Effect of travel effort on movement vigor during foraging

Shruthi Sukumar
Department of Computer Science
University of Colorado
Boulder, CO-80309
`shruthi.sukumar@colorado.edu`

Reza Shadmehr
Department of Biomedical Engineering
Johns Hopkins School of Medicine
Baltimore, MD-21205
`shadmehr@jhu.edu`

Alaa A. Ahmed
Department of Mechanical Engineering &
Department of Integrative Physiology
University of Colorado
Boulder, CO-80309
`alaa@colorado.edu`

Abstract

Research in patch foraging decisions is generally concerned with how long an animal or human should stay in a patch, or after how much reward intake. However the question of how to select travel vigor to further optimize foraging performance isn't generally considered. Here, we investigate how travel vigor is affected by the utility rate of a foraging environment when the effort associated with that travel is modulated. The computational framework we use here is based on our previous work that extends a normative ecological model of foraging. The extended framework relates selected travel duration to global utility rate of an environment, in which environment utility is modulated by changing difficulty of harvest in an environment. The contribution of this study is to investigate the effect of changing travel effort on vigor of movement in the environment, based on the hypothesis that this travel vigor is selected to optimize the global utility rate. We find that travel vigor (peak velocity) is modulated differently across movements with identical effort requirements, in accordance with this extended MVT framework, depending on the global rate of utility in an environment.

Keywords: vigor, decision making, foraging, marginal value theorem

Acknowledgements This research was supported by NIH grant 1R01NS096083

Human decision making has often been studied in the context of simultaneously presented choices and the investigation of the subjective value associated with those choices. Here we consider a class of sequential decision-making tasks in which people are faced with the choice of whether to engage with an available option or search for a better one. Optimal foraging theory proposes normative models of how animals make these decisions while searching for prey [1, 2]. More recently, there has also been much work investigating how humans balance the exploration-vs-exploitation tradeoffs associated with foraging decisions [3, 4, 5]. While these models seek to determine the utility of a given patch in an environment based on the amount of reward and the difficulty of harvesting that reward, few have considered the question of how quickly to travel within such environments in order to optimize reward intake [6].

In a previous study [7], we extended a classical normative framework, the Marginal Value Theorem (MVT) [8], to predict how optimal travel durations varied when environment utility was manipulated by changing harvest difficulty, in a visual foraging task. While this work provides an important extension to a classical normative model, the utility rate of an environment is modulated primarily through effort required to harvest the reward. In the current study, we further investigate the modulation of optimal travel durations, in human arm reaching movements, as the effort associated with travel in an environment changes. Unlike in the case with eye movements, travel effort required in reaching can be modulated explicitly [9], to make it more analogous to patch foraging environments that have been modeled in foraging theory.

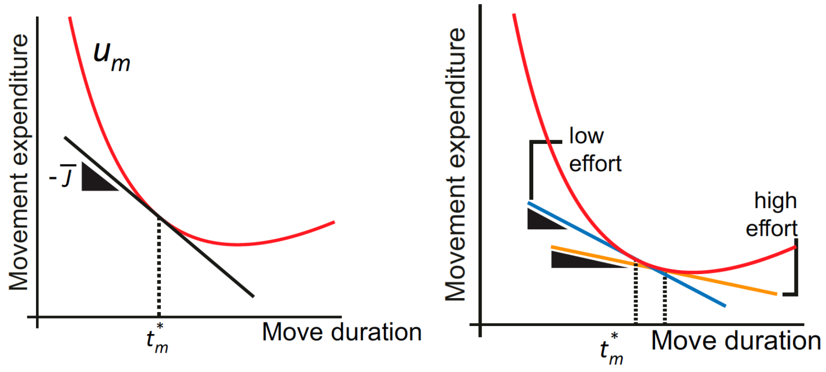
An overview of the extended MVT framework is presented, along with its main predictions regarding travel vigor, in Section 1. The details of our experimental protocol are presented in Section 2 following which we will highlight our empirical findings and results in Section 3. As stated earlier, our results show that individuals modulate their vigor in movements with identical effort requirements, in response to the global utility rate of the environment.

