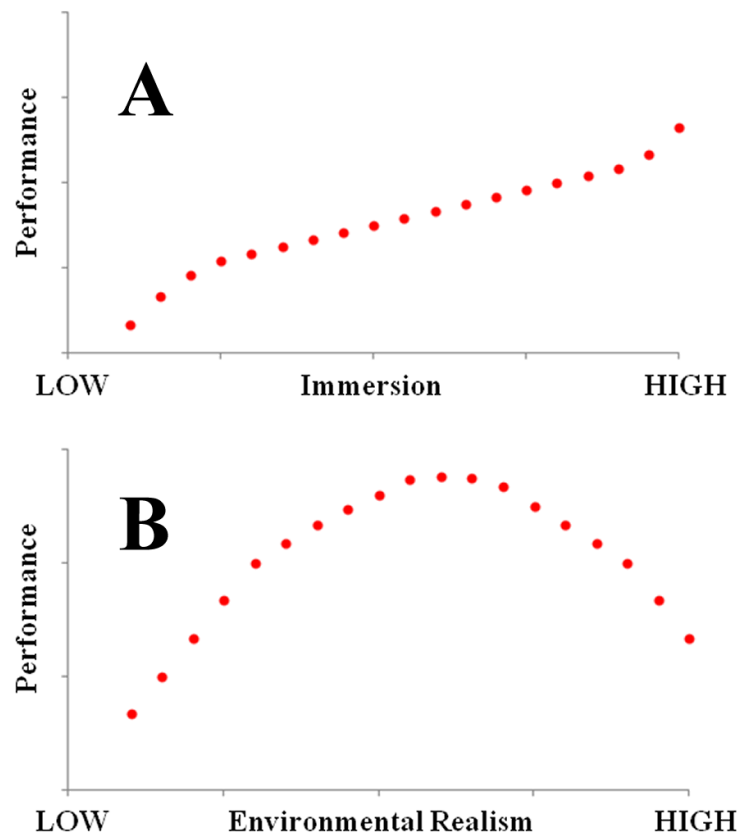
Figure 2. Two expected sets of outcomes related to time dilation (A) and illusion (B).

The neural substrates of time dilation involve structures related to learning and memory, spatial cognition, and time-keeping. In mammals, these include the hippocampus (Jacobs *et al.*, 1990) and frontostriatal-cerebellar connections (Stevens *et al.*, 2007). 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 (Axmacher *et al.*, 2006). Figure 2B shows the theoretical relationship between the degree of environmental realism and task performance.

Challenges and Future Directions

There are a number of hurdles for eliciting the effects of virtuality (illusion and dilation) in animals. Of course, these hurdles are not unique to non-human animals, as VE systems applied to humans are often far from an immersive experience. But animal models provide additional constraints in that systems reliant upon symbolic representations and fictive conditioning may not have much an effect on the individual. While these are key and often complex features of human cognition, depending on the species they may be absent altogether in animal cognition. Taking this into consideration, the best strategy would be to tailor VE system content to specific animal species. In fishes, symbolism is likely absent and fictive conditioning must be done at a highly abstract level. In other animal species such as birds or social insects, symbolism might be used as a means to mediate the encoding of memories.

Another consideration is the interaction between cognitive mechanisms such as attention and memory and psychophysiological mechanisms such as arousal. These connections have been shown to be important in mediating human-VE interactions (Parsons and Courtney, 2011). In non-human animals, the interaction of these mechanisms provides an opportunity to make a stronger link between affect and the effects of virtuality. This also provides a means to understand the traditionally affect-driven Uncanny Valley effect in the context of "Matrix" and "Inception"-like effects, which are primarily a product of higher-level cognition.

Even more interesting is the effect of decoupling affect or other psychophysiological responses from their cognitive context. A simple example might be a virtual version of the nictitating membrane response. This form of conditioned learning can lead to an effect called overexpectation (Rescorla, 2006), which can affect memory formation across taxa for both fear conditioning and perhaps even other forms of acquisition (Kehoe and White, 2004). Coupling simple mechanisms with VE systems might open up new avenues for manipulating and exploring higher-cognitive processes.

