EXPLORING DEPTH ESTIMATION FROM MOTION PARALLAX IN A MOUSE MODEL

by

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A THESIS

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Our eye is not just a camera providing an image of the world around us, but rather a tool that the visual system uses to navigate our environment. One visual ability that separates human vision from cameras is depth perception. Depth perception not only allows us to see three-dimensional images, but it also allows us to properly and productively interact with our environment. One way in which depth is perceived is through motion parallax. Motion parallax is a visual computation that amalgamates both self-motion from the observer and retinal image displacement to determine the distance to objects in the environment. Our larger goal is to determine what neural mechanisms are responsible for this process. To facilitate investigating these neural mechanisms, we adapted a rat/gerbil depth sensation task to mice. In this task, animals must jump from one platform, over a variable gap distance, to another platform in order to receive a reward. To encourage the use of motion parallax and prevent the use of retinal image size as a cue, we varied the landing platform size. Furthermore, to test the role of binocular vision, we sutured one eye closed. From our results, we have determined that animals can learn to estimate distance and accurately jump from the take-off platform to

the landing platform, animals perform specific head movements before initiating a jump, and these head movements are modulated based on the object distance. Establishing this task will allow us to perform further experiments to determine how the visual cortex integrates various sensory signals, enabling us to interact with our environment.

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Introduction

Background

Vision as an active process

Our eye is not just a camera providing an image of the world around us, but rather a tool that the visual system uses alongside other sensory inputs to allow us to perform daily tasks. Vision not only allows us to see the environment we are in but allows us to interact with it in a number of ways. Through visual systems, we can identify an object while also having an awareness of its position in space. Interaction between the visual system and other sensory networks allows us to investigate the world around us.

The intertwined relationship between action and perception is critical when considering cognition. Visual perception provides sensory information necessary for survival, but also relies on other sensory areas to work. Perceived visual information dictates the actions we take, but requires the coordination of sensory information from a feedback loop to continue working.

Visual cues and motion parallax

A key visual ability that separates human vision from cameras is depth perception. Depth perception not only allows us to see three-dimensional images, but also allows us to properly and productively interact with our environment. Retinal image size, the size of an object defined by the angle of the object on the retina, is one visual cue that can be used to perceive depth. For example, if you are familiar with the size of an apple, you could estimate the distance of the apple based on its size on your retina. Binocular disparity, the difference in object placement on the two retinas, is another visual cue that can be used to judge depth. The brain uses information from binocular disparity for depth information in stereopsis, the perception of depth from normal binocular vision. Another visual cue used to determine depth is motion parallax. Motion parallax is a visual computation that amalgamates both self-motion from the observer and retinal image displacement to determine distance to objects in the environment. Retinal image displacement is the change in the position of a stationary object on the retina over time.

Objects that are closer appear to move a greater distance and faster than objects that are farther away, which appear to move less and more slowly. The use of motion parallax as a depth cue has been observed in various animals, including humans.

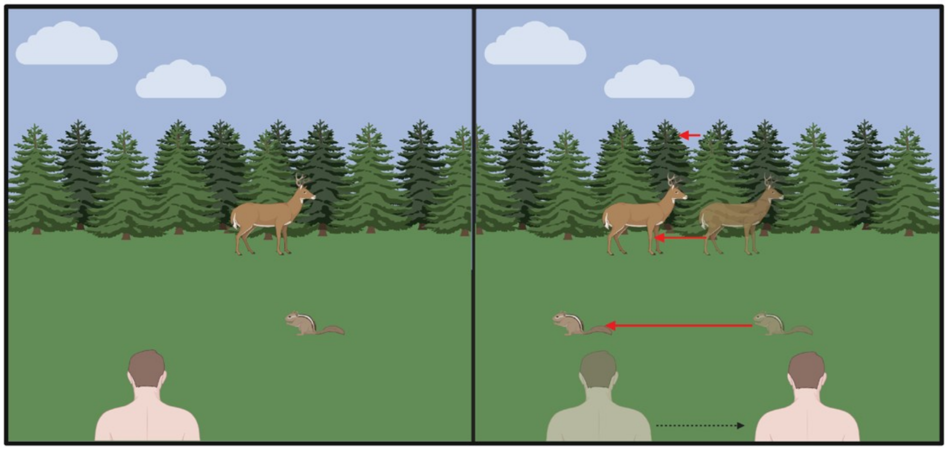


Figure 1: Parallax model

The observer perceives objects in the foreground moving more than objects in the background. This allows the observer to estimate the depth of objects generally.

