



Homing tasks and distance matching tasks reveal different types of perceptual variables associated with perceiving self-motion during over-ground locomotion

Steven J. Harrison^{1,2,3} · Nicholas Reynolds³ · Brandon Bishoff³ · Nicholas Stergiou³ · Eliah White⁴

Received: 26 August 2021 / Accepted: 15 February 2022 / Published online: 24 February 2022
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2022

Abstract

Self-motion perception refers to the ability to perceive how the body is moving through the environment. Perception of self-motion has been shown to depend upon the locomotor action patterns used to move the body through the environment. Two separate lines of enquiry have led to the establishment of two distinct theories regarding this effect. One theory has proposed that distances travelled during locomotion are perceived via higher order perceptual variables detected by the haptic perceptual system. This theory proposes that two higher order haptic perceptual variables exist, and that the implication of one of these variables depends upon the type of gait pattern that is used. A second theory proposes that self-motion is perceived via a higher order perceptual variable termed multimodally specified energy expenditure (MSEE). This theory proposes that the effect of locomotor actions patterns upon self-motion perception is related to changes in the metabolic cost of locomotion per unit of perceptually specified traversed distance. Here, we test the hypothesis that the development of these distinct theories is the result of different choices in methodology. The theory of gait type has been developed based largely on the results of homing tasks, whereas the effect of MSEE has been developed based on the results of distance matching tasks. Here we test the hypothesis that the seemingly innocuous change in experimental design from using a homing task to using a distance matching task changes the type of perceptual variables implicated in self-motion perception. To test this hypothesis, we closely replicated a recent study of the effect of gait type in all details bar one—we investigated a distance matching task rather than a homing task. As hypothesized, this change yielded results consistent with the predictions of MSEE, and distinct from gait type. We further show that, unlike the effect of gait type, the effect of MSEE is unaffected by the availability of vision. In sum, our findings support the existence of two distinct types of higher order perceptual variables in self-motion perception. We discuss the roles of these two types of perceptual variables in supporting effective human wayfinding.

Keywords Odometry · Homing · Distance perception · Self-motion · Haptic perceptual system · Visual perceptual system

Introduction

Humans and animals possess a robust ability for perceiving how their body is moving through the environment during locomotion (Etienne and Jeffery 2004; Harrison and Turvey 2019). The effectiveness of this ability is supported by (1) independent capacities for detecting information about self-motion by the visual, vestibular, and haptic perceptual systems (Ellmore and McNaughton 2004; Harrison 2020; Israel et al. 1997; Schwartz 1999; Srinivasan et al. 2000), and (2) the ability to flexibly and adaptively integrate, or switch between, these sources of information (Campos and Bulthoff 2012; Campos et al. 2014; Carriot et al. 2013; Chen et al. 2017; Frissen et al. 2011; Harrison et al. 2021; Kearns 2003; Zhao and Warren 2015). For humans, the capacity

Communicated by Francesco Lacquaniti.

✉ Steven J. Harrison
steven.john.harrison@gmail.com

¹ Department of Kinesiology, University of Connecticut, Storrs, CT 06269, USA

² Center for Ecological Study of Perception and Action, University of Connecticut, Storrs, USA

³ Department of Biomechanics, University of Nebraska at Omaha, Omaha, USA

⁴ Department of Psychological Science, Northern Kentucky University, Highland Heights, USA

for perceiving self-motion can also be roughly approximated with explicit cognitive strategies such as counting the number of steps taken or by mentally timing the number of seconds elapsed (Lederman et al. 1987). In the face of context-dependent variation in gait (e.g., walking or running) and gait parameters (e.g., gait speed or step length), explicit cognitive strategies are poor substitute for perceptual solutions. For example, in the mobility training of sight impaired individuals, explicit counting strategies are actively discouraged, and only advised in highly constrained situations such as climbing stairs (Williams et al. 2014).

Self-motion perception has been investigated by studying the ability to complete simple homing tasks (see Harrison and Turvey 2019). Simple homing tasks involve a participant travelling outbound from an initial starting location, before turning around, and then attempting to travel inbound, directly back to where they started. When homing tasks are performed without the aid of vision (i.e. by blindfolded participants), homing task performance is quite reliable for distances of up to 100 m (Durgin et al. 2009; Schwartz 1999) and is unaffected by many changes in the conditions of inbound and outbound travel (Schwartz 1999; Turvey et al. 2009).

The ability to accurately complete a homing task depends upon whether or not the outbound and inbound gaits are of the same gait type (Harrison 2020; Turvey et al. 2009). Two gait types have been identified (Harrison 2020). Walking, jogging, running, and backwards-walking have been shown to belong to one gait type classification group (Isenhower et al. 2012; Turvey et al. 2009). Skipping, two-legged hopping, gallop–walking, and hesitation-walking have been shown to belong to another gait type classification group (Harrison 2020; Harrison et al. 2021; Turvey et al. 2009, 2012). When outbound and inbound gaits are of the same gait type (e.g., walking and backwards-walking), homing task performances are no different from when outbound and inbound gaits are identical. In contrast, if outbound and inbound gaits are different gait types (e.g., walking and gallop–walking), then homing task performances are systematically biased. Each gait type has been associated with a different higher order perceptual variable. The systematic bias of homing task performance that results from a change in gait type has been interpreted to be a consequence of mismatches in the haptic perceptual variables implicated in the outbound and inbound phases of the task (Harrison et al. 2021). Theories concerning the form of these higher order variables include gait symmetry theory (Turvey et al. 2009) and spatial reference frames theory (Harrison 2020).

