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(Don't) Look Where You Are Going:
Evidence for a Travel Direction Signal in Humans
That Is Independent of Head Direction

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We often assume that travel direction is redundant with head direction, but from first principles, these two factors provide differing spatial information. Although head direction has been found to be a fundamental component of human navigation, it is unclear how self-motion signals for travel direction contribute to forming a travel trajectory. Employing a novel motion adaptation paradigm from visual neuroscience designed to preclude a contribution of head direction, we found high-level aftereffects of perceived travel direction, indicating that travel direction is a fundamental component of human navigation. Interestingly, we discovered a higher frequency of reporting perceived travel toward the adapted direction compared to a no-adapt control—an aftereffect that runs contrary to low-level motion aftereffects. This travel aftereffect was maintained after controlling for possible response biases and approaching effects, and it scaled with adaptation duration. These findings demonstrate the first evidence of how a pure travel direction signal might be represented in humans, independent of head direction.

Public Significance Statement
Travel direction was tested in a first-person motion adaptation paradigm in humans, while head direction and optic flow were controlled throughout the study. Adaptation in the direction of travel is the first evidence of travel direction signals. These findings demonstrate how a pure travel direction signal might be represented in humans, independent of head direction.

Keywords: spatial cognition, path integration, motion adaptation, sensory recalibration, virtual reality

Supplemental materials: https://doi.org/10.1037/xge0001538.supp

In daily navigation, for activities as simple as going to a grocery store, we form a path of our movement through space (i.e., travel trajectory). How do we use self-motion information to form this travel

trajectory? Travel trajectory is derived from time and velocity. Velocity in turn is composed of speed and travel direction, which is the direction of one's body movement. Although head direction—the

direction that one's head is facing toward (also called facing direction)—is typically assumed to be the direction of travel, in reality, these two factors offer different spatial information. For instance, when we walk on the street, we constantly look around at our surroundings, changing our head direction while maintaining a constant travel direction. Thus, from first principles travel direction, rather than head direction or facing direction, is the most important component in forming a travel trajectory, as well as in maintaining spatial-vector memory over time (Hulse et al., 2021; Stone et al., 2017).

Only a handful of human and rodent studies have examined whether travel direction is coded separately from head direction. Although they do not offer the same amount of information, spatially tuned head direction cells have previously been used as a theoretical basis for the formation of a travel trajectory. Indeed, head direction cells have been discovered in the rat brain, which selectively fire in the direction a rat is facing toward, independent of its location (Chen et al., 1994; Ranck, 1984; Taube, 1995; Taube et al., 1990), demonstrating that head direction is a fundamental component of the internal orientation system of navigation. These head direction cells are found in the thalamus (Taube, 1995), retrosplenial cortex (Chen et al., 1994; Cho & Sharp, 2001), presubiculum (Ranck, 1984), extrastriate cortex (Chen et al., 1994), and entorhinal cortex (Frank et al., 2000; Quirk et al., 1992). Head direction cells could fire independently of whether an animal is moving or motionless (Taube, 1998), whereas travel direction should involve motion, therefore it might be more difficult to record activity related to travel direction. One study that contrasted head and travel direction found that head direction is coded more strongly than travel direction in a population of rodent entorhinal neurons (Raudies et al., 2015). A previous behavioral study in humans also showed different roles of body orientation and head orientation in forming spatial reference systems in memory (Waller et al., 2008). Further experimental findings in rodents and *Drosophila* also suggest the existence of neural signals for travel direction (Lu et al., 2022; Lyu et al., 2021). Taken together, while there is evidence to suggest a dissociation between coding of head direction and travel direction, the role that travel direction plays in the internal representation system of human navigation remains unclear.

The goal of this study was to determine whether there are behavioral signatures of travel direction as a fundamental component of human spatial navigation, independent of facing direction. To test the role of travel direction in human navigation, we utilized a motion adaptation paradigm adopted from vision science. In motion adaptation, neurons selective for visual motion features (e.g., moving downward) will adapt to visual stimuli that correspond to its selective firing properties after prolonged exposure to the same stimuli (Barlow, 1990). This adaptation often results in a decrease in the neural response to the same stimuli, compared to an unadapted stimulus (Brown & Masland, 2001; Lisberger & Movshon, 1999; Maffei et al., 1973; Miller et al., 1991). This neuronal change is represented at the behavioral level as a motion aftereffect (MAE)—a visual phenomenon produced after motion adaptation such that a stationary stimulus will appear to move in the opposite direction of the previously viewed motion. These MAEs are suggested to be associated with an amalgam of adaptation of motion-selective opponency cells at several visuocortical sites (Antal et al., 2004; Ashida & Osaka, 1994; Bach & Ullrich, 1994; Barlow & Hill, 1963; Bex et al., 1999; Culham et al., 1998; Kohn & Movshon, 2003; Mather et al., 2008; Sutherland, 1961; Verstraten et al., 1998). Thus, our study operates under the

assumption that if travel direction exhibits adaptation-like effects, then it is a fundamental component of the representation system for human navigation.

In the present study, participants were adapted to travel direction by viewing movement in a hallway in a constant direction. To dissociate travel direction from head direction, head direction was randomly reversed while travel direction was kept constant during adaptation (Figure 1 and video). We expected to observe MAEs compared to a control condition with no adaptation. Typically, MAEs are found in the opposite direction to the adapted motion (Anstis et al., 1998; Mather et al., 1998), and so we predicted MAEs in the opposite direction of travel. However, high-level MAEs are frequently seen in the same direction as the locally adapted motion because they use nonretinotopic visual features, although they might go in the opposite direction from the globally perceived movement (Culham et al., 2000; Dubé & Von Grünau, 1992; Hiris & Blake, 1992; Nishida & Sato, 1995; Von Grünau, 1986). MAEs in other sensory modalities have been reported to go in the same direction as travel. For example, in a podokinetic (walking-based) adaptation study, blindfolded people were adapted to a circular trajectory but perceived themselves to be going straight; when released to move freely, they formed the same circular trajectory (Earhart et al., 2001). This occurred both when walking forward or backward, indicating that the motion adaptation could be transferred to both directions of locomotion. Navigation is considered high-level cognition (Wolbers & Hegarty, 2010) whose information processing generally centers around higher level brain regions rather than visual areas (Chrastil, 2013; O'Keefe & Nadel, 1978), and navigation processes are typically nonretinotopic (Chrastil et al., 2019; Giudice, 2018; Loomis et al., 1993). Thus, we theorized that we could instead observe high-level MAEs in the same direction as the motion adaptation.

In addition, as far as we know, motion adaptation paradigms have only been used previously to study motion from the third-person view. The present study is the first to utilize such a paradigm to study a first-person view of motion—self-motion. This novel implementation of the motion adaptation paradigm may also lead to different adaptation effects than observed in previous visual perception studies. Regardless of the direction of the effect, an MAE would be a behavioral signature of travel direction selectivity that is represented in a particular way in the human brain, potentially operating as a fundamental basis function in human navigation.

Experiment 1: High-Level MAEs of Travel Direction

To test whether there is a travel direction signal in humans, we used a visual motion adaptation paradigm in desktop virtual reality (VR), designed to isolate travel direction from the contribution of head direction. In the initial adaptation phase, participants experienced 60 s of visual self-motion toward a cardinal direction (toward a sun or toward a moon, Figure 1a and b) along a virtual hallway (Figure 1c). In the test phase, participants then experienced a series of visual back and forth movements, toward and away from the initial cardinal direction (Figure 1e). We then asked participants to report their net travel direction during the test phase. Critically, in both adaptation and test phases, the head direction alternated occasionally, canceling out any effect of overall head direction, to dissociate head direction from travel direction. To maintain an adaptation state, participants experienced shorter 10-s "top-up" adaptation between each trial.

