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Walking: How visual exploration informs step choice

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We rely on gaze to guide subsequent steps during walking, more so when the terrain ahead is more uncertain. New research shows that the increased visual exploration during walking as the terrain becomes more uncertain reflects our preference for accuracy over effort in step choice.

Winters in Colorado come with the frequent advice to "watch your step!" to avoid the scourge of ice on sidewalks or slushy puddles. In such environments, first we must use our gaze to collect relevant information regarding where to step, and then we must perform the action of stepping on the selected location. How do we decide where to look — how does the iciness of the sidewalk affect our gaze? Do we look only at the upcoming icy foothold or do we shift our gaze to the side, exploring for a potentially safer, yet wider step to the right? Further, how does our decision regarding where to look ultimately impact our choice of where to step? Recent research reported in this issue of *Current Biology* by Domínguez-Zamora and Marigold[1] reveals how gaze strategy is changed by the precision and energetic cost requirements of walking, and how this strategy ultimately influences our subsequent step choices.

Research has shown that humans minimize energetic cost with their choice of step width[2], stride frequency[3] and speed[4] when walking through a flat, obstacle-free environment. In such environments, what role does gaze play in guiding movements? Interestingly, we don't rely on continuous visual information for our upcoming foot placement. Rather, gaze is only required right before the foot leaves the ground, and is no longer necessary as the foot swings towards the next step location[5]. Furthermore, while walking on flat terrain, only roughly about half of gaze time is spent looking at where we should step. But when the terrain becomes more uncertain, the role of gaze in walking becomes more important. When more step precision is required, the time spent gazing at the footholds ahead exceeds 90%[6]. Furthermore, in rough terrains, where the next foothold is not necessarily obvious, there is an increased spread in gaze allocation in the side-to-side (medio-lateral) direction for each step. One question that remains unexplored is how do the available step choices determine gaze allocation from side-to-side? In their new study, Domínguez-Zamora and Marigold[1] investigated how motor costs and visual uncertainty affect gaze decisions, and how this ultimately dictates where people step. Their contribution builds on previous work by controlling for available step choices in the medio-lateral direction and assigning them competing motor costs and visual uncertainty. The authors test the effects of these costs on the choice of where to look, and how that in

turn determines where people choose to step.

Why is this research important? That we rely on vision to direct ourselves while walking has been repeatedly observed in many vision[7] and locomotion studies. In fact, previous studies have shown how gaze is affected by terrain uncertainty, step width requirements[8] and gaze allocation time relative to the stance phase of the previous step. But how gaze is related to ultimate step choice is unknown, especially in the context of different objectives or outcomes. Further, studies focused on what dictates ultimate gaze choice have considered eye movements as standalone tasks providing primary or proxy rewards in response to saccades and gaze[9,10]. In their work, however, Domínguez-Zamora and Marigold[1] used a two alternative forced choice paradigm (Figure 1) for walking step choice to study gaze allocation in a decision-making task where choice is realized through another movement, namely walking.

Briefly, the four-step walking task that Domínguez-Zamora and Marigold[1] developed required subjects to walk while placing their steps on *targeted* footholds displayed in white on a black surface using a projector (Figure 1). Each step was called a row; one of the rows was deemed the decision row in which there was a choice between two target steps for that foothold position (Figure 1A). One had a large step width, while the other had a smaller step-width requirement, closer to the experimentally determined preferred width for human walking. Further, there were six different uncertainty conditions in which the closer step-width target had increasing amounts of added gaussian noise to its visual appearance (Figure 1B), while the farther target was always noiseless (Figure 1C). Subjects performed two tasks — one was the precision-relevant task, in which subjects were required to be as close to target centers as possible, and the other was precision-irrelevant, in which step precision was not required. Where they gazed and ultimately stepped was measured throughout the task.

The results of this study[1] replicate a fundamental finding — an increase in precision requirements for a given step increases the amount of gaze time allocated to the step targets, resembling
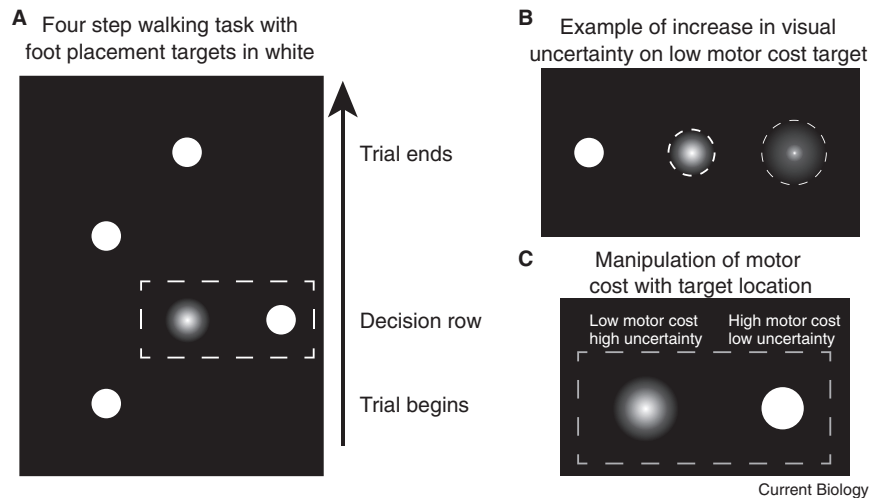