The effect of gait type can be examined by looking at the ratio of inbound-to-outbound distances (i.e., $D_{\text{inbound}}/D_{\text{outbound}}$) as a function of the particular pairing of outbound and inbound gaits. In Turvey et al. (2012), the gait pairing of gallop–walk–walk (i.e., where gallop–walk

is the outbound gait and walk is the inbound gait) led to an underestimation bias. $D_{\text{inbound}}/D_{\text{outbound}}$ was 0.842 for the gait pairing of gallop–walk–walk and 0.971 for walk–walk. Note that a gallop–walk gait pattern involves starting with feet together, stepping out with a lead foot, and then bringing the trailing foot forwards, so that the feet are together again. The homing task underestimation bias associated with a gallop–walk–walk gait pairing was replicated by Harrison et al (2021), although they obtained numerically different values. They determined $D_{\text{inbound}}/D_{\text{outbound}}$ to be 0.939 (SD 0.20) for gallop–walk–walk, and 1.073 (SD 0.17) for walk–walk. In Harrison (2020), the gait pairing of two-legged-hopping–walk led to an underestimation bias. $D_{\text{inbound}}/D_{\text{outbound}}$ was 0.787 for the gait pairing of two-legged-hopping–walk (i.e., where two-legged hopping is the outbound gait and walk is the inbound gait), and 0.900 for walk–walk. To compare the effect of gait type across experiments, it is useful to scale determined values to a control value. In the aforementioned experiments, we can use the walk–walk condition as the control condition. From the results from Turvey et al. (2012), if we scale $D_{\text{inbound}}/D_{\text{outbound}}$ for the gallop–walk–walk condition by the $D_{\text{inbound}}/D_{\text{outbound}}$ value for the walk–walk condition, we obtain $0.842/0.971 = 0.867$. Throughout this paper, we refer to a value that is calculated in this way as a scaled effect. For Harrison et al. (2021), we obtain a scaled effect of $0.939/1.073 = 0.876$, and for Harrison (2020), we obtain $0.787/0.900 = 0.874$. Here, we see that the scaled effect of gait type yields consistent values across experiments. Scaled effect values of 1.000 indicate that there was no effect of manipulating outbound phase gait. Values less than 1.000 indicate that inbound reports for the gallop–walk–walk condition were underestimated compared to the walk–walk condition. The calculation of scaled effect values involves two rescaling operations. First, report distances are expressed as a function of outbound distances (i.e., $D_{\text{inbound}}/D_{\text{outbound}}$). This operation normalizes the data for differences in given set outbound distances. Second, $D_{\text{inbound}}/D_{\text{outbound}}$ values for the condition in which gait type was manipulated (e.g., gallop–walk–walk) are scaled relative to $D_{\text{inbound}}/D_{\text{outbound}}$ values obtained for the condition in which gait type was not manipulated. The second operation is designed to further normalize the data and to adjust for potential differences between experiments such as the effects of the specifics of the environment in which different experiments are conducted (Harrison et al. 2020; Witt et al. 2007).

Self-motion perception has also been investigated by studying distance matching tasks (Abdolvahab et al. 2015; Glasauer et al. 2007; Harris et al. 2000; White et al. 2013). Unlike a homing task, where a participant is tasked with returning to where they started, in a distance matching task, a participant travels a set distance, pauses momentarily, and then attempts to walk a matching distance. In contrast to the outbound and inbound phases of the homing task, the

distance matching task is comprised of measure phase and a report phase. During the measure phase, the participant has the goal of perceptually measuring how far they have travelled. In the report phase, the participant has the goal of reproducing the measure phase distance by walking a matching distance.

White and colleagues (White 2012; White et al. 2013; see also Witt and Riley 2014) proposed a theory of self-motion perception based on the detection of a higher order variable termed multimodally specified energy expenditure (MSEE). MSEE captures the metabolic cost of locomotion per unit of perceptually specified traversed distance. They propose that MSEE is specified multimodally, and that it provides a basis for perceiving self-motion during locomotion. To test their theory, White (2012) first determined the MSEE for walking and gallop–walking. They obtained measures of 0.345 and 0.266 L of oxygen per meter travelled for gallop–walking and walking, respectively. Based on these values, they hypothesized that performances of a distance matching task where gallop–walk was the report gait and walk was the measure gait would satisfy the relation $D_{\text{measure}}/D_{\text{report}} = 0.345/0.266 = 1.297$. To test this prediction, they studied a treadmill-based distance matching task. In this task, participants experienced distance based on (1) the movements of their legs during treadmill locomotion, and (2) movement along a virtual corridor presented in a head mounted display. In the measure phase, participants travelled set distances using a walk gait pattern. In the report phase, participants verbally signaled when they perceived they had travelled a distance equal to the measure phase distance. In the report phase, participant's either (1) gallop–walked, (2) walked, or (3) walked while wearing ankle weights. In the walking with ankle weights' condition, the mass of ankle weights was adjusted, so that the MSEE was equal to that of the gallop walk condition. Consistent with predictions based on MSEE, they observed a $D_{\text{measure}}/D_{\text{report}}$ value of 1.238 (SD 0.28) in the gallop–walk condition and 1.198 (SD 0.22) in the walk with ankle weights' condition. Both of these values differed from the value of 1.009 (SD 0.16) obtained for the walk (with no ankle weights) condition. These results are consistent with the idea that MSEE provides a basis for perceiving self-motion. Given that a difference was found between the walking and walking with ankle weights' conditions, these results contradict predictions based on gait type.

Current study

The present study was motivated by the idea that gait type and MSEE implicate two distinct perceptual functions associated with self-motion perception. We consider the potential theoretical basis for this distinction in the discussion section. The effect of gait type is associated with detection of distance-specifying variables detected by the

haptic perceptual system. The effect of MSEE is associated with detection of the perceptual consequences of the metabolic cost of locomotion per unit of traversed distance. We hypothesized that the behavioral expression of these distinct forms of self-motion perception depends upon the specifics of the methods used. Specifically, we hypothesized that the effect of gait type is revealed in homing task performances, and the effect of MSEE is revealed in distance matching task performances. To test this hypothesis, we conducted an experiment that replicated Harrison et al. (2021) in all details bar one. Rather than examining a homing task, participants performed a distance matching task. In other words, the outbound phase of the homing task performed in Harrison et al. (2021) was replaced with a measure phase, and the inbound phase was replaced by a report phase. Following the design of Harrison et al. (2021), the measure phase gait was either a gallop–walk or a walk, and the report phase gait was walk. The current study was conducted in the same environment as Harrison et al. (2021). It also used the same equipment and the same research team.