Why we use a mouse model:

Historically, cats and non-human primates, such as macaques, have been used to study the visual system because of their anatomical similarities to humans. Only recently has there been a shift towards utilizing the mouse. Although mice have lower visual acuity, as well as eyes and visual pathways much smaller than humans, the fundamental circuitry of the visual system is very similar between mouse and human. Furthermore, a major benefit to using a mouse model is the variety of tools that can be used. Using genetic modification, it is now possible to label, observe, and manipulate specific cells and circuitry (Huberman & Niell, 2011). For example, we can use genetically modified mice to specifically target which neural networks we want to manipulate. In conjunction, tools such as Designer Receptors Exclusively Activated by Designer Drugs (DREADDs) and optogenetics allow us to enhance or suppress activity in these targeted neural networks. Adapting a previous study that used gerbils into a mouse model allows us to utilize new tools with natural behavior to potentially discover the contributions of different brain areas, as well as determine the neural computations in calculating distance to objects in an environment.

Previous Research and Relevance

The concept of depth discrimination from motion parallax is not new to the field of Neuroscience. In 1909, Florence Richardson pioneered a set of studies on sensory control in the rat, including one in which she trained rats to jump from one platform to another across a variable gap distance. Utilizing this task, researchers began to notice that rodents, locusts, and some other animals performed a series of head translations prior to executing a jump (Kral, 2003). The behavior was first observed by a research group studying locusts (Wallace, 1959). They would move the landing target in accordance to head translations, either countering head movements or moving alongside. This resulted in conclusive evidence that head translations were used to determine object distance; for example, when they moved the target in the opposite direction of the head movements, the apparent object motion was greater and therefore perceived to be closer, resulting in the locust under-jumping the target (Wallace, 1959). This study provided the necessary support that self-motion can be used as a behavioral tactic to assess the distance to objects in the environment.

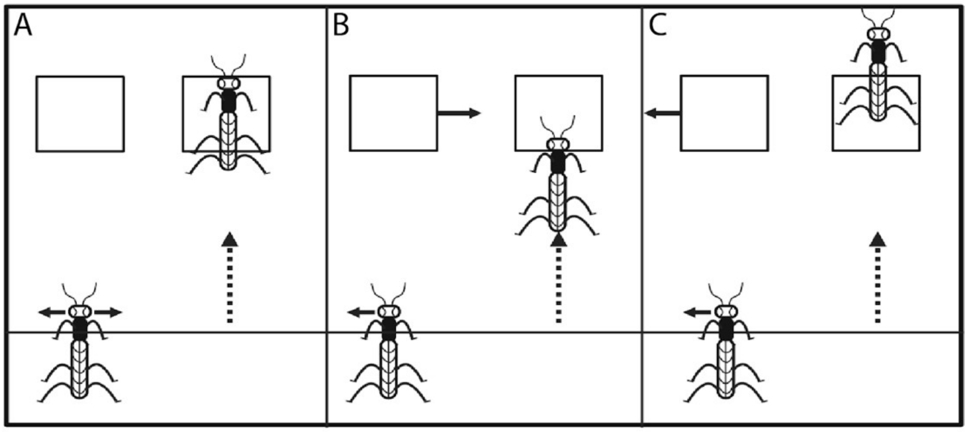


Figure 2: Early experiments establishing the use of motion parallax in locusts (Wallace, 1959), schematic adapted from Kral, et al.

(A) Depicts the locust gaining depth information from side to side head translations. The second and third frame shows how moving the platform in accordance (C) or in opposition (B) to head movement causes the locust to incorrectly calculate distance.

After observing this behavior in a number of animals, researchers began to focus studies around the behavior. Ellard and Goodale used these findings to further test similar behavior in Mongolian gerbils. They performed lesions of various visual areas in the brain in an attempt to find which neural pathways were critical to this behavior (C. G. Ellard, Goodale, Scorfield, & Lawrence, 1986). From these lesions, they determined that accuracy was drastically affected when the visual cortex was lesioned, resulting in a failure rate close to 50%. Although vision was clearly impaired, gerbils still generated head bobs (in fact of even larger amplitudes), meaning the execution of this motor skill is independent of visual cortex. Lesioning other areas of the brain did not result in any changes in jump accuracy, suggesting this behavior requires an intact visual cortex (C. G. Ellard et al., 1986).

The task in this study is adapted from Ellard and Goodale’s earlier work on this behavior. Previously, researchers using this task were not able to utilize the techniques discussed above in *Why we use a mouse model*, because the genetic tools available in a mouse model are not available in species such as gerbils. Today, we can use this task to perform an ethological study, a study of animal behavior with an emphasis on natural conditions, while taking advantage of modern technology to fully determine the neural basis behind these behaviors.

Research Question/ Hypothesis

Our research goal is to determine what neural mechanisms are responsible for depth estimation from motion parallax, i.e., what cells and circuits of the brain are necessary for computing distance based on self-motion signals and visual input. To investigate these neural mechanisms, we adapted a rat/gerbil depth sensation task to work with mice. We aim to utilize this task to determine how the brain integrates various sensory signals, enabling us to interact with our environment.