Figure 1
Experiment 1
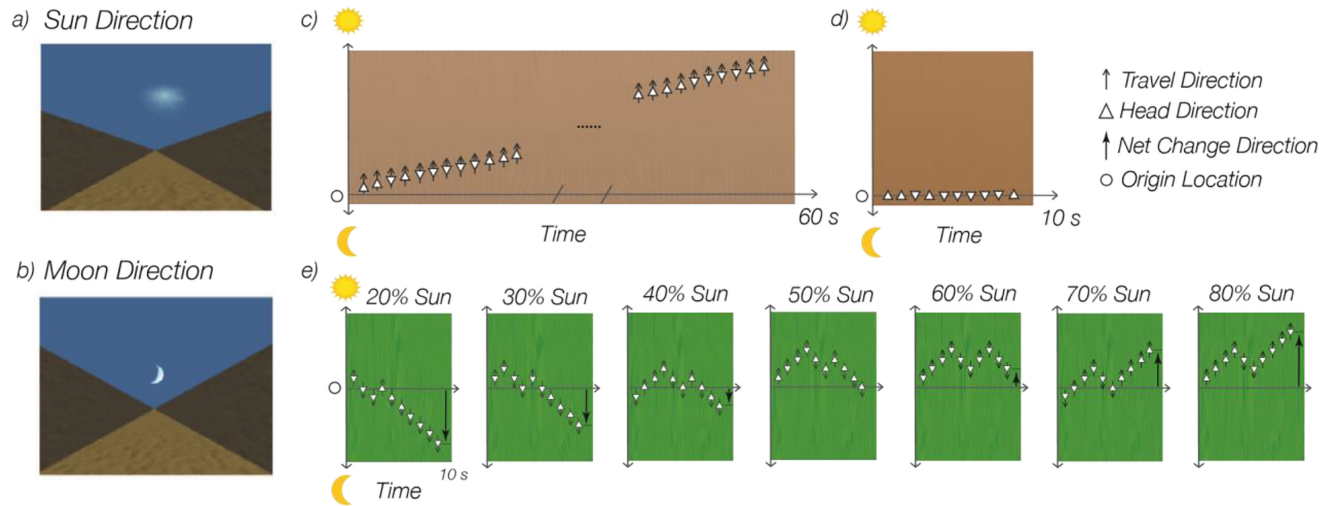
Note. Hallway during the adaptation phase, facing the (a) sun or (b) moon direction. Note that in the virtual environment, both the sun and the moon were rendered to move with the viewer at a constant distance; the size of the moon and the sun did not change with self-motion and participants could not evaluate distance change based on perceptual changes in either the sun or the moon. The extreme length of the hallway and random textures also precluded using changes in the hallway itself for location cues. The ground for the hallways turned green during the test phase to provide a visual cue for when to start tracking movement direction. (c) Overhead illustration of the 60-s adaptation phase for the sun group. During the adaptation phase, visual movement traveled toward the sun while the facing direction occasionally changed. Half the participants were adapted to a similar moon condition, with travel direction toward the moon. (d) Overhead illustration of the 10-s initial phase for the control session, which was the same for both the sun and moon groups. There was no visual travel, but the facing direction randomly changed. (e) The test phase, which was the same for all sessions in all conditions. Visual movement traveled back-and-forth between the sun and the moon during a 10-s interval. Participants were asked to decide whether the total movement was more toward the sun or more toward the moon in that interval. The facing direction randomly changed during the test phase. Here, we show one example from each of the seven test phase conditions of the percent of net movement toward the adaptation direction (20%, 30%, 40%, 50%, 60%, 70%, and 80%). See also the online supplemental materials for links to experimental videos. See the online article for the color version of this figure.

We compared the adaptation condition to a no-adapt control condition, in which participants viewed a static hallway with occasional facing changes (Figure 1d); the control condition had the exact same test phase as the adaptation condition. By parametrically manipulating the coherence of global travel direction (Figure 1e), we acquired psychometric functions for perceived travel direction, which allowed us to assess whether travel direction adaptation shifted the psychometric function, relative to the control.

To guard against response bias for one of the cardinal directions (i.e., a preference for selecting the sun or the moon), we divided the participants into two groups through random assignment, with each group adapting to either the sun or the moon direction. (Figure 1a–e; method). The groups were combined for analysis (see Figure S2 in the online supplemental materials for analysis of each group separately).

Method

Transparency and Openness

Data and codes are available on Open Science Framework at https://osf.io/38a6p/ (Chrastil et al., 2023).

Participants

Participants consisted of 77 University of California, Santa Barbara (UCSB) undergraduates who participated in return for course credit or monetary incentive ($12/hr). Our task is novel, thus there is limited previous data to use for a power analysis. Therefore, we based our sample size on previous studies of movement adaptation that used within-subjects designs (Culham et al., 2000; Earhart et al., 2001) and desktop navigation tasks (Weisberg et al., 2014; Weisberg & Newcombe, 2016). These studies yielded a target of 30 participants per condition. We used the outcomes of Experiment 1 for power analysis of subsequent experiments. The four criteria for prescreening participants were (a) no history or a current condition of psychiatric problems, (b) no learning disability or attention deficit disorder, (c) not currently taking psychoactive drugs, and (d) no history of head trauma.

Participants were discarded for either not completing both control and adaptation sessions ($n = 15$), responding with the same key all the time ($n = 1$), or responding too slowly (reaction time > 10 s; $n = 1$). The final pool consisted of 60 participants (29 males, 31 females; 38 not Hispanic or Latino, 15 Hispanic or Latino, seven not reported; 20 Asian, 18 White, two African American, three American Indian/Alaskan Native, one Native Hawaiian/Pacific Islander, three more than one race, 13 not reported), with 30 participants randomly assigned in the moon condition virtual environment (16 males, 14 females) and 30 participants randomly assigned in the sun condition virtual environment (13 males, 17 females). Ages of the remaining 60 participants ranged from 18 to 30 ($M = 20.32$). Participants chose from options for sex, race, and ethnicity and filled in a blank for age. All participants signed an informed consent form in agreement with the UCSB Institutional Review Board (Approval 5-17-0756) requirements in accordance with the Declaration of Helsinki.

Stimuli

The virtual environment was generated on a PC (Origin, NVIDIA GeForce GTX 980 graphics card, 15-inch display, $1,920 \times 1,080$ pixels display resolution) using Vizard software (WorldViz) to render the images. Participants experienced visual self-motion in a long (8,566 virtual units) landmark-free virtual hallway (see Figure 1). The hallway was long enough such that the visual angle to the end of the hallway did not change during movement and therefore could not act as a cue to the distance traveled. The translational speed of self-motion was randomly sampled from 10 to 15 virtual units/s in each trial. The rotational speed of self-motion was randomly sampled from 130° to 150°/s. Speeds for adaptation and test phases were sampled separately in each trial. The hallway consisted of two walls and a ground surface with coarse grained texture; the textures were designed to prevent participants using them for location cues during movement. The walls were always colored dark brown, while the ground was colored light brown during the adaptation phase and was colored green during the test phase (see Figure 1a and b). At one end of the hallway, in the sky, there was a sun and at the other end there was a moon. The sun and the moon were designed to be cardinal frames of reference and were rendered to move with the viewer at a constant distance. Therefore, the size of the moon and the sun did not change with self-motion, and participants could not evaluate distance change based on perceptual changes in either the sun or moon. In the moon condition, participants would initially move toward the moon frame of reference, and vice versa for the sun condition. See the online supplemental materials for links to videos of the task.

Task

The task consisted of an adaptation period followed by test trials (see Figure 1c–e). In the adaptation phase for both the sun and the moon adaptation groups, each block started with 60 s of virtual travel toward the sun or the moon as the global travel direction, depending on their group (see Figure 1c). During the adaptation phase, participants were instructed to pay attention to the movement in the hallway on the computer screen. To dissociate travel direction from heading direction, we included occasional 180° turns to change the local facing direction while maintaining the constant global travel direction. This heading change occurred through a rotation, such that the view turned around, rather than a sharp flip. The number of turns in all experiments were randomly sampled from a range varied by the time length of each trial (zero to two turns for 10 s trials, five to seven turns for 60 s initial adaptation phase).

The control was the same for both groups, where the "adaptation" phase consisted of a still screen without movement. This phase only lasted 10 s, but with occasional 180° turns to change the facing direction (see Figure 1d).

Immediately after the adaptation phase was a 10-s test phase. The test phase was the same for all conditions. The ground in the hallway would turn green, signifying the 10-s test period. In the test phase, the travel direction would change, such that participants experienced back-and-forth movement toward both the sun and the moon. The facing direction changed during the test phase, just like in the adaptation phase, with between zero and two turns. The amount of back-and-forth movement on each trial was expressed in terms of a percentage of movement toward one of the two cardinal frames of reference (see Figure 1e). The percentage of movement in one direction is complementary to the other direction such that they add up to 100%. For example, 20% of virtual movement toward the sun is equivalent to 80% of virtual movement toward the moon. In order to compare the sun and the moon conditions, all analyses are described as oriented toward the sun direction so that we could easily see the effect of adaptation in each condition.

In addition to the experimental condition (adaptation vs. control), this percentage of virtual movement was the primary independent variable in the study, ranging from 20% to 80% in 10% steps. Participants were instructed to pay attention to the overall direction they traveled in during the test period. When the movement in the test period stopped, on-screen text asked participants to judge whether their movement during the test period was overall more toward the sun or more toward the moon direction. They used their left hand to press the "D" key to indicate that they moved closer to the sun and used their right hand to press the "K" key to indicate that they moved closer to the moon. Although the task was untimed, participants were instructed to respond as quickly and accurately as possible.