Our null hypothesis was that the results of the present experiment would not differ from those of Harrison et al. (2021). Based on the results of Harrison et al. (2021), we can predict a gait type-based scaled effect of 0.876. Our research hypothesis was based on the distance matching results of White (2012). Given that White (2012) investigated a walk–gallop–walk condition rather than gallop–walk–walk condition, we formed our predictions by calculating the inverse of the values they observed. This gives us a $D_{\text{report}}/D_{\text{measure}}$ value of $1/1.238 = 0.808$ for the gallop–walk–walk condition, and $1/1.009 = 0.992$ for the walk–walk condition. Based on these values, we get a predicted an MSEE-based scaled effect of $0.808/0.992 = 0.815$. It should be noted that we could also form our prediction based on measurements of the MSEE for walking and gallop–walking. This would yield $MSEE_{\text{report}}/MSEE_{\text{measure}}$ values of $0.266/0.345 = 0.771$ for the gallop–walk–walk condition, and $0.266/0.266 = 1.000$ for the walk–walk condition. From this, we get a predicted scaled effect value of $0.771/1.000 = 0.771$. Based on these values, we hypothesized that observed scaled effect values would be less than 0.876.

Following the methods of Harrison et al. (2021), we also manipulated whether vision was available during the measure phase. Specifically, during the measure phase, participants either wore (1) a partial blindfold that permitted optic flow information about self-motion, or (2) a full blindfold. Harrison et al. (2021) observed that the availability of optic flow led to change in the scaled effect from a value of $0.939/1.073 = 0.876$ to a value of $1.008/1.060 = 0.951$. The effect of vision shifted the scaled effect value closer 1.000 (i.e., towards no effect). In contrast, White (2012) observed a scaled effect of $0.808/0.992 = 0.815$, in spite of the fact

that optic flow was available throughout the task. Based on these findings, we hypothesized that the availability of vision would not affect scaled effect values.

Methods

Participants

Twelve (9 male and 3 female) participants aged between 19 and 28 years ($M=21.45$; $SD\ 3.34$) were recruited. All participants signed an informed consent form. The consent process and study procedures were approved by the University of Nebraska Medical Center Institutional Review Board. This research complied with the Declaration of Helsinki. One participant was removed from the analysis after reporting that they had repeatedly used a step-counting strategy.

Materials and design

The experiment was conducted on the artificial surface of a synthetic turf football pitch. Trials were completed within the confines of a 55 m \times 30 m test area located between the top of the penalty arc and the center circle of the football pitch (Fig. 1A). There were no white lines (i.e., pitch marking) within this area. Researchers cleared the test area of litter and leaves before each data collection session.

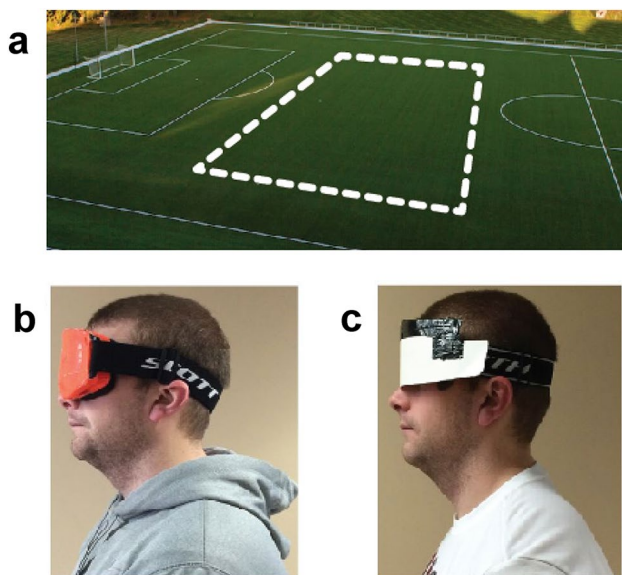


Fig. 1 **A** The studied distance matching task was performed on a soccer pitch, within the area that has been highlighted with the white dashed line drawn on the image. The availability of vision was manipulated by participants either wearing **B** a full blindfold that permitted no visual information, or **C** a partial blindfold that permitted optic flow-based information about self-motion

Participants performed a distance matching task. The task was comprised of a measure phase and a report phase. The starting location and initial facing direction for the task were varied on each trial. In the measure phase, participants moved forwards until instructed to stop by an experimenter. An experimenter rolled a distance measuring wheel (i.e., a surveyor's wheel) behind the participant and monitored the incrementing distance values that were displayed. The instruction to “stop” walking was issued as the measured distance value approached the target distance for that trial. Participants were stopped at set distances of either 6.5 m, 13.0 m, or 19.5 m. The gait pattern used during the measure phase was manipulated to be either a walk or a gallop–walk. Measure phase gait was controlled via instructions given to participants at the start of each trial. The availability of optic flow was also manipulated. Measure phase optic flow was controlled by having participants wear a full blindfold or a partial blindfold (see Fig. 1B, C, respectively). The full blindfold produced a condition in which no optic flow was available. The partial blindfold produced a condition which prevented sight of distal features of the surrounding environment, and allowed detection of the lamellar component of optic flow known to be especially important for optic flow-based self-motion perception (Banton et al. 2005). See Harrison et al. (2021) for images of both the test environment and the two types of blindfolds used in this research.

In the report phase, participants were tasked with reproducing the distance they experienced in the measure phase. They did this by walking forwards again. Participants continued to wear either the full or partial blindfold worn during the measure phase. During the report phase, they closed their eyes. The decision for participants to close their eyes behind both the full and partial blindfolds was motivated by the known effects eye-closing per se, on both visual and haptic perception (Brodoehl et al. 2015; Marx et al. 2003) and perceptuomotor and attentional processes (Xu et al. 2014). Report distances were determined using a distance measuring wheel rolled behind the participant.

The three set distances, two gait patterns, and two optic flow conditions in our study design were all within-subjects manipulations of the measure phase. Each condition was repeated 3 times, for a total of 36 trials. Two practice trials were completed prior to starting the main experiment. In practice trials, participants wore a full blindfold. The first practice trial used a gallop–walk as the measure phase gait. The second practice trial used a walk gait. For half of the participants, measure phase set distances were 4 m and 22 m for the first and second trials, respectively. For the remaining participants, this was reversed.