This research focused on three different potential visual mechanisms used by the mice to perform the task. One potential mechanism is using a visual cue, such as binocular disparity, to determine depth. Another potential mechanism is determining depth based upon retinal image size. The third mechanism is using motion parallax which combines self-motion and object displacement to determine depth.

Methods

Animals

Male and female mice (n=7), bred in-house in a C57/BL6J background, began training around postnatal day 40. Mice are housed in a reverse 12-hour light-dark cycle room in standard cages in a small social group (no more than 4 mice) with basic necessities - food, water, nesting/bedding material, as well as a shelter or running wheel. Weights are monitored daily, and water restriction is stopped if a mouse's weight drops below 75% of baseline. All procedures are performed in accordance with the University of Oregon Institute for Animal Care and Use Committee (IACUC) and Animal Care Services standard operating procedures.

Behavioral Apparatus

The arena in which the experiment takes place is a plastic circular enclosure ~30 cm high and ~60 cm across. Within the arena there are two platforms: a "take-off" platform and a "landing" platform. Unlike the landing platform, the take-off platform has a ledge protruding from the front, indicating where the mouse should prepare to jump. The take-off platform is roughly 15 cm tall and the landing platforms are roughly 20 cm tall. We chose these heights in an attempt to discourage animals from jumping up to the landing platform from the floor, or repeatedly aborting the task by easily dismounting the take-off platform. There are three landing platforms that are used interchangeably, ranging from 8.9 to 11.4 cm in width. We use different widths to ensure that the mice cannot use other cues, such as retinal image size, to determine the distance to the platform. If there is only one platform size, they can determine distance without head bobs/motion parallax; multiple platform sizes provide ambiguity. Each platform top is covered in rubber to prevent slipping.

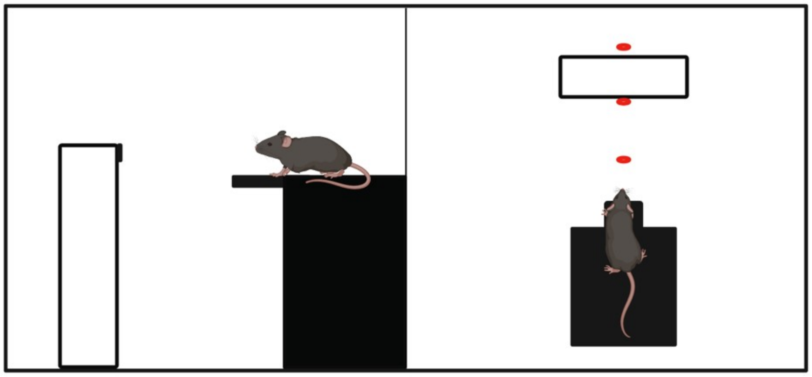
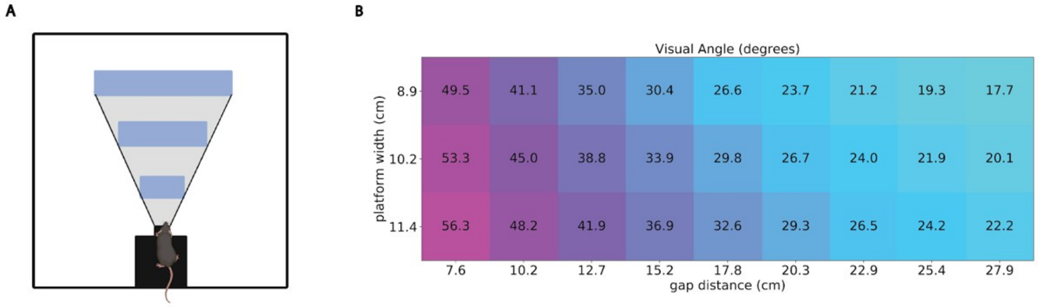


Figure 3: Schematized model of the experimental set up in the arena.



platform width (cm) \ gap distance (cm)	7.6	10.2	12.7	15.2	17.8	20.3	22.9	25.4	27.9
8.9	49.5	41.1	35.0	30.4	26.6	23.7	21.2	19.3	17.7
10.2	53.3	45.0	38.8	33.9	29.8	26.7	24.0	21.9	20.1
11.4	56.3	48.2	41.9	36.9	32.6	29.3	26.5	24.2	22.2

Figure 4: Schematic of platform size and distance resulting in retinal image size ambiguity.

(A) Top down view depicting how different sized platforms at different distances have the same resulting visual angle for the mouse on the take-off platform. (B) Visual angle, color coded by similar visual angles, that result from combinations of platform widths at various gap distances.