As soon as participants pressed a response key, the hallway would turn brown again for 10 s as a "top-up" adaptation phase. The top-up adaptation of the next trial started with the same facing direction as the last screen of the previous testing trial so that participants could have a more coherent experience in the virtual environment. During the 10-s top-up phase, participants would experience the same movement as the initial 60-s adaptation (i.e., the same initial travel direction with occasional changes of facing directions) but for a shorter time length. Then, participants would be given another 10-s test of travel direction. In the control condition, the top-up was 10 s in the hallway without movement, but with occasional facing changes. The task continued alternating between the original travel direction top-up adaptations (brown) and test phase (green) until the block ended, and then participants could take a break (up to 5 min). Reported direction and reaction time for each trial were recorded.

Design

A 2 (experimental condition: adaptation, control; within-subjects) $\times$ 7 (actual percentage of movement toward the sun: 20%, 30%, 40%, 50%, 60%, 70%, 80% rate; within-subjects) within-subjects design was used. Each test condition was repeated for 12 trials, for a total of 84 trials (7 test conditions $\times$ 12 trials/test condition). These 84 trials were randomly separated into three blocks with a short break between blocks. A new 60-s adaptation occurred after each break to reinstate the adaptation. All stimuli were presented in random order for all participants.

In order to control for the influence of a particular adapting direction and of response bias, half of subjects were randomly assigned to the sun adaptation group, and the other half were assigned to the moon adaptation group. We combined the sun and moon adaptation groups for analysis, although we also analyzed them separately (see the online supplemental materials). The experiment was conducted over two sessions for each participant, with one session the experimental task and the other session as the control. The order of completing these two sessions were counterbalanced among participants within each group.

Procedure

Participants first were greeted in the lab, given information about the study, and given consent forms to sign. They then completed a

participant screening form and were given an instruction sheet to learn about the task.

Next, they performed the motion adaptation task. Participants sat approximately 50 cm in front of the computer screen. Before beginning the formal experiment, they were given additional instructions and the experimenter answered any questions. They completed five practice trials (the adaptation time and test conditions were different from the experimental trials), and then any additional questions were answered.

Each session lasted approximately 1 hr. Participants completed the two sessions on two separate days to prevent fatigue, with no more than 1 week between sessions. Finally, after each session, participants were asked to rate the difficulty of the task based on a 1–7 Likert scale (1 meant *very easy* and 7 meant *very difficult*) and to respond to an open-ended question about their strategy.

Data Analysis

R-studio and MATLAB were used for data analysis. We first removed outlier trials that were 3 *SD*s above or below of the mean of each subject's reaction time. Approximately 0.33% of trials were removed: no trials were removed in the sun group, and in the moon group 0.04% trials were removed from the experimental session and 1.27% trials were removed from the control session. From the remaining trials for each participant, we calculated the percent of trials selecting the adapted direction of movement toward the adaptation direction (i.e., sun or moon direction) as well as mean reaction time for each percentage level.

First, we conducted a 2 (experimental condition: adaptation, control; within-subjects) × 7 (actual percentage toward the adaptation direction: 20%–80% rate of actual movement toward the adaptation direction; within-subjects) repeated-measures analysis of variance (ANOVA). The primary comparison was the difference between the adaptation and the control conditions within each actual percentage of movement since a MAE would lead to a shift in the curve for the adaptation conditions. Because this difference between adaptation and control was the primary outcome measure, we also conducted Tukey honestly significant difference (HSD) paired *t* tests between adaptation trials and control trials within each actual percentage of movement.

We then analyzed the data by fitting results with a Weibull function. In the current study, the Weibull function assumes that the perceived movement contrast between the moon and the sun scales proportionally to the signal-to-noise ratio of the actual movement contrast that supports the perception. Separate Weibull functions were fit to individual participants' data for each experimental condition (adaptation and control) and each percentage of movement in the adaptation direction (20%–80%) using Palamedes toolbox in MATLAB (Prins & Kingdom, 2018). Two parameters were derived for each fitted function: the α value (i.e., the point of subjective equality) measures a bias to respond the "sun" or the "moon" direction in the task, and the β value reflects the detectability of the difference in the task. We then filtered nine subjects' data (three from the sun adaptation group, six from the moon adaptation group) whose α or β value were beyond 2 *SD*s above or below the mean, and conducted paired *t* tests of the α and β values between the adaptation and control condition. In addition, we reran the same ANOVAs of reported rate and reaction time on the filtered data. Throughout the article, "all subjects" refers to all the subjects

whose data were used for the initial analyses, including subjects who were later excluded based on implausible parameter estimates from the Weibull function fitting procedure.

Based on poststudy questionnaires, participants generally reported the same strategies for both adaptation and control sessions. More specifically, more than half of the subjects (*n* = 36) reported using counting strategies (e.g., mentally counting time, counting steps, physically counting by tapping fingers, etc.). The next set of subjects (*n* = 18) reported keeping focus on a certain part of the environment (e.g., wall, hallway, ground, sky, etc.) for distance estimation. Each of the remaining people (*n* = 6) used a unique strategy. For the filtered data, there were still subjects using counting (*n* = 31), focusing on a part of the environment (*n* = 14), and a unique strategy (*n* = 6). We controlled for the influence of strategies by adding strategy as a factor in the above ANOVA analyses for reported rate and reaction time.

Results

ANOVA Results

We observed significant MAEs of travel direction in the adaptation condition compared to the control, $F(1, 59) = 11.38$, $p = .001$, $\eta_p^2 = .162$, 95% confidence interval (CI) [0.028, 0.332] (Figure 2). Although we found a significant shift in the function with adaptation, the pattern was not in the direction we initially predicted: motion adaptation increased travel estimation in the same direction as the adaptation, instead of producing a traditional opponent-process aftereffect in the opposite direction. As expected, there was a main effect of the actual percentage of motion on perceived direction, $F(2.14, 126.49) = 522.34$, $p < .001$, $\eta_p^2 = .899$, 95% CI [0.882, 0.912], with the perceived percentage of movement in the adaptation direction increased with the actual percentage. There was also an interaction between the experimental condition and the actual percentage of movement, $F(4.22, 248.94) = 4.91$, $p < .001$, $\eta_p^2 = .077$, 95% CI [0.021, 0.122], which indicates that the difference between the adaptation and control conditions depended on the actual percentage of movement in the adaptation direction. Post hoc analyses revealed that the adaptation significantly increased the perceived percentage of movement in the adaptation direction in several conditions where the actual percentage was below 60%. These planned comparisons further confirmed that the adaptation condition was increased toward the adaptation direction compared to the control condition (Figure 2).

We conducted several additional analyses to preclude possible explanations besides a MAE. We separately analyzed results from the sun and moon adaptation groups and found the same result as the combined data (with somewhat weaker effects for the moon group), which ensured that neither the particular adaptation direction nor response bias disproportionately affected the results (Figure S2 in the online supplemental materials). We also found no serial position effects (i.e., no primacy or recency effects), suggesting that no particular portion of the test phase disproportionately contributed to the reported rate (e.g., participants only paid attention to the last second of the movement; Figure S3, A6 in the online supplemental materials). We found no reaction time differences between conditions. We only found the expected higher reaction time at the 50%, indicating that participants found the condition with equal amounts of travel in each direction difficult to
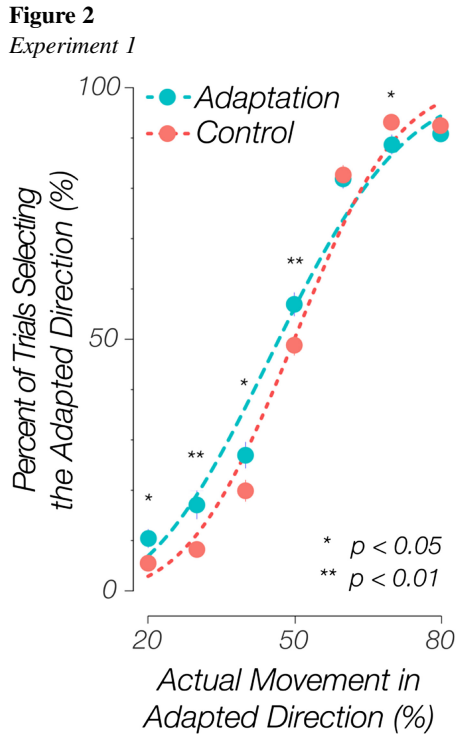
Figure 2