Figure 1. The two-alternative forced choice walking task of Domínguez-Zamora and Marigold[1].
(A) Task protocol from subject's perspective; subjects are faced with four steps to complete the task. Each step is indicated by a white target projected onto the mat in front of them. One of the steps entails a choice between two step options on the decision row with the closer (low motor cost target) having more visual uncertainty associated with it. (B) Increasing uncertainty on the closer target; there are six conditions overall with three shown here. (C) Focusing on decision row in (A): motor cost is manipulated by step width requirement. Figure adapted from Domínguez-Zamora and Marigold[1] (Figure 1).

the results shown in previous work outlined above. Therefore, on the question of how to allocate gaze, subjects decided to spend more time looking at the steps ahead in precision walking when they had to be sure of where they placed their step. Further, when high precision is required — when they are asked to aim for the center of the target — their gaze behavior starts to correlate with their ultimate step decision.

At first, in both tasks, subjects looked towards the closer target in the decision row indicating their inclination towards reducing motor cost in walking. But as the visual uncertainty associated with the closer target increased, their gaze began to switch more towards the high motor cost target leading to them sampling from both choices in the medio-lateral direction. More importantly, the higher probability that subjects looked at both targets (not just the closer target), the higher their probability of stepping towards the farther target. In other words, as they explored more in the medio-lateral direction, the subjects were more likely to value certainty of outcome over motor cost. In short, if subjects used their gaze to reduce *decision* uncertainty (not to be confused with visual uncertainty) by sampling both choices in the decision row, then they were more likely to step on

the more certain but high motor cost target.

Domínguez-Zamora and Marigold[1] explain this phenomenon as follows. Gaze seeks to gain information — of intrinsic value to, and a primary goal of, vision — regarding target choice and corresponding costs. The redirection of gaze towards exploration of choices in the medio-lateral direction seeks to reduce decision uncertainty regarding the outcome of the choice. The more subjects visually sample the farther, more motorically costly target, the more likely they are to ultimately choose that step target. Therefore, a reduction in decision uncertainty by visual exploration of the high motor cost target leads to subjects choosing that target.

But can these results be explained by a simpler framework, one in which gaze behavior merely foreshadows ultimate step choice, both determined by a common objective function? Domínguez-Zamora and Marigold[1] acknowledge that their current protocol cannot on its own sufficiently distinguish between this simplified framework and one in which gaze seeks to reduce decision uncertainty, thereby determining ultimate step choice. Based on past literature, however, they stress that information gain has intrinsic value for eye gaze, which in

humans and other animals supersedes primary rewards like money or food[11–13]. This intrinsic value arises from the fact that this information gain from gaze informs the subsequent decision about where to step. Therefore, taking their new results together with existing literature, Domínguez-Zamora and Marigold[1] conclude that gaze causally affects ultimate step choice, and that a willingness to visually sample high motor cost targets indicates a bias towards outcome accuracy (stepping to the center of target) over motor cost. Additional experimentation and modeling work could effectively disentangle this confound, furthering our understanding about how gaze informs step choice.

In summary, Domínguez-Zamora and Marigold[1] have addressed a phenomenon that is ubiquitous in our daily activities: locomotion when precise foot placement matters. Whether it be walking on an icy sidewalk, hiking on a rocky trail, or avoiding the Legos strewn across the floor by a child, in all cases we could either continue on our minimum

energy path or switch to a new one. This study suggests that if your eyes choose to seek out a new path, it's highly likely your feet will follow. It will be exciting to explore how these findings generalize to other behaviors as well as other forms of costs.

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Colour opponency: Chromatic and achromatic circuits in the mix

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The molecular genetic dissection of *Drosophila* colour vision circuitry reveals converging pathways previously categorized as being chromatic versus achromatic. Amacrine-like Dm8 cells receive direct and indirect inputs with different spectral sensitivity tuning, thereby forming the second stage of colour-opponent processing.

Most animals share the ability to distinguish objects based on their spectral content and irrespective of their relative intensity[1]. This ability always relies on comparing the outputs from different photoreceptor classes, each expressing a distinct opsin gene that largely defines the spectral sensitivity, as for instance in human short- (S), mid- (M), and long- (L) wavelength cones. In most

cases, these signals are then processed by so-called color-opponent circuit elements, whose hallmark properties involve combining hyperpolarizing and depolarizing responses to visual stimuli of different wavelengths[2]. This integration occurs in both time and space: for instance, 'yellow–blue' opponency in the primate retina results from comparing S cone signals to combined L+M cone

signals, leading to the formation of ON- or OFF-pathways whose receptive fields can manifest characteristic center-surround organization[1]. While the physiology of spectral processing in the retina has been very well characterized in different vertebrate species, much less is known about the molecular and cellular mechanisms underlying colour-opponent responses in the insect visual system. In