Behavioral Training & Task

Before we begin training for the task, the mice go through several days of habituation and handling. We handle the mice before placing them in the arena with the platforms for behavioral habituation. The goal of handling and habituation is to have the mice feel comfortable in the arena, while also allowing them to explore the new environment before training. When we begin training the mice for the task, we start with the take-off platform touching the landing platform, allowing the mouse to step from one platform to the next to receive a reward. With each consecutive trial, the landing platform is moved farther away, increasing the gap until jumping is required to reach the landing platform. This process of training can take 7-10 days before the mouse consistently jumps. Once the mouse can perform jumps at variable distances, the three landing platforms are randomly presented at different distances, ranging from 7.6 to 27.9 cm. For this task, mice are water restricted and only receive water and a piece of tortilla chip as a reward for successfully performing the task, reaching the landing platform directly from the take-off platform. If a mouse jumps but does not land on the platform (failure), they do not receive a reward. If a mouse climbs down from the landing platform (abort), we do not present the landing platform for one trial (time-out).

Surgical Procedures

For a subset of experiments, mice will have one eyelid sutured closed to test the use of monocular visual cues. Anesthesia is administered, 2-5% isoflurane in oxygen gas with 1-3% isoflurane maintenance, prior to suturing the left (n=3) or right (n=4) eyelid with two to three mattress sutures. Mice are returned to their cage and monitored for proper healing. Once the mouse recovers, they are once again water restricted for performing the behavioral task. Once the eye is no longer fully sutured, usually three days after surgery, mice have restored vision to both eyes.

Data Analysis

Video data acquired during the task is analyzed using DeepLabCut, which uses machine learning to perform supervised, automatic labeling of the animal's features (nose, eye/s, ears, etc.) (Mathis et al., 2018). After labeling, all tracking data are combined with trial outcome information using custom analysis in Python in order to determine the relationship between the animal's movements leading up to the jump and their performance on the task. All data are first averaged within animal (across days) and then across animals within a group (monocular, binocular). Abort trials were not considered in trial outcome, only success and failure outcomes after jumping were used in calculations. To cluster movements into groups, we use principal component analysis to determine the first ten principal components, then feed these into an agglomerative clustering algorithm (scikit learn, Python). Selecting a distance threshold then yields distinct clusters of movements. Statistical significance is determined using analysis of variance and the student's t-test with Bonferroni corrections for multiple comparisons.

Figure 5: Single video frame of a mouse in position on the take-off platform overlaid with tracked points from DeepLabCut analysis (nose, whisker pad, right and left ear, left foot, base of tail, and end of tail). The tracking permits measuring the displacement of each point across time in x/y space.

Results

Mice can estimate distance and therefore accurately jump from a take-off platform to a landing platform. Figure 6A displays the probability of completing a jump at different gap distances, and from this figure we can determine that the behavior does not rely on binocular visual cues because it is not impaired under monocular deprivation. In both conditions, success rate decreases as gap distance increases, which can be observed in Figure 6A. Figure 6B demonstrates the actual distance jumped compared to the gap distance between the take-off platform and landing platform. The dotted line in Figure 6B depicts where jump distance would perfectly match gap distance, from this figure, we can observe that on success trials, monocular animals consistently jump farther than the gap distance, when compared to binocular animals. From Figure 6B, we can see that when animals failed, under both binocular and monocular conditions, they appeared to be drastically under-jumping. Lastly, Figure 6C and D show that success rate, actual distance jumped, and visual condition are independent from platform size.