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 to illustrate potential neural mechanisms that might be involved in producing behavioral 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 (Figure 3).

Elicitation of these behavioral effects is dependent on the configuration of the virtual environment itself. Unlike natural environments, virtual environments are highly stereotyped and do 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 (Blascovich and Bailenson, 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 (Bohil *et al.*, 2011). Since there are a range of possible design configurations for animal research-oriented VE systems, many of which can be tailored to a scientific question and organism of interest, the possibilities for further application and future research are potentially endless. Furthermore, costs can be minimized through clever design features.

Tailoring the virtual world to the perceptual specializations of a given organism would help in this regard. One example is the high critical fusion frequency (CFF) of the housefly (Healy *et al.*, 2013). Tightly-controlled environments can be constructed by using the fly's natural visual sampling rate as a baseline. The rate of presentation can then be systematically varied. Another example is the electrosensory capabilities of South American weakly electric fish (Gymnotiformes). A virtual environment that models the fluid environment could enable the creation of perceptual ambiguities, which could then allow for the power of sensory illusion to be leveraged. These type of examples ultimately provides the experimentalist with a highly-controllable, selectively enriched (Nithianantharajah and Hannan, 2006), and customizable environment.
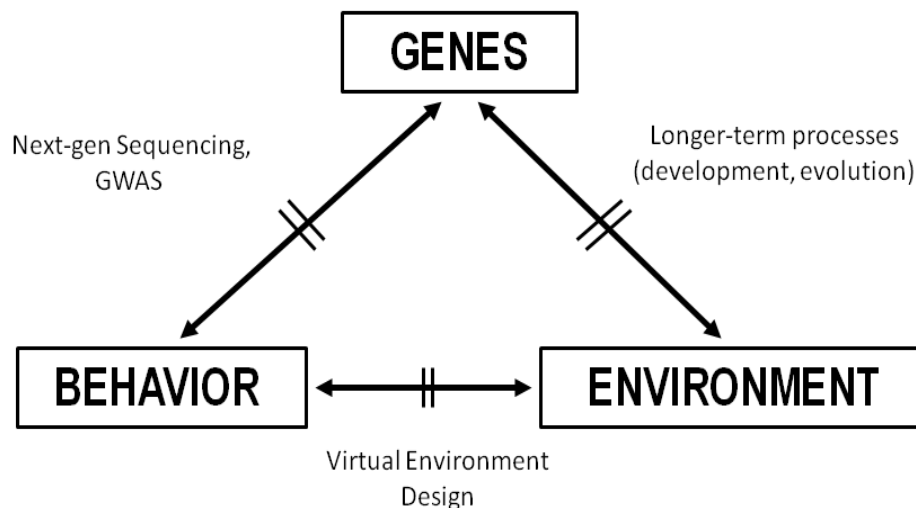
Figure 3. The role of VE in the milieu of interactions (genes, behavior, and environment) that define an organism's world.

The benefit of this might be also considered in terms of gene-environment interactions (Figure 3). One way in which virtual environments might be able to assist in uncovering gene-environment interactions is by using a logic similar to that which twin studies rests upon. In twin

studies, the genetic similarities of identical twins are used to control for unknown genetic variation (van Dongen et.al, 2012). In a similar manner, virtual environments might be employed to control for unknown environmental noise. For experimental purposes, a random sample exposed to the same highly-controlled environment is predicted to exhibit minimal environmental variation. This should allow for the effects of the genetic background to be magnified, enabling stronger associations between genes and behavior to be made.

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.

While the link between genotype and controllable environment is more speculative, the promise of VEs for the study of animal behavior and cognition is real and the returns can be immediate. I have shown how different forms of VE have been used to elucidate and perhaps even augment animal behavior. In fact, VE might be particularly useful in understanding particularly difficult-to-define problems such as neural coding (Kumar *et al.*, 2010) and human-animal interaction (Wilson and Barker, 2003). Overall, however, VE systems provide a flexible mode of investigation for both general and specific mechanisms that govern brain and behavior. In addition, two specific types of manipulation (illusion and dilation) can be used to produce novel experimental outcomes. These effects of virtuality provide an opportunity to advance the natualistic study of animal brain and behavior.

Acknowledgements

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17