Procedure

Participant's read and signed a consent form detailing the tasks they would perform. They then received training on how to perform the walking and gallop–walking gait patterns. This training began with a visual demonstration of each gait pattern performed by an experimenter. For the gallop–walk gait pattern, participants were instructed (1) to use their right foot as the leading-out foot, (2) to try to minimize over-stepping or under-stepping when bringing the left foot up next to the right foot, and (3) to only pause briefly when the feet came together so as to maintain a constant rhythm to the motion. Each gait pattern was first practiced with eyes open, and then with eyes closed. This practice was performed along the half-way line of the football pitch. This line allowed for corrective feedback to be given on each participant's ability to walk in a straight-line during eyes-closed practices. Next, both the full and partial blindfolds were fitted. To fit the partial blindfold, the participant was asked to face forward with their head positioned as if they were looking out to the horizon. The visor on the front of the partial blindfold was adjusted up or down, so that a tennis ball placed on the ground 2 m in front of them was just visible. Instruction was provided on how to perform the distance matching task. Two experimenters acted out the roles of experimenter and participant to familiarize the participants with the procedure of each trial. They were instructed to perform the distance matching task without overthinking it. Participants were instructed not to use mental strategies, such as counting and matching the number steps produced in the measure and report phases (e.g., Cohen et al. 1963; Lederman et al. 1987). They were advised to simply pay attention to how far they travelled during the measure phase, and to reproduce that distance in the report phase, stopping as soon as it felt like they had walked an equivalent distance. Similar instructions have been used in related studies (Harrison 2020; Turvey et al. 2009, 2012), and have been shown to be effective in stopping participants from changing the perceptual distance matching task into a cognitive step-counting or mental timing task. Participants were told that they would always use a walking gait to complete the report phase.

Trial was started from a pseudo-randomly selected location within the test area. The first trial was started in the approximate center of the test area. Once standing at the selected starting location, the participant was given and then put on the blindfold for that trial. The participant was then reminded of the task, and told which gait pattern they should use in the measure phase. Following a “go” instruction, they started to walk or gallop–walk an approximately straight-line path until instructed to “stop” by the experimenter. Participants were then instructed to close their eyes, and to reproduce the distance they just travelled. Following

this instruction, participant walked forwards, and stopped themselves when they perceived that they had walked a distance that matched the distance they experienced in the measure phase. As soon as they had stopped, participants were reminded to keep their eyes closed. If, at this point, they wore a blindfold that was different from the blindfold required for the next trial it was switched. With eyes remaining closed, the participant was led to the next starting location within the test area. The starting location for the next trial was selected using the following criteria. The new starting location should (1) be at least 4 m from the ending location of the previous trial, and (2) allow for a comfortable margin of report phase overshoot, thereby minimizing the risk of the participant exiting the test area with their walked reports.

All participants were debriefed to establish whether an explicit step-counting strategy had been used. They were each asked the open question, “If you were to describe to a friend how you managed to walk a matching distance, what would you tell them?” With one exception, all recruited participants responded in a way that suggested that they stopped when they just felt they had walked the correct distance. When directly asked whether they had counted steps or seconds, all participants, bar one, responded that they had not.

Results

We analyzed the report distances scaled to measure distances (i.e., $D_{\text{report}}/D_{\text{measure}}$). In the optic flow condition, $D_{\text{report}}/D_{\text{measure}}$ was 0.758 when the measure gait was a gallop–walk, and 0.945 when the measure gait was a walk. From these results, we get a scaled effect of $0.758/0.945 = 0.806$ (i.e., $D_{\text{report}}/D_{\text{measure}}$ values for the gallop–walking condition were 80.6% of the values observed for the walking condition). This is similar to the scaled effect value of 0.815 predicted from a change in MSEE (White 2012). In the no optic flow condition, $D_{\text{report}}/D_{\text{measure}}$ was 0.714 when the measure gait was a gallop–walk, and 0.902 when the measure gait was a walk. From these results, we get a scaled effect of $0.714/0.902 = 0.795$. Again, this is similar to the scaled effect value of 0.815 predicted from a change in MSEE.

Planned one-sample t tests (one-tailed) were used to test the hypotheses that presently obtained scaled effect values would be less than the scaled effect value of 0.876 predicted by a change of gait type (Harrison et al. 2021; Turvey et al. 2012). This hypothesis was supported for both the values obtained in the optic flow condition ($M = 0.806$, $SD = 0.102$), $t(10) = -2.26$, $p < 0.05$, and the no optic flow condition ($M = 0.795$, $SD = 0.138$), $t(10) = -1.94$, $p < 0.05$.

One sample t tests (two-tailed) were used to examine whether the presently obtained scaled effect values differed from the scaled effect values predicted by MSEE (i.e., the

change in MSEE associated with changing gait from a walk to a gallop–walk). For the value of 0.771, predicted from a scaled effect of $MSEE_{\text{report}}/MSEE_{\text{measure}}$ values, no difference was observed for either the optic flow condition ($M=0.806$, SD 0.102), $t(10)=1.15$, $p=0.28$, or no optic flow condition ($M=0.795$, SD 0.138), $t(10)=0.59$, $p=0.57$. For the value of 0.815, predicted from a scaled effect of $D_{\text{report}}/D_{\text{measure}}$ values, no difference was observed for either the optic flow condition ($M=0.806$, SD 0.102), $t(10)=-0.28$, $p=0.79$, or no optic flow condition ($M=0.795$, SD 0.138), $t(10)=-0.47$, $p=0.65$. These results further suggest that the presently studied distance matching reports are consistent with predictions based on MSEE.

A planned 3 (set distance) $\times 2$ (measure gait) $\times 2$ (vision) ANOVA was performed on $D_{\text{report}}/D_{\text{measure}}$ values. Consistent with previous studies investigating the effects of both gait type and MSEE, $D_{\text{report}}/D_{\text{measure}}$ was smaller when gallop–walking was the outbound gait, $F(1, 10)=31.69$, $p<0.001$, and the magnitude of this underestimation bias increased with set distance, $F(2, 20)=5.90$, $p<0.05$. $D_{\text{report}}/D_{\text{measure}}$ decreased with set outbound distance, $F(2, 20)=26.96$, $p<0.001$, with a direct comparison of the means revealing differences between the 6.5 m and 13.0 m conditions, and between the 6.5 m and 13.0 m conditions.