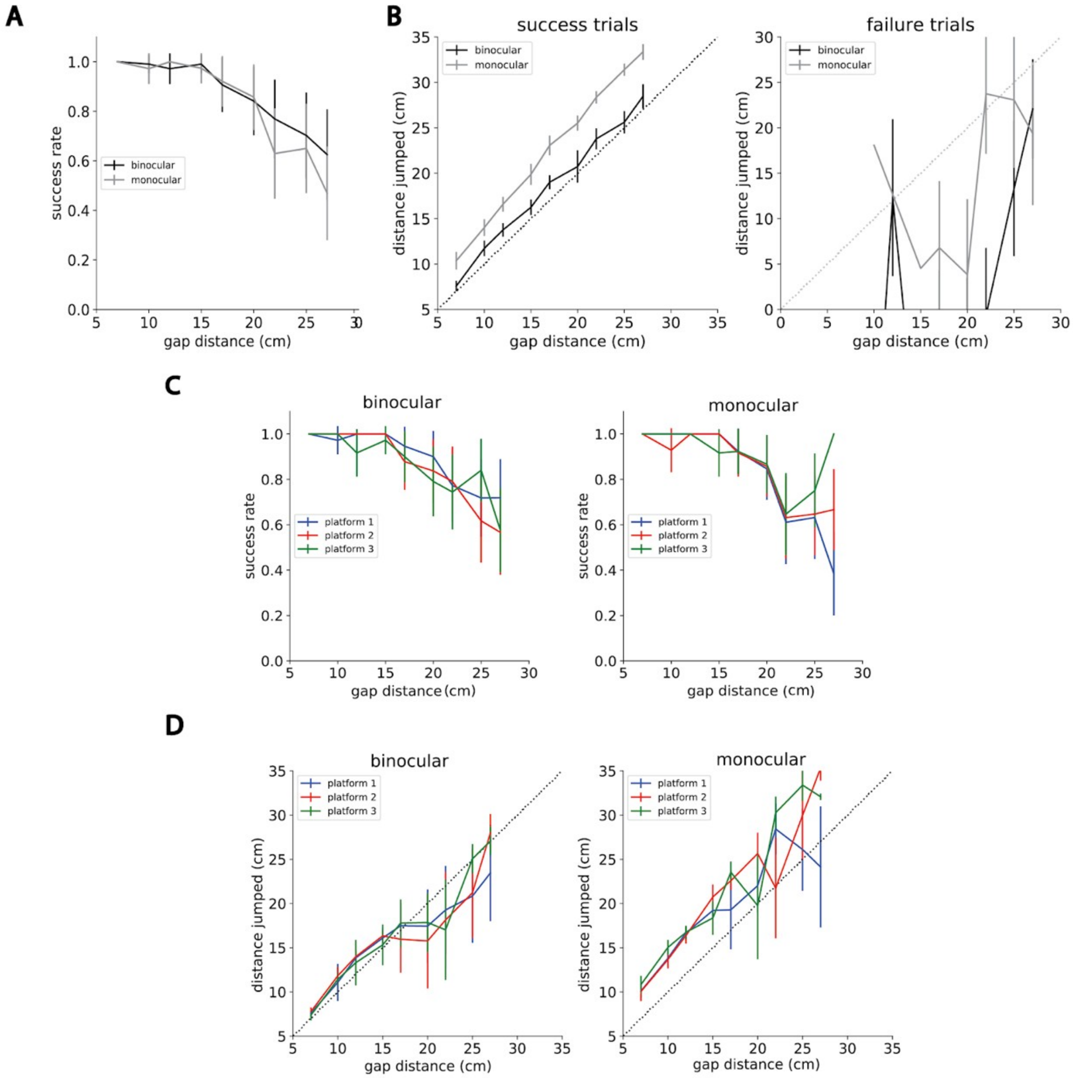


Figure 6: Distance Estimation

(A) Success rate versus gap distance; individual trials are scored as 1 for success and 0 for failure. Binocular results are shown in black, monocular results are in gray. (B) Actual distance jumped compared to gap distance. The dotted line is the unity line where distance jumped would be equivalent to gap distance. (C) Success rate by platform as gap distance increases. Platform 1 has the narrowest width, and Platform 3 has the widest width. (D) Actual distance jumped by platform across gap distance.

Figure 7 shows that mice do produce specific head movements prior to initiating a jump. Panel A is the raw trace of eye position, in the horizontal (x) and vertical (y) planes. Panel B shows an individual head movement when you plot the x and y movements against each other. We extracted the traces associated with each individual movement, and used the clustering algorithm to determine the shapes of the movements performed, disregarding the size. Panel C is a hierarchical dendrogram resulting from agglomerative clustering of the first ten principle components of all of the movements; the six resulting clusters are grouped by common shape (see Methods). The UMAP in panel D shows that movements from the same cluster are indeed close together in multi-dimensional space, suggesting clusters are in fact composed of similar movements. In panel E, six specific movement clusters can be seen. It is important to note from panel C and E that “movement 5” is a conglomeration of many movements, potentially including “noisy” nonspecific movements.