1 Marginal Value Theorem And Movement Vigor

For a patch foraging task, the marginal value theorem in essence prescribes a patch-leaving rule which states that it is optimal to leave any patch when the local rate of utility of that patch drops below the environment's overall global rate of utility. In the extended framework [7], the overall global rate is optimized not just with respect to patch residence time, but also movement vigor between patches. Stated another way, the new model not only solves for an optimal distribution of harvest durations in all the patches, but also an optimal distribution of travel durations between patches. Equation (1) specifies the global utility rate that is being optimized as a sum of the utilities of every patch minus the movement effort of the patch divided by the sum of all the time spent harvesting in and travelling from the patch. Here, $f^{(n)}\left(t_h^{(n)}\right)$ denotes the harvest utility of a patch n and $u_m\left(d^{(n)}, t_m^{(n)}\right)$ denotes the effort of moving out of patch n. $t_h^{(n)}$ and $t_m^{(n)}$ denote the harvest and travel durations associated with patch n respectively.

$$\bar{J} = \frac{\sum_{n=1}^{N} f^{(n)}\left(t_h^{(n)}\right) - u_m\left(d^{(n)}, t_m^{(n)}\right)}{\sum_{n-1}^{N} t_h^{(n)} + t_m^{(n)}} \tag{1}$$

As seen in [7, 8], an analytical expression for optimal durations associated with a single patch cannot be obtained by optimizing the function in Equation (1) since all the durations associated with the remaining patches need to be known ahead of time to compute $\bar{J}$ and vice versa. However, the solutions do prescribe how these durations are modulated by changes in environment utilities and we will therefore compare those predicted changes to what we empirically observe. Since, we are primiarily concerned with movement vigor in this study, we pictorially depict the predictions of extended MVT framework (Figure (1)) for optimal movement durations and changes in these optimal durations for changes in the level of effort in the environment (mathematical derivations and other predictions can be found in [7]). As can



(a) (b)

Figure 1: (a): Optimal movement t_m^*duration occurs when the movement effort equals (negative) average rate of the environment $\bar{J}$. (b): Optimal movement duration increases with an increase in overall effort in the environment. Note: These comparisons are only valid while considering identical patches in low vs high effort environments since the movement expediture curve remains constant across both. (Figure adapted from [7])

be see in Figure (1a), the optimal duration for travel between patches is not the duration for which movement effort is minimized, but rather one for which the movement effort reaches a value equal to the negative of the global utility rate of the environment. Furthermore, when comparing identical travel costs across different environments, the optimal travel duration increases for the patch belonging to the high effort environment which has low global utility rate, as opposed to one that belongs to the low effort environment with the high global utility rate (seen in Figure (1b)).

2 Experiment

To test if these predictions hold for a foraging task with arm reaching movements, we designed a protocol that emulated the classic patch foraging task design.We created a computer game in which subjects had to perform arm reaches while holding the handle of a robotic manipulandum (InMotion 2; Interactive Motion Technologies) as seen in Figure (2). By moving the robot handle subjects could controls the movement of a cursor on the monitor in front of them. The monitor displayed a game screen in which they were cued to move to different targets, causing them to make reaches in different directions in the horizontal plane. The end of the robot handle was attached with a grasp sensor that measured the grip force of the subject. Additionally, the robot had motors that can produce forces; here we leveraged this by having the robot produce acceleration-dependent resistive forces to simulate the effect of adding mass to the arm to movement in the horizontal plane. The use of increased mass to manipulate effort is motivated by our previous findings in [9] that describe effort costs in arm reaching as a function of movement duration and added mass.