A main effect of vision was observed, $F(1, 10)=9.33$, $p<0.05$, with $D_{\text{report}}/D_{\text{measure}}$ values being higher in the optic flow condition ($M=0.852$, SD 0.175) compared to the no optic flow condition ($M=0.808$, SD 0.187). Unlike the results of Harrison et al. (2021), the effect of vision was not found to interact with measure phase gait, $F(1, 10)=0.00$, $p=0.95$. The effect of vision was not found to interact with set distance, $F(2, 20)=0.08$, $p=0.93$. No three-way interaction of vision, measure gait, and set distance was observed, $F(2, 20)=0.34$, $p=0.71$.

Linear regressions on the mean D_{report} values in the no optic flow condition yielded slopes of 0.498 (intercept=2.284, $r=0.634$) for the gallop–walk–walk condition and 0.701 (intercept=2.136, $r=0.828$) for the walk–walk condition. For the optic flow condition, the slopes were 0.505 (intercept=2.207, $r=0.717$) for the gallop–walk–walk condition and 0.772 (intercept=1.837, $r=0.896$) for the walk–walk condition.

Discussion

The present study was motivated by the idea that self-motion perception during over-ground locomotion is supported by two distinct types of perceptual variables. The first type of variable is a higher order variables detected by the haptic perceptual system. This variable carries information about distance traversed during locomotion and depends upon gait type. The second type of variable is a higher order variable

termed multimodally specified energy expenditure (MSEE). This variable depends upon the perceptual consequences of the metabolic cost of locomotion per unit of traversed distance. We hypothesized that the implication of these distinct perceptual variables is related to the particular methods that have been used in empirical studies of self-motion perception. Specifically, we hypothesized that the effect of gait type is revealed in performances of homing tasks, and the effect of MSEE is revealed in performances of distance matching tasks. As hypothesized, in the presently investigated distance matching task, the observed scaled effect values were different from the value of 0.876 predicted for an effect of gait type, and were similar to the value of 0.815 predicted for an effect of MSEE. Taken together with the results of Harrison et al. (2021), our results suggest that there are two distinct perceptual functions associated with perceiving self-motion during over-ground locomotion, and the behavioral expression of these functions relies upon the task that is studied (i.e., homing vs. distance matching).

Our claim that the effects of gait type and MSEE are associated with distinct perceptual functions finds additional support when we examine the effect of vision. In the homing task studied by Harrison et al. (2021), the availability of visual information about self-motion (i.e., optic flow) was associated with a shift in scaled effect values closer to 1.000 (i.e., towards no effect). This was taken to suggest that (1) the effect gait type specifically affects the haptic perceptual measurement of distance traversed, (2) visual information about distance traversed is not affected by the effect of gait type, and (3) the integration of visual and haptic information about distance traversed reduces the homing task bias resulting from the effect of gait type (Harrison et al. 2021). In the distance matching task studied here, the availability of visual information about self-motion did not change the scaled effect values. We interpret this to suggest that although MSEE is influenced by visual information about self-motion (White et al. 2013), visual information about self-motion is not necessary for the perceptual measurement of this variable (c.f. White 2012, Experiment 4).

Two perceptual functions for perceiving self-motion

The effect of gait type in homing task performances has been associated with an ability for invariantly perceive distances travelled during legged locomotion (Harrison 2020; Harrison and Turvey 2019). Specifically, as long as the gait patterns used during legged locomotion are of the same gait type, then distance travelled can be equivalently perceptually measured by the haptic perceptual system. We suggest that homing tasks lend themselves to the behavioral expression of the effect of gait type, because homing tasks emphasize the ability to return to a particular location in the environment. In other words, the effect of gait type implicates a

perceptual measurement that is distance-specific, since the only perceptual measurement that can satisfy the demands of a homing task is one where physical distance is invariantly measured across outbound and inbound phases.

The effect of MSEE in distance matching tasks reveals an ability to detect the perceptual consequences of the metabolic cost of locomotion per unit of traversed distance (White et al. 2013). The effect of MSEE implicates a multimodal perceptual measurement that is action-specific and relates to the traversability of an environment in terms of the effort that must be expended (Harrison and Turvey 2009; Witt and Riley 2014). We suggest that distance matching tasks lend themselves to the behavioral expression of MSEE, because (1) the task constraint of needing to return to a particular location in the environment is absent, and (2) a distance matching task is a type of magnitude estimation task. Studies in which participants are required to estimate the magnitude of environmental dimensions have shown that participant's responses can reflect the perceivers' capacity to act with respect to those dimensions, rather than the environmental dimension per se (Witt and Riley 2014). For example, magnitude estimations of the physical heaviness of manually wielded objects have been shown to reflect action relevant properties related to tool use, such as the movability of a tool (Shockley et al. 2004; Carello and Turvey 2016). Similarly, magnitude estimations of target size in the context of performing an archery task have been shown to reflect how hittable a target is, given the skill of the archer (Lee et al. 2012). These findings have been interpreted to be the result of an intrinsic bias towards perceiving variables that reflect the proper function of biological perceptual systems (Shockley et al. 2004; Turvey et al. 1999). A proper function is a function that has warranted reproduction in the history of one or more species following its successfully execution (Millikan 1984, 1993).