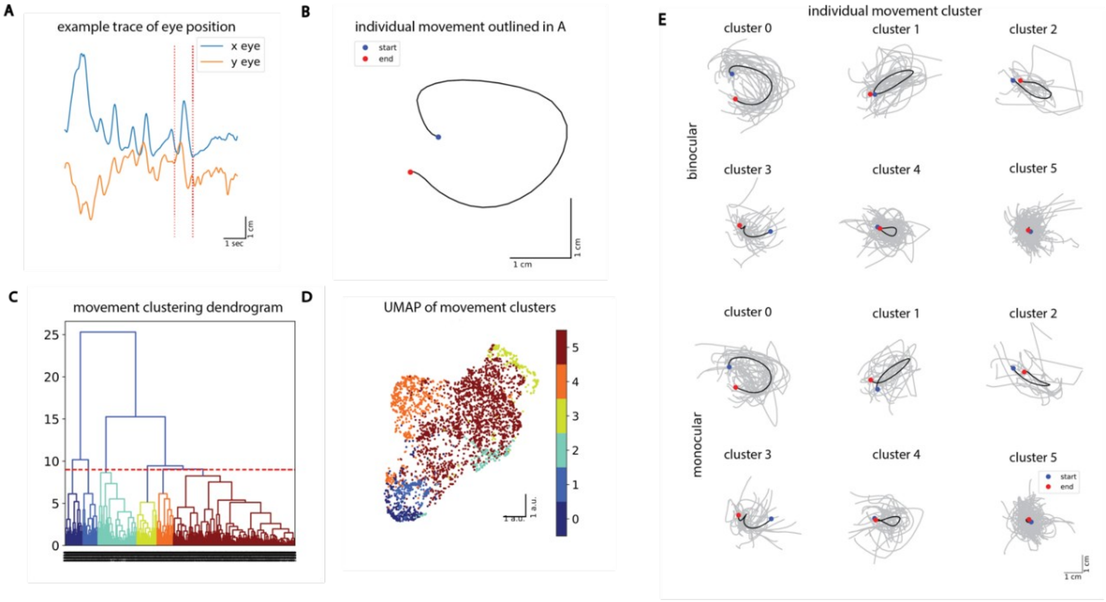


Figure 7: Head movements before a jump

(A) Raw x/y trace of the eye leading up to the jump. Red dotted lines are the time window for the movement plotted in B. (B) A single movement pulled from the raw x/y trace in A. Blue dot denotes the beginning of the movement, and the red dot is the end of the movement. (C) Hierarchical dendrogram of movements prior to a jump and the division between different movement clusters. The red line shows the experimenter-selected cut off, resulting in 6 movement clusters. (D) UMAP plot (from first 10 principle components) of each movement cluster, each point in a cluster is a movement with the color corresponding to the clusters in C. (E) Movement clusters; all the movements from each cluster in gray and the average trace in black. Blue dot is the start of the movement, and the red dot is the end.

We found that mice modulate their movement depending on distance. Figure 8A, shows that as gap distance increases, average head movement is modified. More specifically, Figure 8B, shows that amplitude in the vertical dimension increases as a function of gap distance in both binocular and monocular conditions. As seen in both panel A and B, this modification is not dependent on binocular vision.

We combined the amplitude of head movement with the gap distance to determine how far the image of the platform would move on the retina, in terms of visual angle. We found that as mice modulate the amplitude of their movements, the change in visual angle of the platform stays relatively constant (~6 degrees), as shown by panel 8C. Figure 8D, shows the probability of success when a head movement is present prior to initiating a jump. The results, demonstrated in Figure 8D, show that success rate is higher in the binocular condition on trials when the mice perform a head movement, versus when no movement occurs before a jump is initiated, especially at longer distances. The right side of panel D shows that under monocular condition, movement before a jump to longer distances does not result in a higher rate of success, even though binocular vision is not required for this task. On the left side of Figure 8E, when binocular mice used movement, the jump distance was more accurate especially at longer gap distances. In the monocular condition, mice jumped the same distance regardless of whether they first performed a movement.