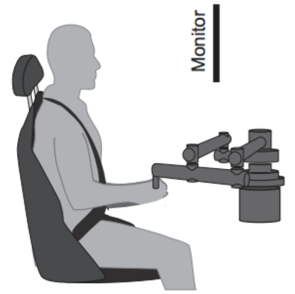
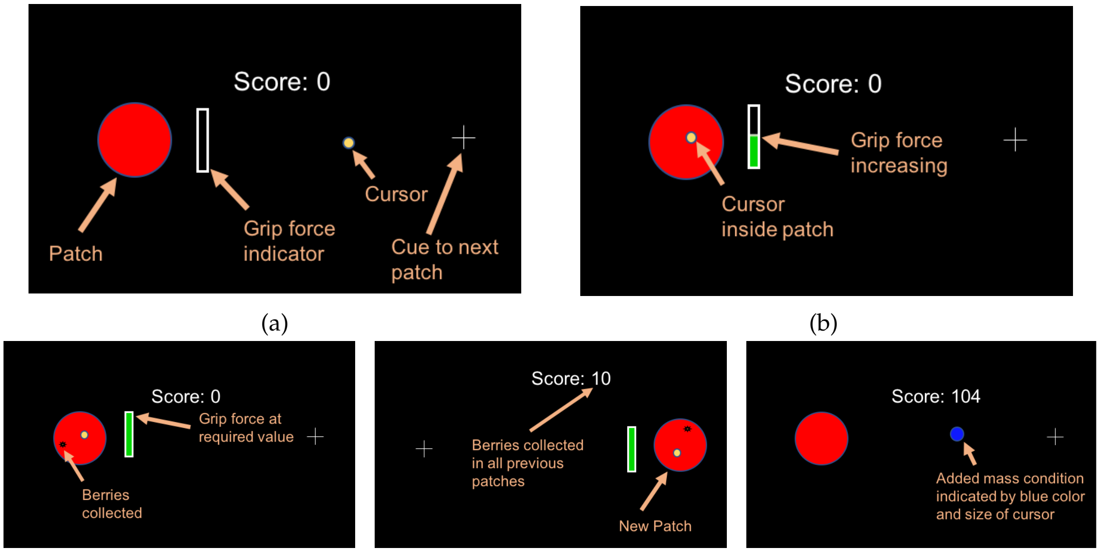


Figure 2: Participants were seated in front of a computer monitor while grasping the end of a robotic manipulandum; the grasping end of the robot handle was affixed wth a grasp sensor that measured their gripping force

Design: Subjects ($n = 10$) were brought into the lab for testing their behaviour in this foraging protocol. A brief familiarization session was conducted to acquaint them to the passive inertial forces of the robot arm as well as the acceleration-dependent forces after which subjects were given instructions regarding the main foraging experiment. In the foraging experiment, subjects played a game in which they need to collect berries from sequentially appearing berry patches. On the monitor appeared the game graphic, as seen in Figure 3 wherein the subject needed to move into a cued patch, indicated by the red circle on the screen. Once inside the patch, the subject started harvesting berries by increasing grip force on the robot handle; the amount of grip force required and their current grip force were both indicated to them by an indicator bar next to the patch seen in Figure 3b. Berries were harvested at a declining rate as the grip force reached the requisite level indicated, by means of a small orange circle quickly appearing and disappearing, accompanied with a beeping sound; we call this a berry pop. Each berry pop corresponded to one berry being harvested and occured in a random locations inside the patch. The total number of berries collected over a duration t_h is given by the function $r(t_h) = \alpha\Big(1 - \frac{1}{1+\beta t_h}\Big)$. Here, α represents the maximum reward and β represents rate of decline in reward harvested. As stated above, in order to continue harvesting berries, a constant grip force of 30 N had to be applied at the handle. When the grip force fell below this required value, the berry harvesting stopped until force was increased again. When collecting berries in a patch, subjects also saw a cue indicating the position of the next expected patch. They were told that they were free to leave a patch at any point in time towards the cued position where a new patch would appear. Once a patch was exited, it disappeared and a new replenished patch appeared in the new location (indicated by a white plus sign in Figure 3a). Patches always appeared at the same two positions thereby keeping the travel distance constant across the entire experiment. Subjects were also instructed not to increase the grip force during travel between patches, in order to decouple harvest and movement efforts. If they chose to travel with increased grip force ($> 10N$), the game paused and a message appeared on screen asking them to reduce their grip force. Additionally, subjects were informed that the entire experiment would take about one hour and fifteen minutes outside of instruction and consent procedures. Subjects were also informed that every 10 berries collected would correspond to 1¢ in monetary bonus, to increase task engagement.