A reasonable guess as to the *proper functions* associated with haptic self-motion perception during over-ground locomotion include (1) attunement to information about how the body is moving in space relative to the environment during legged locomotion, as suggested by theories of gait type (Harrison 2020; Turvey et al. 2009), and (2) attunement to information about the neuro-biomechanical resources that should be martialled to actualize a specific act of legged locomotion (Patla 1997; Warren 1984), as suggested by MSEE. This way of characterizing the proper functions associated with gait type and MSEE is motivated by a conceptual distinction that has previously been drawn between the target and manner parameters of goal directed actions (Shaw and Kinsella-Shaw 1988; Shaw et al. 1992). Target parameters denote the form of the kinematic relationship that exists between an agent and environment given some goal. Manner parameters denote the character of the kinetic resources that are needed to transform (or maintain)

the kinematic relationship. In this theory, a specific action is realized when kinetic resources are allocated with respect to the kinematic constraints that are defined by the target parameters. To appreciate the theoretical utility of the target versus manner parameter distinction, we can consider how these two concepts might be defined for perceptually guided navigation. The target parameters of perceptually guided navigation include (1) the spatially or spatiotemporally invariant structure associated a particular form of navigation (Dang et al. 2021; Harrison 2020; Heft 1996; Lee 2017; Warren 2019), and (2) the styles of spatiotemporal transformation that constitute the conceivable space–time paths of travel. Manner parameters for perceptually guided navigation include the particular kinetic mode associated with how the body is transported through the environment (Holt et al. 2010; Roberts and Azizi 2011) and related principles of action organizational style and efficiency (Diedrich, and Warren 1995; Saunders et al. 1953; Kuo 2007; Turvey et al. 1996). In the specific case of gait type, the relevant spatially or spatiotemporally invariant structure has been theorized to be either (1) the symmetries of gait revealed in models of the dynamics of muscle activation patterns (Turvey et al. 2009), or (2) the distinction between propriospecific and proextero-specific spatial reference frames embedding the perceptual measurement of legged locomotion.

Implications from reinterpreting prior research: Abdolvahab et al. (2015)

Abdolvahab et al. (2015) used a treadmill distance matching task over set distances of 9.0 m, 18.0 m, and 27.0 m to study the effect of gait type. In light of our current conclusions, it seems that what was actually studied in this experiment was an effect of MSEE. Consistent with this reinterpretation, Abdolvahab et al. (2015) observed $D_{\text{report}}/D_{\text{measure}}$ values of 0.866 for the gait pairing of gallop–walk–walk and 1.033 for walk–walk. This gives us a scaled effect value of $0.866/1.033 = 0.838$. This value is numerically closer to the scaled effect value predicted for MSEE than it is to the scaled effect value predicted for gait type. If we assume that MSEE was in fact implicated in the results of Abdolvahab et al., then we can draw some new insights. Unlike the studies by White and colleagues (White 2012; White et al. 2013), Abdolvahab et al. (2015) did not use a head mounted display to create visual information about self-motion. Instead, participants simply walked on a treadmill with their eyes open. The potential implication here is that visual information about self-motion is not needed to perceive MSEE, and instead, the haptic perceptual system may support the perceptual specification of traversed distance.

Implications from reinterpreting prior research: Chrastil and Warren (2014)

The specific hypotheses for the present study were formed using numerical predictions drawn from four previous studies of gait type (Harrison 2020; Harrison et al. 2021; Turvey et al. 2009, 2012). The results of these experiments were markedly consistent with one another when expressed as scaled effect values. The observed numerical consistency is likely due to similarities in study designs. All four studies considered direct homing tasks that were performed on flat terrain, within open, and uncluttered environments, and with similar instructions given to participants. The designs of each of these studies contained a three similar measure phase distances, with distances of 6.5 m, 13.0 m, and 19.5 m studied by Harrison et al. (2021), and distances of 8.0 m, 16.0 m, and 24.0 m studied by Harrison (2020), Turvey et al. (2009), and Turvey et al. (2012). The homogeneity of these motivating studies raises questions about the ability to apply the specific numerical predictions made here to other studies with different designs. A useful test case for these concerns is the results of Chrastil and Warren (2014). Chrastil and Warren (2014) reported effects of manipulating gait to be either a walk or a gallop–walk in an experiment that differed markedly in design from those that we used to generate our predictions. They studied a task in which blindfolded participants travelled five set distances of 2.0 m, 4.0 m, 5.0 m, 6.0 m, and 8.0 m, before turning 90° and attempting to match the outbound distance with a walked report. The directions of measure and report phase travel were tightly controlled by having participants use a white cane to follow verges on the ground.

The data from Chrastil and Warren (2014, Experiment 2b) yield average $D_{\text{report}}/D_{\text{measure}}$ values of 0.955 for the gallop–walk–walk condition, and 0.989 for the walk–walk condition (E. Chrastil, personal communication, October 11th 2021). This yields a scaled effect value of 0.966 that is inconsistent with our predictions for both MSEE and gait type. If, alternatively, we calculate a scaled effect value based on regression slope values, rather than condition means, we obtain a value of $0.777/0.892=0.877$. This is consistent with the predicted effect of gait type. Given the much shorter distances investigated Chrastil and Warren, this suggests that scaled effects calculated on condition mean values may be especially sensitive the set of distances investigated. This potentially suggests that reporting scaled effects based on regression slope values may support more robust predictions. To test this, we reexamined the data from Harrison et al. (2021). We performed linear regressions on the mean D_{report} values and found slopes in the no optic flow condition of 0.662 (intercept = 3.005, $r=0.764$) for the gallop–walk–walk condition and 0.814 (intercept = 2.741, $r=0.869$) for the walk–walk condition.

For the optic flow condition, the slopes were 0.660 (intercept = 3.744, $r=0.776$) for the gallop–walk–walk condition and 0.753 (intercept = 3.377, $r=0.858$) for the walk–walk condition. These values yield a slope-based scaled effect value of 0.813 for the no optic flow condition, which does not appear to align well with the results of Chrastil and Warren. Motivated by this inconsistency, we explored a different strategy; rather than using slope-based values, we entered the set distance value of 14.5 m (i.e., the average of set distance values used in Harrison et al. 2021; Turvey et al. 2009) into the regression equations reported by Chrastil and Warren (2014, Experiment 2b). Using this strategy, we obtain a scaled effect of $D_{\text{report}}/D_{\text{measure}}$ values of $0.828/0.920=0.899$ which appears to align with the values of 0.874, 0.876, and 0.867 reported by Harrison (2020), Harrison et al. (2021), Turvey et al. (2009), and Turvey et al. (2012), respectively.