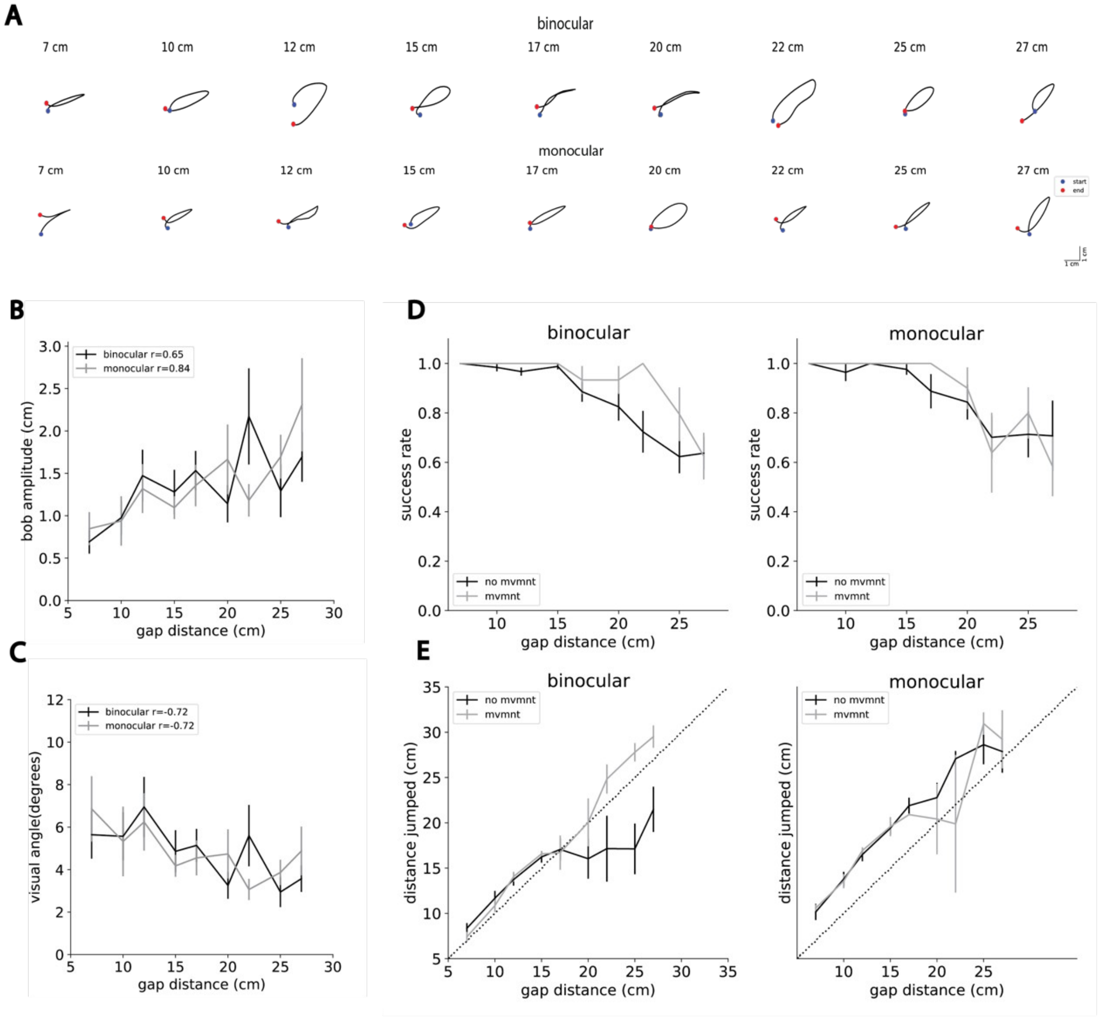


Figure 8: Head movements change based on distance

(A) Average trace of movement 1 across distance for binocular and monocular conditions. Start is labeled with a blue dot and the end is labeled with a red dot. (B) Head “bob” amplitude in the vertical dimension for movement 1 versus gap distance. Binocular condition is in black and monocular in gray. (C) Change in visual angle for movement 1 across gap distance (same color scheme as B). (D) Success rate across gap distance with (gray) and without (black) the presence of movement 1. Binocular success rate on the left, and monocular success rate on the right. (E) Actual distance jumped across gap distance with (gray) and without (black) movement 1. Binocular condition on the left, and monocular condition on the right.

Discussion

From our results, we can tell that mice can accurately estimate the distance from the take-off platform to the landing platform (Colin G. Ellard, Goodale, & Timney, 1984). First, we wanted to determine if binocular vision, such as stereopsis or binocular disparity, could be used to determine the distance. Based on our data, and the previous literature (Colin G. Ellard et al., 1984), we can rule out binocular visual cues as a necessary source of information. Figure 6A definitively shows that monocular deprivation does not impact the success rate. Figure 6B shows that, although binocular mice may be more accurate at jumping to the exact gap distance, monocular mice modulate their jump distance linearly, though they consistently jump farther than in the binocular condition. Figure 7E and Figure 8A show that both binocular and monocular animals perform certain head movement patterns that correlate to one another, indicating that the visual cue and head movement are independent from binocular vision. Ellard et al., 1986 found that after lesioning various brain areas, incidence of head movements increased and accuracy was not affected, suggesting that increased generated head movements are performed to compensate for loss of information, similar to monocular deprivation.

After determining that this behavior does not require binocular vision, the second suggested mechanism was the use of retinal image size to determine distance. Goodale et al., 1990, confirmed that if trained on a single platform, gerbils will use retinal image size to determine distance. Once platform sizes were changed, gerbils did not recalibrate jump amplitude and their trajectory was too short (under-jumping) on larger platforms, and conversely they over-jumped smaller platforms. To rule out the use of retinal image size, we trained and ran behavior tasks with multiple platform sizes at randomized distances. From Figure 6C and D, it can be observed that mice performed similarly regardless of which platform they were jumping to, therefore, unlike previous work with gerbils which found consistent under-jumping and/or over-jumping, platform size did not have an effect with mice on success rate or distance jumped. The platforms were wide enough that mice could land without high accuracy, so this “over-jumping” that monocularly deprived animals are exhibiting on Figure 6B, could be an effort by the mouse to land on top of the platform rather than at the edge. This over-jumping behavior was independent from platform size as shown in Figure 6D.