Experiment 1

Note. The perceived percentage of movement in the adaptation direction compared with the actual percentage for all subjects ($n = 60$). Solid dots indicate the grand average value, and error bars indicate standard errors. Dashed lines indicate the average psychometric Weibull functions. The adaptation condition had an overall significantly higher percent of trials selecting the adapted direction than the control condition ($p = .001$). The adaptation condition showed significantly higher percent of trials selecting the adapted direction than corresponding control conditions at 20%, 30%, 40%, and 50%, supporting the aftereffect. This result suggests an aftereffect in the same direction of travel. There was also a significant interaction between condition and the actual percentage. The bias psychometric function (i.e., α) for the adaptation condition did not significantly shift compared to the control ($p = .252$). The uncertainty psychometric function (i.e., β) became more flattened when adapted, indicating that observers' detectability of the difference between the two directions was decreased by adaptation ($p = .007$). See the online article for the color version of this figure.
* $p < .05$.   ** $p < .01$, Tukey correction.

judge, which is an indication that our task was effective (Figure S1 in the online supplemental materials). We also specifically analyzed just the first test trials in each block after the initial 60-s adaptation and found similar patterns of results as the entire data set; this finding suggests that the opposite MAE was not due to insufficient adaptation during the top-ups (Figure S7 in the online supplemental materials). Further, the test trials were the same for the control and test conditions, so it is unlikely that remembering the movement direction they experienced for more or less time (availability

heuristic) would underlie the aftereffect. In addition, the pattern of results was stable after we controlled for strategies in the analyses (see Data Analysis section and Experiment 1 in the online supplemental materials). Finally, we filtered out nine subjects (around 15% of the subjects; three from the sun adaptation group, six from the moon adaptation group), based on a Weibull function (Mood et al., 1974) and the results from the remaining subjects still revealed the same pattern as the raw data. This finding suggests that the observed opposite MAE was not due to outlier subjects (see Data Analysis section for details of the filtering procedure; Figure S8 in the online supplemental materials).

Weibull Analysis Results

To quantify the magnitude of the aftereffect, we fitted each participant's data with a Weibull function (Mood et al., 1974). α and β values were derived for each fitted function: α means a bias to respond to the "sun" or the "moon" direction in the task, while β means the detectability of the difference in the task (methods). We found no difference in the bias (α) between the adaptation and the control conditions, $t(59) = 1.16$, $p = .252$, Cohen's $d = 0.196$, 95% CI [−0.143, 0.536], *ns*. The detectability (β) in the adaptation condition was significantly lower than in the control condition, $t(59) = −2.79$, $p = .007$, Cohen's $d = −0.439$, 95% CI [−0.765, −0.113], indicating that people had more uncertainty in making judgments in the adaptation condition (Figure 2).

Discussion

In summary, our first experiment found a significantly increased perception of movement toward the direction of adaptation, consistent with a MAE. Participants also exhibited more uncertainty after the adaptation, compared to control, suggesting that the adaptation was affecting their judgments of movement direction during the test periods. Together, these findings are consistent with a role for travel direction that is independent of head direction.

Experiment 2: MAEs Remain When Adaptation of Head Direction Is Orthogonal to Travel Direction

In Experiment 2, we attempted to address additional questions about response biases and approaching effects from Experiment 1. Specifically, we wondered whether in Experiment 1 people felt like they were approaching the adapted direction due to the alignment of head and travel directions along the same axis. Although we separated travel direction from head direction by randomly flipping head direction throughout the task, travel direction was still on the same axis as head direction—the direction that aligns with the front-back body axis. One possible outcome of this alignment of travel direction and head direction is that people might more easily generate a feeling of approaching the adapted travel direction. Thus, to test this alternative possibility and to preclude approaching effects during the adaptation, in Experiment 2 we changed the facing direction to be perpendicular to travel direction (Figure 3a–e and experimental videos; method). Because travel direction and facing direction were never aligned, this experiment provides an even more stringent test of our MAE hypothesis.

Figure 3
Experiment 2
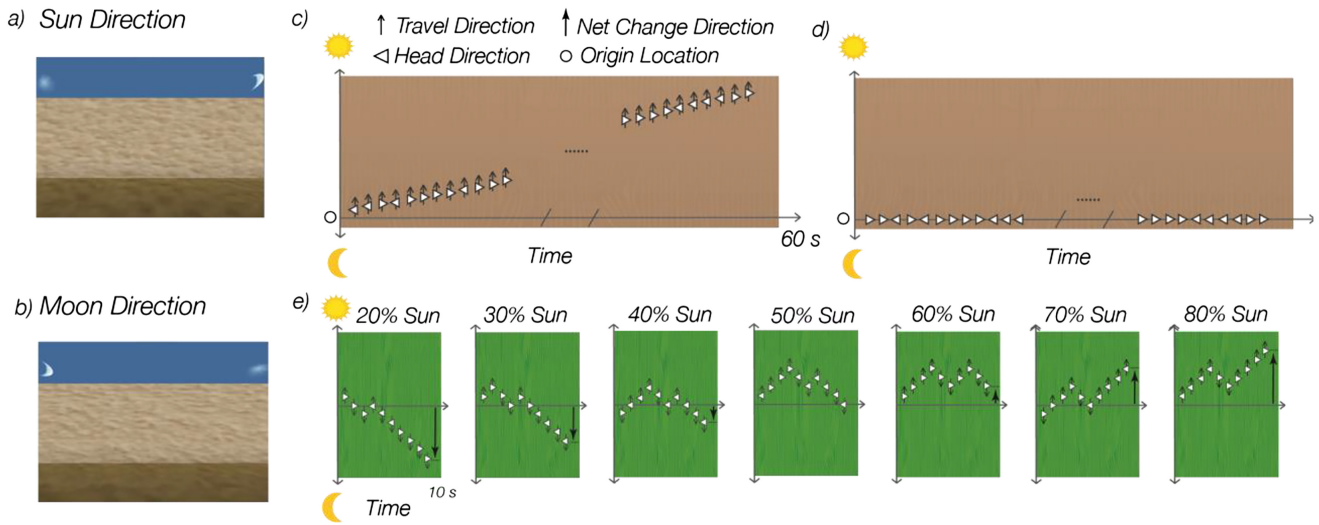
Note. (a) Hallway during the adaptation phase, adapting to the sun direction. (b) Hallway during the adaptation phase, adapting to the sun direction, but with the opposite facing direction compared to (a). The ground for the hallways turned green during the test phase to provide a visual cue for when to start tracking movement direction. (c) Overhead illustration of the 60-s adaptation phase for the experimental condition. During the adaptation phase, visual movement traveled toward the sun while the facing direction occasionally changed. (d) Overhead illustration of the 60-s initial phase for the control session. There was no visual travel, but the facing direction randomly changed. (e) The test phase, which was the same for all sessions in all conditions. Visual movement traveled back-and-forth between the sun and the moon during a 10-s interval. Participants were asked to decide whether the total movement was more toward the sun or more toward the moon in that interval. The facing direction randomly changed during the test phase. Here we show one example from each of the seven test phase conditions of the percent of net movement toward the adaptation direction (20%, 30%, 40%, 50%, 60%, 70%, and 80%). See the online supplemental materials for links to the experiment video. See the online article for the color version of this figure.

Method

Participants

The sample size in Experiment 2 was determined based on power analysis using the results of Experiment 1. We used G*Power software (https://www.gpower.hhu.de/; Erdfelder et al., 1996) with an $\alpha = .05$, power $= .8$, and Cohen's f measurement of effect size $= 0.176$ which is based on the weakest effect size (i.e., the interaction effect of the moon condition, see Figure S2c in the online supplemental materials) from Experiment 1. The resulting sample size for within-group comparison was 24. Using this power analysis, we recruited 33 participants for Experiment 2, which is more than adequate for the main objectives of this study and which matched closely with the participant numbers from the Experiment 1 sun condition. Participants consisted of 33 University of California, Irvine (UCI) students who participated in return for monetary incentive ($12/hr). Three participants were discarded for misunderstanding the task instruction ($n = 1$), wrongly pressing the reverse response buttons ($n = 1$), or not completing both control and adaptation sessions ($n = 1$). The final pool consisted of 30 participants (14 males, 16 females; 20 not Hispanic or Latino, nine Hispanic or Latino, one not reported; 14 Asian, 11 White, two African American, one American Indian, one other, one not reported). Participants chose from options for sex, race, and ethnicity and filled in a blank for age. Ages of the remaining 30 participants ranged from 18 to 34 ($M = 22.93$). All participants signed an informed consent form in agreement with the UCI Institutional Review Board requirements (Approval 2019-5315) in accordance with the Declaration of Helsinki.

The stimuli, task, design, and procedure were the same as Experiment 1, except that tasks were modified such that the head direction was always orthogonal to the travel direction (see Figure 3). See the online supplemental materials for links to videos of the task. For simplicity, we only conducted adaptation to the sun direction. The initial control adaptation period lasted 60 s in Experiment 2.

Data Analysis

The analysis was largely the same as Experiment 1. We first removed outlier trials that were 3 *SD*s above or below of the mean of each subject's reaction time. Approximately 2.12% of trials were removed: 2.18% trials were removed from the experimental session and 2.06% trials were removed from the control session. From the remaining trials for each participant, we calculated the percent of trials selecting the adapted direction of movement toward the sun as well as mean reaction time for each percentage level.