This above analysis supports the conclusion that the results of Chrastil and Warren (2014, Experiment 2b) are due to gait type. Given that the task studied by Chrastil and Warren was not a homing task (i.e., participants turned 90° at the end of the measure phase), this conclusion is at odds with our initial theorizing about the specific contextual constraints that lead to the implication of MSEE versus gait type. The results of Turvey et al. (2009) may provide some relevant insight. They observed no difference in $D_{\text{report}}/D_{\text{measure}}$ values between conditions where participants turned 180° versus 145° at the end of the measure (i.e., outbound) phase. One interpretation of this finding is that a within-subjects study design that includes both 180° and 145° turns can lead participants to treat the trials with 145° turns as if they were a homing task. Said differently, the trials with 180° turns create implicit task constraints that emphasize a specific location in the environment. This interpretation can also be applied to the complex within-subjects design of Chrastil and Warren. The design of Chrastil and Warren had aspects that emphasized specific locations in the environment. This included (1) participants encountering specific environmental structure (i.e., strips of foam attached to the floor) that acted to demarcate the measure phase distances, (2) trials being performed in close proximity to walls in an indoor space, and (3) participants' prior experience of trials in which they viewed targets positioned on the ground with the aim of perceiving the distance to those targets. An alternative interpretation is that turning per se is the relevant contextual constraint that leads MSEE or gait type to be implicated in these perceptual reports. In other words, it is that the act of performing a turn that matters, even if the turn is not 180°. Consistent with this interpretation, the act of turning has been attributed some special significance in theories of navigation. For example, the experience of sharp turns during navigation is believed to reset place and grid cell activity (Derdikman et al. 2009; Navratilova and

McNaughton 2014) and constrain how space is perceptually segmented (Brunec et al. 2018).

Summary

In conclusion, we believe that our reanalysis of the previous literature, together with the new data presented here, constitutes a reasonably compelling case for the existence of two distinct perceptual functions associated with the capacity to perceive how the body is moving relative to the environment during legged locomotion. It is clear from our results that any investigation of these perceptual functions requires careful attention to the specific contextual and task constraints that influence their expression in experimentally measured responses. The further development of a theory of context to explain the nature of these contextual and task constraints is clearly warranted.

Funding This research was supported by the University of Nebraska at Omaha (Fund for Undergraduate Scholarly Experiences). Dr. Stergiou is supported by grants from the National Institutes of Health (NIGMS/P20GM109090, NIA/R15AG063106, and NINDS/R01NS114282).

Data availability statement The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest None of the authors demonstrate any conflict of interest regarding this submission.

References

- Abdolvahab M, Carello C, Pinto C, Turvey MT, Frank TD (2015) Symmetry and order parameter dynamics of the human odometer. *Biol Cybern* 109(1):63–73
- Banton T, Stefanucci J, Durgin F, Fass A, Proffitt D (2005) The perception of walking speed in a virtual environment. *Presence Teleoper Virtual Environ* 14(4):394–406
- Brodoehl S, Klingner CM, Witte OW (2015) Eye closure enhances dark night perceptions. *Sci Rep* 5:10515
- Brunec IK, Moscovitch M, Barense MD (2018) Boundaries shape cognitive representations of spaces and events. *Trends Cogn Sci* 22(7):637–650
- Campos JL, Bühlhoff HH (2012) Multimodal Integration during self motion in virtual reality. In: Murray MM, Wallace MT (eds) *The neural bases of multisensory processes*. CRC, Boca Raton, pp 603–627
- Campos JL, Butler JS, Bühlhoff HH (2014) Contributions of visual and proprioceptive information to travelled distance estimation during changing sensory congruencies. *Exp Brain Res* 232(10):3277–3289
- Carello C, Turvey M (2016) Dynamic (effortful) touch. *Scholarpedia of touch*. Atlantis Press, Paris, pp 227–240
- Carriot J, Brooks JX, Cullen KE (2013) Multimodal integration of self-motion cues in the vestibular system: active versus passive translations. *J Neurosci* 33(50):19555–19566
- Chen X, McNamara TP, Kelly JW, Wolbers T (2017) Cue combination in human spatial navigation. *Cogn Psychol* 95:105–144
- Chrastil ER, Warren WH (2014) Does the human odometer use an extrinsic or intrinsic metric? *Atten Percept Psychophys* 76(1):230–246
- Cohen J, Cooper P, Ono A (1963) The hare and the tortoise: a study of the tea-effect in walking and running. *Acta Physiol (oxf)* 21:387–393
- Dang S, Wu Y, Yan R, Tang H (2021) Why grid cells function as a metric for space. *Neural Netw* 142:128–137
- Derdikman D, Whitlock JR, Tsao A, Fyhn M, Hafting T, Moser MB, Moser EI (2009) Fragmentation of grid cell maps in a multicompartment environment. *Nat Neurosci* 12:1325–1332
- Diedrich FJ, Warren WH Jr (1995) Why change gaits? Dynamics of the walk-run transition. *J Exp Psychol Hum Percept Perform* 21(1):183–202
- Durgin FH, Akagi M, Gallistel CR, Haiken W (2009) The precision of locomotor odometry in humans. *Exp Brain Res* 193(3):429–436
- Ellmore TM, McNaughton BL (2004) Human path integration by optic flow. *Spat Cogn Comput* 4(3):255–272
- Etienne AS, Jeffery KJ (2004) Path integration in mammals. *Hippocampus* 14(2):180–192
- Friszen I, Campos JL, Souman JL, Ernst MO (2011) Integration of vestibular and proprioceptive signals for spatial updating. *Exp Brain Res* 212(2):163–176
- Glasauer S, Schneider E, Grasso R, Ivanenko YP (2007) Space-time relativity in self-motion reproduction. *J Neurophysiol* 97(1):451–461
- Harris LR, Jenkin M, Zikovitz DC (2000) Visual and non-visual cues in the perception of linear self motion. *Exp Brain Res* 135(1):12–21
- Harrison SJ (2020) Human odometry with a two-legged hopping gait: a test of the gait symmetry theory. *Ecol Psychol* 32:58–78
- Harrison SJ, Turvey MT (2009) Load affects human odometry for travelled distance but not straight-line distance. *Neurosci Lett* 462(2):140–143
- Harrison SJ, Turvey MT (2019) Odometry. In: Vonk J, Shackelford T (eds) *Encyclopedia of animal cognition and behavior*. Springer, Cham
- Harrison SJ, Bonnette S, Malone M (2020) For humans navigating without vision, navigation depends upon the layout of mechanically contacted ground surfaces. *Exp Brain Res* 238:917–930
- Harrison SJ, Reynolds N, Bishoff B, Stergiou N (2021) Assessing the relative contribution of vision to odometry via manipulations of gait in an over-ground homing task. *Exp Brain Res* 239(4):1305–1316
- Heft H (1996) The ecological approach to navigation: a Gibsonian perspective. In: Portugali J (ed) *The construction of cognitive maps*. Springer, Dordrecht, pp 105–132
- Holt KG, Wagenaar RO, Saltzman E (2010) A dynamic systems: constraints approach to rehabilitation. *Braz J Phys Ther* 14:446–463
- Isenhour RW, Kant V, Frank TD, Pinto CM, Carello C, Turvey MT (2012) Equivalence of human odometry by walk and run is indifferent to self-selected speed. *J Mot Behav* 44(1):47–52
- Israel I, Grasso R, Georges-Francois P, Tsuzuku T, Berthoz A (1997) Spatial memory and path integration studied by self-driven passive linear displacement. I. Basic Properties. *J Neurophysiol* 77(6):3180–3192
- Kearns MJ (2003) The roles of vision and body senses in a homing task: the visual environment matters (Unpublished doctoral dissertation). Brown University, Providence
- Kuo AD (2007) The six determinants of gait and the inverted pendulum analogy: a dynamic walking perspective. *Hum Mov Sci* 26(4):617–656