The last proposed mechanism was the use of motion parallax to estimate platform distance. From our results in figure 7B and E, we can see that there are consistent movements that are performed before initiating a jump. Figure 7C and E show that these movements have consistent patterns and can be grouped across animals. Figure 8A and B show that movement performed before initiating a jump is modulated in amplitude based on the platform’s distance. This change in amplitude contributes to maintained change in visual angle that ranges from ~4° to 6°, shown in Figure 8C. Previous literature has found that neurons in the primary visual cortex (V1) respond to stimuli as small as ~3°(Niell & Stryker, 2008), while behavioral tasks suggest mice can discriminate visual stimuli as small as ~2° (Prusky, West, & Douglas, 2000). This change in amplitude has a linear relationship with platform distance, which is supported by previous findings (Colin G. Ellard et al., 1984). Ellard et al. (1984) also determined that as amplitude changed by distance, so did the frequency of head movements; our data did not show any relationship between frequency of head movements and gap distance (data not shown).

Figure 8D and E have unexpected results; monocularly deprived animals do not follow the same pattern as binocular animals. When a movement is present prior to jumping in the binocular group, they have a higher success rate and more accurate distance jumped. Other studies in the Mongolian gerbil found jump accuracy and head movement have a relationship but did not explore how success rate was related to head movement incidence (Colin G. Ellard et al., 1984). For monocularly deprived animals, the presence of a head bob does not impact the success rate or distance jumped. For this data set, any trials that were aborted were not included in the success rate, which means that the plotted outcomes for monocular data on panel D may not accurately represent this relationship in monocularly deprived animals, i.e., it would not be apparent if animals systematically aborted trials in which they made no head movements. Another possible explanation is other cues were being used that provided depth information. Animals may be disinclined to perform head bobs if they have gained distance information from other visual cues. Using visual cues that involve movement may not be preferred given that in a natural environment it draws unnecessary attention from predators (Goodale, Ellard, & Booth, 1990). Based on previous results in this study, it seems the explanation of aborts is more likely causing the unforeseen trends on these plots.

Conclusion

Future Directions

To further this research, there are two direct approaches: shutting down brain areas to test their involvement in this behavior, and recording neural activity to determine how the brain actually computes depth information. A major advantage of using the mouse model is the toolkit of genetic modifications that can be utilized in research. Optogenetics and chemogenetics provide researchers the opportunity to temporarily "shut down" certain areas of the brain to test what areas are required in various tasks. As neuroscience has adopted the mouse as a keystone research animal, brain anatomy and circuitry are well known, therefore defined areas and circuits can easily be tested in order to determine the "pathway" used in motion parallax-based depth estimation.

Another advantage of the genetic capabilities of using a mouse model is the opportunity to see defined visual cell types and map the connections. After determining what areas are involved, the next step could be recording neural activity in order to determine how the brain actually encodes the visual and motor information. Given the consistency of our results with previous experiments in other species, we can now begin experiments to causally link cells to different aspects of vision. This further research has the potential to finally connect the behavior to underlying physiology and anatomy.

Importance

Ultimately, studying the brain's cells and circuitry enables researchers to understand the link between structure and function; this in turn allows for better prevention, treatments, and cures to brain disorders. Understanding the mechanisms involved in motion parallax can provide insight to an individual’s critical ability to navigate through their environment. Vision is important not only to avoid obstacles, but also plays a major role in locomotion; it is tied to balance, gait speed, etc. (Logan et al., 2010). Throughout locomotion, the body experiences a series of balance perturbations, resulting in postural sway. To avoid losing balance, the body must mitigate postural sway by making specific adjustments. There has been promising research that confirms that motion parallax is used to control postural sway and may provide more effective information especially when paired with other visual cues, like optic flow, the pattern of apparent movement by objects due to relative motion between an observer and a scene (motion of objects is parallel to self-motion) (Bardy, Warren, & Kay, 1996).

Neurodegenerative diseases can limit an individual's ability to perform tasks that were once simple and effortless. This observable decline is often due to the loss of gross motor and sensory skills. Unfortunately, neurodegenerative diseases are rarely curable and the only treatment involves alleviating a subset of symptoms. Parkinson’s Disease (PD) is one of the most common neurodegenerative diseases and is often associated with motor dysfunction. Research using virtual reality locomotion found that optic flow speed had a greater effect on PD patients' direction of movement than asymmetry in gait (Young et al., 2010). Other studies have found that many cerebral structures related to motion parallax and other visual cues can be easily impaired in patients with diseases like Parkinson’s (Lee, Ko, Suh, & Park, 2015). Using this information about Parkinson’s patients and the perception-action feedback loop, one can begin to understand how intertwined visual information and motor information truly are.

“We must perceive in order to move, but we must also move in order to perceive”

-Gibson, 1979

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