Protocol: The experiment session was conducted in two main blocks of 200 trials each, representing two foraging environments, one with high movement effort between patches and the other with lower movement effort. As stated earlier, movement effort was modulated by changing the added mass simulated by forces. The low effort environment had no added mass, i.e., subjects only experienced passive inertial forces of the robot arm. The high effort environment added a mass of 3.5kg. Of the 200 trials in each environment, 40 trials were designated as probe trials (grouped together in sub-blocks of 10) during which subjects had to move between patches with an intermediate added mass value of 2kg. Probe trials ensured comparison across movements with the same effort requirement to elicit vigor modulation due to just the global utility rate of an environment. Throughout the experiment, the values of maximum reward α and reward



(a) (b)

(c) (d) (e)

Figure 3: This figure depicts the game screen as seen by participants during different phases of the experiment(a): They are cued a patch into which they need to move the cursor so they can collect reward (b)Once they move the cursor into the patch they can start increasing grip force to begin harvesting berries; their current force is indicated by the height of the green bar and the max required force is indicated by the height of the outer white bar in the grip force indicator (c) Once the required force is applied, berries are harvested by an audio visual stimulus in the patch corresponding to each berry pop (d) Subjects could move out any any point to the next cued location of the patch where they continued to collect reward. the number of berries they collect in that patch is added to a score on the screen (e) Depending on the environment, subjects experienced more mass while moving between patches; this was visually indicated by a blue solid circle on the cursor whose size indicated how heavy the arm was going to be.

depletion rate β were also kept constant at 40 and 0.5 respectively. Half the subjects ($n = 5$) performed foraging in the high effort environment first.

3 Results And Discussion

The empirical results revealed that there was a significant main effect of global utility rate of the environment on the vigor of movements (Figures (4) & (5); left panels). This showed that subjects responded to an increase in added mass by reducing their speeds, in accordance with our previous findings regarding effort costs in arm reaches [9]. More importantly, we looked at the effect of environment effort levels on probe trials separately from the non-probe trials. Recall that probe trials have an added mass of 3kg in travel effort regardless of whether they're embedded in a low or high effort environment. If environment had no effect, then we would expect vigor in these probe trials to be the same between environments. Interestingly, we found that movement vigor in probe trials belonging to the low effort environment was higher than in the high effort environment (Figure (4), right panel; t-test reveals $p < 0.01$). This result of the effect of environment on probe trials revealed a similar trend in travel duration, though not significant (Figure (5), right panel; t-test $p = 0.06$). Overall, these results support the predictions of the extended MVT framework which states that individuals must reduce their movement vigor in response to foraging in an environment with lower global utility rate.

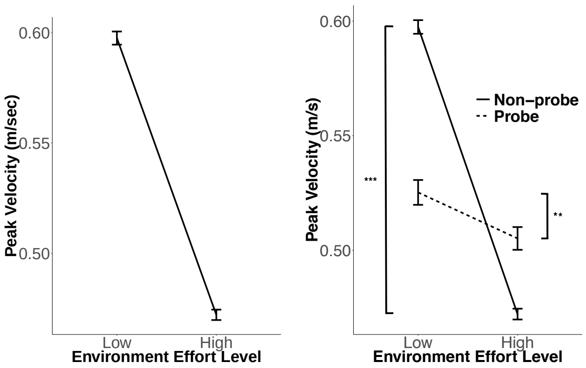


Figure 4: Left Panel : Peak velocity in arm reach is plotted as a function of environment effort level for averaged across all subjects.Right Panel : Peak velocity displayed as a function of environment effort level, separated by whether they were probe trials or not. All errorbars represent standard error about the mean

Interestingly, we also found a significant 2-way interaction between the environment as well as order in which subjects experienced the two environments during their visit for both peak velocity as well as travel durations, as seen in Figure