First, we conducted a 2 (experimental condition: adaptation, control; within-subjects) × 7 (actual sun percentage: 20%–80% rate of actual movement toward the sun; within-subjects) repeated-measures ANOVA analysis. Because the primary comparison was the difference between the adaptation and the control conditions within each actual percentage of movement, we also conducted Tukey HSD paired t tests between adaptation trials and control trials within each actual percentage of movement. We then filtered seven subjects' data and analyzed the data using parameters derived from Weibull fits, similar to Experiment 1.

Based on poststudy questionnaires, participants generally reported the same strategies for both adaptation and control sessions. Same as we had observed in Experiment 1, people reported three main types of

strategies in Experiment 2: counting strategies ($n = 13$), keeping focus on a certain part of the environment for distance estimation ($n = 7$), and a unique strategy ($n = 10$). For the filtered data, there were still subjects using counting ($n = 12$), focusing on a part of the environment ($n = 4$), and a unique strategy ($n = 7$). Again, we controlled for the influence of strategies by adding strategy as a factor in the above ANOVA analyses for reported rate and reaction time.

Results

ANOVA Results

We observed a trend for a difference between the perceived percentage in the adaptation and the control conditions, but it was not statistically significant, $F(1, 29) = 2.92$, $p = .098$, $\eta_p^2 = .092$, 95% CI [0.000, 0.321], *ns*. As expected, there was a main effect of the actual percentage report, $F(2.10, 60.89) = 232.24$, $p < .001$, $\eta_p^2 = .889$, 95% CI [0.861, 0.909], that showed the perceived percentage increased with the actual percentage. There was no interaction between the experimental condition and the actual percentage, $F(3.31, 95.97) = 2.07$, $p = .103$, $\eta_p^2 = .067$, 95% CI [0.000, 0.122], *ns*. However, for the planned Tukey HSD paired *t* tests between adaptation trials and control trials within each actual percentage, we found that adaptation increased the perceived percentage where the actual percentages were 20% and 40%. These planned comparisons found that the adaptation condition was increased toward the adaptation direction, compared to the control condition (Figure 4), consistent with Experiment 1.

Furthermore, after controlling for people's self-reported strategies by including types of strategies (e.g., counting, focusing on part of the environment, and others) as a factor in the analyses (see Data Analysis section), the difference between the adaptation and the control condition became more distinguishable, such that adaptation increased people's reported rate, $F(1, 27) = 5.58$, $p = .026$, $\eta_p^2 = .171$, 95% CI [0.000, 0.418]. There was also a significant interaction between condition and the actual percentage, $F(3.53, 95.40) = 3.23$, $p = .020$, $\eta_p^2 = .107$, 95% CI [0.012, 0.178]. Tukey HSD analyses revealed that people reported significantly more travel toward the adaptation direction in the adaptation session than in the control session at 20% ($p = .003$), 40% ($p = .005$), 50% ($p = .031$), and marginally more at 30% ($p = .070$; see Experiment 2 in the online supplemental materials for more details). The MAE also got stronger after excluding seven subjects (about 25% of subjects) based on implausible parameter estimates from the Weibull function fitting procedure (Figure B2 in the online supplemental materials; see Data Analysis section for details of the filtering procedure).

Weibull Analysis Results

We fit each subject's data into the Weibull function as we did in Experiment 1. We found no difference between the adaptation and the control conditions in either response bias (α), $t(29) = 0.43$, $p = .670$, Cohen's $d = 0.112$, 95% CI [−0.409, 0.633], *ns* or detectability (β), $t(29) = -1.28$, $p = .210$, Cohen's $d = -0.251$, 95% CI [−0.648, −0.147], *ns* (Figure 4).

Discussion

Thus, the observed aftereffects in Experiment 2 were weaker compared with those observed in Experiment 1, but still largely

Figure 4
Experiment 2
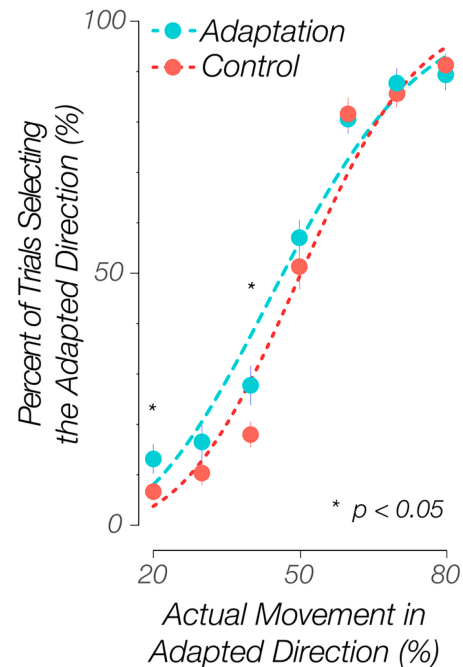
Note. The perceived percentage of movement in the adaptation direction compared with the actual percentage for all subjects ($n = 30$). Solid dots indicate the grand average value, and error bars indicate standard errors. Dashed lines indicate the average psychometric Weibull functions. The adaptation condition showed significantly higher percent of trials selecting the adapted directions than corresponding control conditions at 20% and 40%, supporting the aftereffect. This result suggests an aftereffect in the same direction of travel. The bias psychometric function (i.e., α) did not significantly shift when adapted ($p = .670$). The uncertainty psychometric function (i.e., β) indicates that observers' detectability of the difference between the two directions was not significantly decreased by adaptation ($p = .210$). See the online article for the color version of this figure.
* $p < .05$, Tukey correction.

followed the pattern of a MAE in the direction of travel. Experiment 2 had fewer participants than Experiment 1; the sample size was based on our power analysis from the Experiment 1 results. This weaker aftereffect could be also due to the unusual travel direction in the task: in daily life, people experience walking forward or backward more often than walking laterally. Moreover, especially for the adaptation condition, tracking four directions (front-back for head direction and left-right or sun-moon directions for travel direction) in Experiment 2 was likely more challenging than in Experiment 1, where people only tracked two directions (front-back or sun-moon directions for both travel direction and head direction). After including the strategy as an additional factor or excluding subjects based on implausible parameter estimates from the Weibull function fitting procedure, we observed much stronger MAEs, indicating that we were able to successfully

replicate the results from Experiment 1 in this more challenging scenario.

Experiment 3a: MAEs Scale With Duration of Adaptation

In Experiment 3a, we attempted to address remaining questions from Experiments 1 and 2 about the adaptation duration. An alternative explanation for the "opposite" adaptation effect is that the adaptation time used in the previous two experiments might be too long or too short to induce a sufficient adaptation effect for travel direction. We initially set the adaptation time (i.e., 60 s initial adaptation, 10 s top-ups) based on previous visual adaptation studies, but since adaptation effects of travel direction have never been studied before, we had few a priori expectations regarding whether adaptation duration would produce larger or smaller effects. Based on previous visual adaptation literature, the magnitude of a classic MAE should scale depending on the amount of adaptation, as increased adaptation time yields a greater decrease in the neural responsiveness to the same stimuli (Fang et al., 2005; Fang & He, 2005; Leopold et al., 2005; Vautin & Berkley, 1977).

Another motivation for modulating the response time was to address questions of response bias, availability heuristics, and demand characteristics. If a participant simply was biased to press the adaptation direction because they had seen it more often or because of other cognitive biases, then all adaptation times would show similar effects. In contrast, differences between adaptation times would suggest that participants are less influenced by other biases. We address this question again in Experiment 3b.

To take a closer look at whether and how adaptation time affects MAEs of travel direction, we conducted an experiment where we tested four adaptation time periods: 18, 36, 54, and 72 s. Motion was in the direction of the hallway like in Experiment 1, and for simplicity we only used the sun direction for this study. Because we added more adaptation conditions, we also only tested three levels of percentage of actual movement in the adaptation direction: 30%, 50%, and 70% (see method).

Method

Participants

Similar to Experiment 2, we calculated a sample size of 24 for within-group comparison in Experiment 3a determined based on power analysis using G*Power software (https://www.gpower.hhu .de/; Erdfelder et al., 1996) based on the weakest effect size from Experiment 1 (Figure S2c in the online supplemental materials). We recruited 28 participants for Experiment 3 (12 males, 16 females; 26 not Hispanic or Latino, one Hispanic or Latino, one not reported; 19 Asian, nine White), which is more than adequate for the main objectives of this study. All participants were UCI students who participated in return for monetary incentive ($12/hr). Ages of the participants ranged from 18 to 30 ($M = 24.71$). Participants chose from options for sex, race, and ethnicity and filled in a blank for age. All participants signed an informed consent form in agreement with the UCI Institutional Review Board (Approval 2019-5315) requirements in accordance with the Declaration of Helsinki.