- Lederman SJ, Klatzky RL, Collins A, Wardell J (1987) Exploring environments by hand or foot: time-based heuristics for encoding distance in movement space. *J Exp Psychol Learn Mem Cogn* 13:606–614
- Lee SA (2017) The boundary-based view of spatial cognition: a synthesis. *Curr Opin Behav Sci* 16:58–65
- Lee Y, Lee S, Carello C, Turvey MT (2012) An archer's perceived form scales the "hitableness" of archery targets. *J Exp Psychol Hum Percept Perform* 38:1125–1131
- Marx E, Stephan T, Nolte A, Deutschländer A, Seelos KC, Dieterich M, Brandt T (2003) Eye closure in darkness animates sensory systems. *Neuroimage* 19(3):924–934
- Millikan R (1984) Language, thought and other biological categories. MIT, Cambridge
- Millikan R (1993) White queen psychology and other essays for Alice. MIT, Cambridge
- Navratilova Z, McNaughton BL (2014) Models of path integration in the hippocampal complex. In: Derdikman D, Knierim JJ (eds) Space, time and memory in the hippocampal formation. Springer, Heidelberg, pp 191–224
- Patla AE (1997) Understanding the roles of vision in the control of human locomotion. *Gait Posture* 5(1):54–69
- Roberts TJ, Azizi E (2011) Flexible mechanisms: the diverse roles of biological springs in vertebrate movement. *J Exp Biol* 214(3):353–361
- Saunders JB, Inman VT, Eberhart HD (1953) The major determinants in normal and pathological gait. *J Bone Joint Surg* 35(3):543–558
- Schwartz M (1999) Haptic perception of the distance walked when blindfolded. *J Exp Psychol Hum Percept Perform* 25(3):852
- Shaw R, Kinsella-Shaw J (1988) Ecological mechanics: a physical geometry for intentional constraints. *Hum Mov Sci* 7(2–4):155–200
- Shaw RE, Kadar E, Sim M, Repperger DW (1992) The intentional spring: a strategy for modeling systems that learn to perform intentional acts. *J Mot Behav* 24(1):3–28
- Shockley K, Carello C, Turvey MT (2004) Metamers in the haptic perception of heaviness and moveableness. *Percept Psychophys* 66(5):731–742
- Srinivasan MV, Zhang S, Altwein M, Tautz J (2000) Honeybee navigation: nature and calibration of the "odometer". *Science* 287(5454):851–853
- Turvey MT, Holt KG, Obusek J, Salo A, Kugler PN (1996) Adiabatic transformability hypothesis of human locomotion. *Biol Cybern* 74(2):107–115
- Turvey MT, Shockley K, Carello C (1999) Affordance, proper function, and the physical basis of perceived heaviness. *Cognition* 73(2):B17–B26
- Turvey MT, Romaniak-Gross C, Isenhower RW, Arzamarski R, Harrison SJ, Carello C (2009) Human odometry is gait-symmetry specific. *Proc R Soc b Biol Sci* 276:4309–4314
- Turvey MT, Harrison SJ, Frank TD, Carello C (2012) Human odometry verifies the symmetry perspective on bipedal gaits. *J Exp Psychol Hum Percept Perform* 38:1014–1025
- Warren WH (1984) Perceiving affordances: visual guidance of stair climbing. *J Exp Psychol Hum Percept Perform* 10(5):683–703
- Warren WH (2019) Non-euclidean navigation. *J Exp Biol* 222:1–10
- White EJ (2012) The role of multimodally specified effort in action relevant distance perception (Unpublished doctoral dissertation). University of Cincinnati, Cincinnati
- White E, Shockley K, Riley MA (2013) Multimodally specified energy expenditure and action-based distance judgments. *Psychon Bull Rev* 20(6):1371–1377
- Williams MA, Galbraith C, Kane SK, Hurst A (2014) Just let the cane hit it" how the blind and sighted see navigation differently. In: Proceedings of the 16th international ACM SIGACCESS conference on computers and accessibility, pp 217–224
- Witt JK, Riley MA (2014) Discovering your inner Gibson: reconciling action-specific and ecological approaches to perception–action. *Psychon Bull Rev* 21(6):1353–1370
- Witt JK, Stefanucci JK, Riener CR, Proffitt DR (2007) Seeing beyond the target: environmental context affects distance perception. *Perception* 36(12):1752–1768
- Xu P, Huang R, Wang J, Van Dam NT, Xie T, Dong Z et al (2014) Different topological organization of human brain functional networks with eyes open versus eyes closed. *Neuroimage* 90:246–255
- Zhao M, Warren WH (2015) Environmental stability modulates the role of path integration in human navigation. *Cognition* 142:96–109

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.