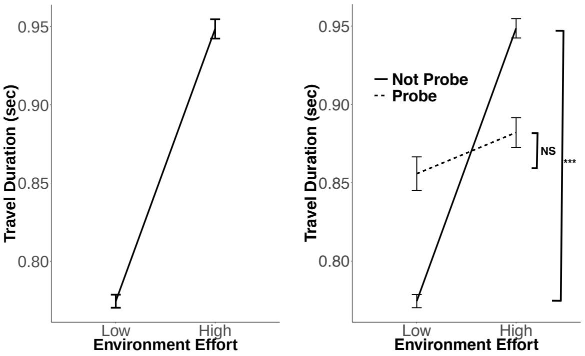


Figure 5: Left Panel: Travel duration in arm reach is plotted as a function of environment effort level for averaged across all subjects. Right Panel : Peak velocity displayed as a function of environment effort level, separated by whether they were probe trials or not. All errorbars represent standard error about the mean

6 respectively. For both orders, the subjects' vigor decreased significantly ($p < 0.001$) in the high effort environment compared to the low effort environment. However, this decrease is more prominent in the case when subjects experience the high effort environment first as compared to when they experience the low effort environment first. This suggests that subjective estimates of the global utility rate of an environment are not entirely decoupled from the previous foraging experience.

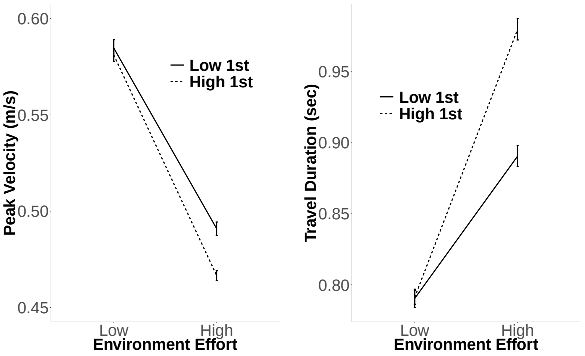


Figure 6: Left Panel :Effect of order and environment on peak velocity, Right Panel: Effect of order and environment on travel duration. Dotted lines indicate that the high effort environment was experienced first whereas solid indicate low effort environment was experienced first

4 Conclusion

In this study, we investigated the role of movement effort of foraging decisions and the extension of Marginal Value Theorem, presented in our previous work [7]. We found that movements with identical effort requirements had lower vigor in environments with higher global utility rate than those in environments with lower global utility rate.

References

[1] David W Stephens and John R Krebs. *Foraging theory*. Princeton University Press, 1986.

[2] Innes C Cuthill, Alejandro Kacelnik, John R Krebs, Patsy Haccou, and Yoh Iwasa. Starlings exploiting patches: the effect of recent experience on foraging decisions. *Animal Behaviour*, 40(4):625–640, 1990.

[3] Sara M Constantino and Nathaniel D Daw. Learning the opportunity cost of time in a patch-foraging task. *Cognitive, Affective, & Behavioral Neuroscience*, 15(4):837–853, 2015.

[4] Jonathan D Cohen, Samuel M McClure, and Angela J Yu. Should i stay or should i go? how the human brain manages the trade-off between exploitation and exploration. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1481):933–942, 2007.

[5] Jonathan S Diamond, Daniel M Wolpert, and J Randall Flanagan. Rapid target foraging with reach or gaze: The hand looks further ahead than the eye. *PLoS computational biology*, 13(7):e1005504, 2017.

[6] Yael Niv, Nathaniel D Daw, Daphna Joel, and Peter Dayan. Tonic dopamine: opportunity costs and the control of response vigor. *Psychopharmacology*, 191(3):507–520, 2007.

[7] Tehrim Yoon, Robert B Geary, Alaa A Ahmed, and Reza Shadmehr. Control of movement vigor and decision making during foraging. *Proceedings of the National Academy of Sciences*, 115(44):E10476–E10485, 2018.

[8] Eric L Charnov et al. Optimal foraging, the marginal value theorem. 1976.

[9] Reza Shadmehr, Helen J Huang, and Alaa A Ahmed. A representation of effort in decision-making and motor control. *Current biology*, 26(14):1929–1934, 2016.