The stimuli and procedure were the same as Experiment 1.

Task

The task was the same as Experiment 1, except for the following:

1. Each block started with different initial adaptation time periods (18, 36, 54, or 72 s), correspondingly followed by different top-up time periods (3, 6, 9, or 12 s). The control adaptation phases and top-up periods had the same corresponding time lengths.

For convenience, we refer to all adaptation trials in terms of their initial adaptation time.

2. Corresponding to the change in the time length for the adaptation phases, we also changed the range of the number of turns of the facing direction that each top-up and adaptation period was sampled from: zero to one turn for 3 s top-ups, zero to two turns for 6 s top-ups, zero to two turns for 9 s top-ups, zero to two turns for 12 s top-ups, one to three turns for 18 s adaptation periods, three to five turns for 36 s adaptation periods, four to six turns for 54 s adaptation periods, and six to eight turns for 72 s adaptation periods. Ranges were calculated based on the following equations:

$$N_{\max} = \lfloor \alpha t + 1 \rceil, \tag{1}$$

$$N_{\min} = \begin{cases} \lfloor \alpha t - 1 \rceil, & \text{if } t \geq 10 \\ 0, & \text{otherwise} \end{cases}, \tag{2}$$

where N denotes the number of turns. α is a coefficient which was set to 0.1. t denotes the number of time step in the trial (either the adaptation or the test phase). $\lfloor \rceil$ denotes round to the nearest integer.

3. To keep the experiment within two sessions, we used three percentages of virtual movement (30%, 50%, and 70%) and reduced the number of trials in each percentage to nine.

Design

A 2 (experimental condition: adaptation, control; within-subjects) × 4 (adaptation time blocks: 3 s top-up with 18 s initial adaptation, 6 s top-up with 36 s initial adaptation, 9 s top-up with 54 s initial adaptation, 12 s top-up with 72 s initial adaptation; within-subjects) × 3 (actual percentage of movement toward the sun: 30%, 50%, 70% rate; within-subjects) within-subject design was used. Each test condition was repeated for nine trials, for a total of 108 trials (4 blocks × 3 percentages/block × 9 trials/percentage, not including the initial trial of each block). Each of the four blocks corresponded to one adaptation time condition. The order of the four blocks was counterbalanced across subjects. The trials with the three different percentages of actual movement toward the sun were presented in random order within each block. There was a short break between blocks. A new initial adaptation period occurred after each break to initiate adaptation of a different magnitude.

The experiment was conducted over two sessions for each participant, with one session the experimental task and the other session as the control. The order of completing these two sessions was counterbalanced.

Data Analysis

The analysis was largely the same as Experiment 1. We first removed outlier trials that were 3 SDs above or below of the mean

of each subject's reaction time. Approximately 1.93% of trials were removed: 1.79% trials were removed from the experimental session and 2.08% trials were removed from the control session. From the remaining trials for each participant, we calculated the percent of trials selecting the adapted direction of movement toward the sun as well as mean reaction time for each percentage level at each adaptation condition (the initial adaptation trial in each block was not included).

First, we conducted a 2 (experimental condition: adaptation, control; within-subjects) × 3 (actual sun percentage: 30%, 50%, 70% rate of actual movement toward the sun; within-subjects) repeated-measures ANOVA for each adaptation time periods (18, 36, 54, or 72 s) separately. Because the primary comparison was the difference between the adaptation and the control conditions within each actual percentage of movement, we also conducted Tukey HSD paired t tests between adaptation trials and control trials within each actual percentage of movement.

Next, we conducted a 4 (adaptation time periods: 18, 36, 54, or 72 s; within-subjects) × 3 (actual sun percentage: 30%, 50%, 70% rate of actual movement toward the sun; within-subjects) repeated-measures ANOVA for each experimental condition (control, adaptation) separately. Because the primary comparison was the difference between different adaptation time periods within each actual percentage of movement, we also conducted Tukey HSD paired t tests between different adaptation time periods within each actual percentage of movement. We then filtered and analyzed the data using the Weibull function, similar to Experiment 1. We filtered four subjects' data from all conditions based on subjects whose results were excluded by more than one adaptation time period condition.

Same as we have observed in Experiments 1 and 2, people reported three main types of strategies in Experiment 3a: counting strategies ($n = 13$), keeping focus on a certain part of the environment for distance estimation ($n = 13$), and a unique strategy ($n = 2$). For the filtered data, there were still subjects using counting ($n = 10$), focusing on a part of the environment ($n = 12$), and a unique strategy ($n = 2$). Again, we controlled for the influence of strategies by adding strategy as a factor in the above ANOVA analyses for reported rate and reaction time.

Results

ANOVA Results

We were again able to successfully replicate the primary results from Experiment 1 and Experiment 2. We observed a tendency for a difference between the experimental and control conditions at the 18 s adaptation time period, $F(1, 27) = 3.88$, $p = .059$, $\eta_p^2 = .126$, 95% CI [0.000, 0.370]. The effect grew to become significant at 36 s, $F(1, 27) = 5.20$, $p = .031$, $\eta_p^2 = .162$, 95% CI [0.000, 0.408], as well as at 54 s, $F(1, 27) = 13.25$, $p = .001$, $\eta_p^2 = .329$, 95% CI [0.070, 0.555], and 72 s adaptation time periods, $F(1, 27) = 7.22$, $p = .012$, $\eta_p^2 = .211$, 95% CI [0.011, 0.455]. This result suggests that the magnitude of the travel MAE scales with adaptation time (Figure 5 and Figure S13 in the online supplemental materials).

Next, we made pair-wise comparisons between the different adaptation time conditions at each percentage of actual movement in the adaptation direction (Figure S11a–f, Figure S12, and Figure S14 in the online supplemental materials). This analysis revealed that when

the actual percentage was at 70%, the 72 s adaptation trials had significantly higher perceived percentage than the 36 s adaptation trials ($p = .014$; Figure S11e in the online supplemental materials) and marginally higher than the 54 s adaptation trials ($p = .055$; Figure S11f in the online supplemental materials).

All patterns of results were maintained after excluding four subjects (around 14% of subjects) based on implausible parameter estimates from the Weibull function fitting procedure (Figures S15–S18 in the online supplemental materials). These findings are consistent with MAEs scaling with adaptation time. These findings were replicated in an independent sample of participants ($n = 31$ participants; 16 females), with slightly different instructions and some blocks having adaptation to the moon direction (see Figures S22–S27 in the online supplemental materials). In addition, the main pattern of results did not shift after controlling for strategies in the analyses for both Experiment 3a and the replication (see Data Analysis section, Data Analysis in the online supplemental materials, Experiment 3a, and Experiment 4). The replication (i.e., Experiment 4, see the online supplemental materials) precludes the possible explanation of demand characteristics because the different instructions occasionally indicated that adaptation would be to the opposite direction than what actually occurred, yet the effect remained in those situations.

Weibull Analysis Results

Further, Weibull analyses showed that when the adaptation time was 54 s, $t(27) = -2.54$, $p = .017$, Cohen's $d = -0.616$, 95% CI [-1.146, -0.086], and 72 s, $t(27) = -1.86$, $p = .074$, Cohen's $d = -0.146$, 95% CI [-0.623, 0.331], people had significantly more uncertainty in making judgments in the adaptation condition compared to the control condition. When adaptation time was 72 s, there was a tendency to bias responses (α) toward the adaptation direction, $t(27) = -2.00$, $p = .056$, Cohen's $d = -0.575$, 95% CI [-1.199, 0.048] (Figure 5).

Discussion

Overall, the results in Experiment 3a successfully replicated effects from Experiment 1 and Experiment 2. Importantly, we observed the same "opposite" MAE of travel direction for differing adaptation time lengths, precluding the alternative explanation that the "opposite" MAE was due to the adaptation time being too long or too short. Furthermore, the travel aftereffect was scaled with adaptation duration, such that longer adaptation duration tended to have larger aftereffects. Together, these findings provide additional support for a MAE for travel direction that is independent of head direction.

Experiment 3b: MAEs Disappear in Delayed Tests

The results of Experiment 3a demonstrated that the travel aftereffect scaled with adaptation duration. Although these results support the hypothesis of an aftereffect rather than other heuristics or biases, we wished to address that question more directly. In Experiment 3b, we allowed the adaptation to "cool off" with a control delay after the adaptation. Under the assumption that any adaptation will decay after some amount of time, we gave participants an additional stationary control period after the initial adaptation. We did the same for the control condition. We reasoned that if there is a response

Figure 5
Experiment 3a
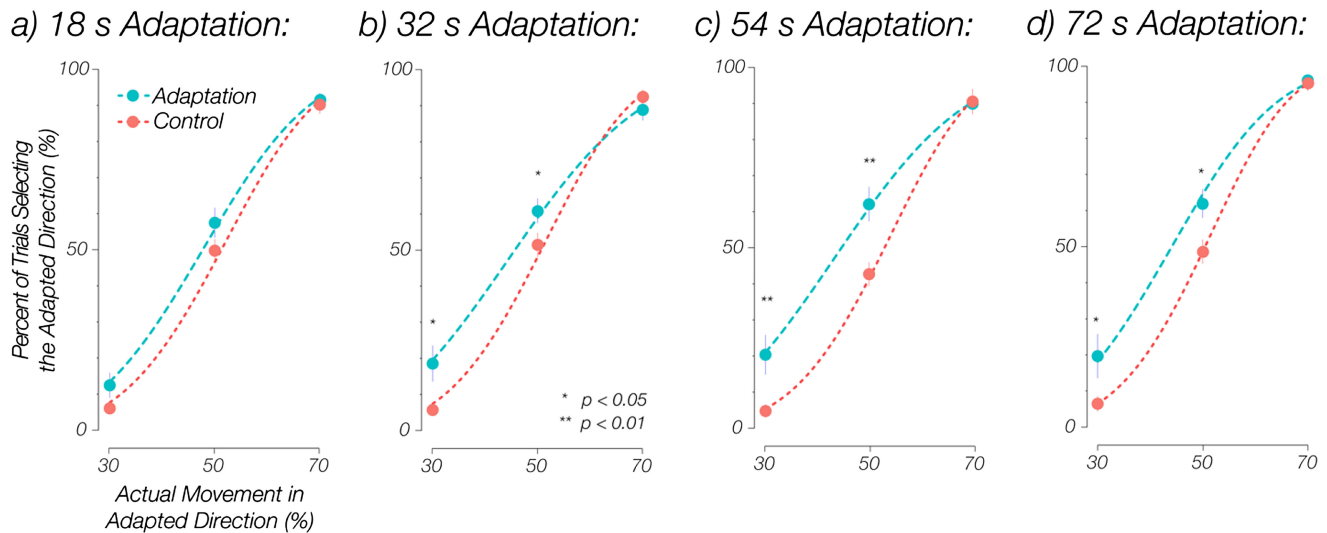
a) 18 s Adaptation: *b) 32 s Adaptation:*   *c) 54 s Adaptation:*   *d) 72 s Adaptation:*

Note. The perceived percentage of movement in the adaptation direction compared with the actual percentage for all subjects, separated by adaptation time periods ($n = 28$). Solid dots indicate the grand average value, and error bars indicate standard errors. Dashed lines indicate the average psychometric Weibull functions. (a) The reported rate for 18 s adaptation trials. The adaptation condition showed a trend for higher percent of trials selecting the adapted directions than the control conditions ($p = .059$). (b) The reported rate for 36 s adaptation trials. The adaptation condition showed significantly higher overall percent of trials selecting the adapted directions than the control conditions ($p = .031$), particularly at 30% ($p = .015$) and 50% ($p = .032$), supporting the aftereffect in the same direction of travel. (c) The reported rate for 54 s adaptation trials. The adaptation condition showed significantly higher overall percent of trials selecting the adapted directions than the control conditions ($p = .001$), particularly at 30% ($p = .007$) and 50% ($p = .001$), supporting the aftereffect. (d) The reported rate for 72 s adaptation trials. The adaptation condition showed significantly higher reported overall percentages than the control conditions ($p = .012$), particularly at 30% ($p = .047$) and 50% ($p = .032$), supporting the aftereffect in the same direction of travel. The bias psychometric function (i.e., α) marginally shifted toward a lower percentage of reported movement toward the adaptation direction when adapted at 72 s adaptation ($p = .056$) time period, but the shift was not significant at 18 s ($p = .315$), 36 s ($p = .407$), or 54 s ($p = .669$) adaptation time periods. The uncertainty psychometric function (i.e., β) indicates that observers' detectability of the difference between the two directions was decreased by adaptation but was not significant at 18 s ($p = .543$) or 36 s ($p = .132$) adaptation time periods, but was significant at 54 s ($p = .017$) adaptation time period and marginally significant at 72 s ($p = .074$) adaptation time period. See the online article for the color version of this figure.
* $p < .05$.   ** $p < .01$, Tukey correction.

bias, demand characteristics, or availability heuristic, then participants would still exhibit a greater tendency to report the adapted direction. In contrast, if the adaptation did reduce over time, then we would expect no differences between the experimental and control conditions. Because we predicted a null result, we followed up our standard analyses with Bayes factor analyses.

Method

Participants

Similar to Experiment 2, we calculated a sample size of 24 for within-group comparison in Experiment 3a determined based on power analysis using G*Power software (https://www.gpower.hhu.de/; Erdfelder et al., 1996) based on the weakest effect size from Experiment 1 (Figure S2c in the online supplemental materials). We recruited 33 participants for Experiment 3b), which is more than adequate for the main objectives of this study. All participants were UCI students who participated in return for monetary incentives ($12/hr). One participant was discarded for task error ($n = 1$). The final pool consisted of 32 participants (10 males, 22 females; 26 not Hispanic or Latino, six Hispanic or Latino; 17 Asian, six White,

three African American/Black, six other). Ages of the remaining participants ranged from 18 to 29 ($M = 20.94$). Participants chose from options for sex, race, and ethnicity and filled in a blank for age. All participants signed an informed consent form in agreement with the UCI Institutional Review Board (Approval 2019-5315) requirements in accordance with the Declaration of Helsinki.

Stimuli and Procedure

Experiment 3b combined features from Experiment 1 and Experiment 3a. We used the same overall adaptation time (60 s) and procedure from Experiment 1. In order to complete the experiment in a single session, we only used the 30%, 50%, and 70% rates of actual movement toward the sun. The control condition was counterbalanced with the experimental condition across participants. The main difference with the other experiments is that we added a 60-s "cool down" period after adaptation, which was just the same as the control session—no movement but with rotations in place to change the facing direction. To be consistent, the control condition also had this cool-down period, which resulted in 120 s of control. The 10-s "top-up" periods between test trials were also followed by a 10-s "cool down." The remainder of the test trials were the

same as in Experiments 1 and 3a. See the online supplemental materials for links to videos of the task.

Data Analysis

The analysis was largely the same as Experiment 1. We first removed outlier trials that were 3 SDs above or below the mean of each subject's reaction time. Approximately 2.49% of trials were removed: 2.68% trials were removed from the experimental session and 2.31% trials were removed from the control session. From the remaining trials for each participant, we calculated the percent of trials selecting the adapted direction of movement toward the sun as well as mean reaction time for each percentage level.

First, we conducted a 2 (experimental condition: adaptation, control; within-subjects) × 3 (actual sun percentage: 30%, 50%, 70% rate of actual movement toward the sun; within-subjects) repeated-measures ANOVA analysis. Because the primary comparison was the difference between the adaptation and the control conditions within each actual percentage of movement, we also conducted Tukey HSD paired t tests between adaptation trials and control trials within each actual percentage of movement. We then filtered 17 subjects' data and analyzed the data using parameters derived from Weibull fits, similar to Experiment 1. Because strategies in previous experiments did not reveal obvious influence on results, a poststudy strategy questionnaire was not implemented. Additionally, because the main hypothesis of the experiment predicts no difference between the two conditions, we computed Bayes factors for these measures using the Bayes Factor package in R. A Bayes factor indicates how stronger a model is preferred than an alternative null model. Because our experiment used a within-subject design, we report comparisons between the experimental factors plus subjects factors and a subject-only model.

ANOVA Results

We observed no difference between the perceived percentage in the adaptation and the control conditions, Figure 6; $F(1, 31) = 1.00$, $p = .325$, $\eta_p^2 = .031$, 95% CI [0.000, 0.221], ns. As expected, there was a main effect of the actual percentage report, $F(1.72, 53.33) = 283.37$, $p < .001$, $\eta_p^2 = .901$, 95% CI [0.855, 0.929], that showed the perceived percentage increased with the actual percentage. There was no interaction between the experimental condition and the actual percentage, $F(1.78, 55.20) = 0.88$, $p = .410$, $\eta_p^2 = .028$, 95% CI [0.000, 0.130], ns. Further, for the planned Tukey HSD paired t tests between adaptation trials and control trials within each actual percentage, we found no difference in perceived percentage between adaptation and control conditions where actual percentages were 30%, 50%, or 70% (Figure 6), indicating the 60 s control phase right after adaptation mitigates the adaptation effects, thus there was no adaptation in the test phase.

Examination of Bayes factors revealed that the condition + subject model was stronger than the subject-only model by a factor of 0.16 ($\pm 2.29\%$), which indicates moderate-to-strong support for the null hypothesis. The Bayes factor for the condition + actual percentage + subject model was 8.70×10^{70} ($\pm 2.06\%$). The strongest model was actual percentage + subject model, with a Bayes factor of 3.70×10^{71} ($\pm 0.64\%$) compared to the subject-only model.

There was still no MAE after excluding 17 subjects (about 53% of subjects) based on implausible parameter estimates from Weibull function fitting procedure (Figure S20 in the online

Figure 6

Experiment 3b
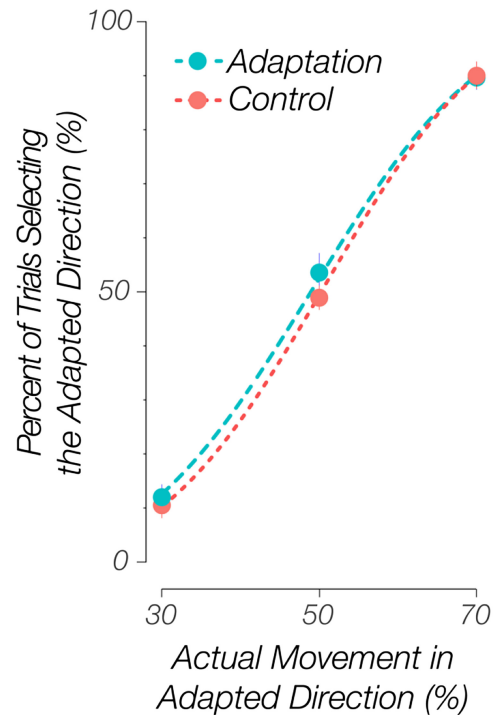
Note. The perceived percentage of movement in the adaptation direction compared with the actual percentage for all subjects. Solid dots indicate the grand average value, and error bars indicate standard errors. Dashed lines indicate the average psychometric Weibull functions. The adaptation conditions showed no difference compared to the control conditions, either overall ($p = .325$) or at any of the percentages. Neither the bias psychometric function (i.e., α; $p = .543$) nor the uncertainty psychometric function (i.e., β; $p = .274$) demonstrated any effects. See the online article for the color version of this figure.

supplemental materials; see Data Analysis section for details of the filtering procedure).

Weibull Analysis Results

We fit each subject's data into the Weibull function as we did in Experiment 1. We found no difference between the adaptation and the control conditions in either response bias (α), $t(15) = -0.64$, $p = .531$, Cohen's $d = -0.233$, 95% CI [−0.984, 0.518], ns, or detectability (β), $t(15) = -0.98$, $p = .341$, Cohen's $d = -0.303$, 95% CI [−0.948, 0.341], ns (Figure 6).

Discussion

Overall, the results in Experiment 3b successfully demonstrated that the addition of a "cool down" period after adaptation eliminates the MAEs. This delay between adaptation and test allowed us to test for other potential explanations of our results, such as response bias or demand characteristics of the experiment. We observed no

support for these other explanations, instead, we found no differences between the experimental and control conditions. These null results were supported by a Bayes factor analysis. Together with the results of Experiment 3a, these findings indicate strong support for an adaptation explanation for our results.

General Discussion

In a series of experiments, we employed a method from visual perception in a novel way to study travel direction during self-motion. We observed systematic travel MAEs across all experiments in both raw data (Figures 2, 4, and 5) and filtered data (Figures S8, S10, and S15 in the online supplemental materials). The aftereffect was not due to response bias for a particular cardinal direction, approaching effects, or serial position effects (Figure 6; Figures S3, S5, S7, and S20 in the online supplemental materials). Moreover, the MAE scaled to a longer adaptation time span. Thus, across the series of experiments, the results consistently indicate that travel direction is a process that can be adapted using a MAE. Although there may be other possible ways that travel direction selectivity could be demonstrated, we provide the first behavioral evidence of this effect. These findings indicate one possibility of how travel direction is coded in the human brain.

The aftereffects were observed in the same direction as the adapted travel direction, which fits the characteristics of previous high-level MAEs paradigms (Culham et al., 1998, 2000). First, the adaptation of travel direction we observed was likely high level. It is unclear whether a high-level aftereffect is more likely to be implemented on the level of a single neuron or through neural systems. We designed the study so that the possible influence of low-level optic flow information would be canceled out due to the constant changes of head direction in the experiment. Second, subjects were instructed to focus on the global net change in position, meaning that they had to integrate their movement over time. Third, the test phase was also dynamic, requiring integration of travel direction over time. The current task differs from previous motion adaptation experiments in that we let participants take a first-person (egocentric) perspective to attentively track self-motion, rather than simply viewing stimuli move across the screen (e.g., the waterfall effect). Taken together, this novel experimental design makes the effects we observed in the current study unique among high-level MAEs, and further study is warranted to understand the mechanisms of this effect.

This "opposite" MAE (which is actually in the same direction of travel) indicates that a nonopponent process underlies the travel direction system. Several previous studies have also found MAEs in the direction of travel, but via different sensory modalities, including the podokinetic aftereffect where spatial orientation is changed via remodeling somatosensory signals between the trunk and feet (Earhart et al., 2001; Gordon et al., 1995; Weber et al., 1998), and the jogging/running-in-place aftereffect that involves recalibration of visuomotor control systems (Anstis, 1995; Durgin & Pelah, 1999; Mulavara et al., 2010).

What could be the possible relationship between the head direction system and the travel direction system in the brain? It is difficult to find direct answers to this question because, as mentioned in the introduction, the two-direction systems have typically been conflated. However, we may get some clues from studies in which head direction and travel direction are perfectly aligned (i.e., heading direction). Several studies have investigated heading direction using

adaptation paradigms or "repetition suppression" in functional magnetic resonance imaging (fMRI) to look at the sensitivity to heading direction of various cortical visual motion areas (Baumann et al., 2010; Cardin et al., 2012; Shine et al., 2016). Researchers observed clear head direction adaptation in the middle temporal, the medial superior temporal (MST) (Cardin et al., 2012), medial parietal lobe (Baumann et al., 2010), as well as bilateral retrosplenial cortex, thalamus, and precuneus (Shine et al., 2016). We can take from these results that when head direction and travel direction are aligned, there is still adaptation taking place in the brain. The brain areas that demonstrate adaptation are higher-level motion systems, suggesting that these systems are involved in encoding heading direction in the human brain.

Possible travel direction pathways are more speculative. They could involve independent sensory inputs (e.g., vision, somatosensation) and feed-forward high-level motion processing pathways (e.g., MST, parietal lobe, hippocampus, etc.; e.g., Chrastil et al., 2016; Sherrill et al., 2015). Recent findings of bidirectional cells in rodent dysgranular retrosplenial cortex (Jacob et al., 2017) may also be a good candidate for cells that are sensitive to travel direction. Further research using fMRI and computational modeling is needed to shed light on the relationship between the travel direction and head direction systems in the human brain, and the degree to which they have independent circuitry.

Additionally, our participants did not actually change their head direction or travel direction during the experiment (all participants were sitting still, facing a computer screen, during the entire experiment), raising concerns of potential differences between self-motion induced by VR and real life. However, several previous studies have shown that vestibular areas could be activated in tasks without real vestibular motions, such as human MST (Smith et al., 2012), cingulate sulcus visual area (Putcha et al., 2014; Smith et al., 2012), and insula vestibular cortex (Putcha et al., 2014), supporting the robustness of using VR to induce vestibular signals.

Finally, we note that participants did not actually respond with how far they perceived that they had traveled. Instead, they simply responded which direction was the main direction of travel. We used this method to match classic psychophysics experiments as closely as possible, but it does not provide a fine-grained estimate of travel direction. Future tests should use alternative methods of probing this effect, including net travel on each trial.

Constraints on Generality

We note that these studies were conducted in a healthy young adult population and may not generalize to aging or patient populations. Our population consisted of both males and females, and we found no effects of sex. Although we do not have any reason to believe that the results depend on characteristics of the participants, materials, or context, these assumptions could be tested in the future. As noted above, testing with alternative measures and outcomes could constrain the generality of these results.

Conclusion

In conclusion, we found high-level MAEs of travel direction using a novel motion adaptation paradigm, which suggests that travel direction is a fundamental component of human navigation and indicates how it might be represented in the brain. Interestingly, the aftereffect

is in the opposite direction to traditional MAEs, suggesting that adapting to a travel direction will result in a greater perception of moving toward the adapting direction. Critically, we dissociated head direction from travel direction across all experiments, indicating that travel direction has separate neural mechanisms from head direction in the human brain. Considering travel direction as a basic navigation component provides a new path to understanding the question of how people form their sense of direction. Furthermore, the results will encourage scientists who study navigation behavior of other species (rodents, birds, insects, etc.) to look for more direct neurological evidence of travel direction, rather than only test for head direction.

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