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Behavior: Knowing When to Walk Away, Knowing When to Run

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A new model has been proposed indicating that humans and other animals weigh the metabolic cost of pursuit in deciding how fast to move toward a given reward, providing a powerful framework for understanding behavior.

Of the many differences between rural Kersey, Pennsylvania (pop. 937) where I grew up and New York City (pop. 8.49 million) were I live and work today, perhaps the most jarring is the pace of life. Whenever I visit my hometown, I'm struck by how unhurried everyone seems to be; when I return to New York the frenetic energy on the streets is palpable. Four decades ago, in a landmark paper [1], Marc and Helen Bornstein examined this phenomenon and found a remarkably strong relationship between a city's size and the speed of its inhabitants (Figure 1). People in big cities move faster. But while this finding comes as no surprise to seasoned urbanites, the underlying neurological mechanisms driving this predictable, seemingly universal aspect of human behavior have proven difficult to pin down.

Humans and other animals have a broad set of evolved neurological mechanisms shaping behaviors to maximize our success in acquiring resources, ultimately aiding our reproductive fitness. Without conscious effort, we integrate a range of sensory and cognitive clues to determine value, explore our environments using efficient search strategies [2], and, at least in lab settings, modify our walking speeds to minimize the cost per kilometer [3]. In deciding how fast to move in pursuing a given reward, the brain must presumably weigh its potential value against the added effort and cost of moving more quickly. How does the brain calculate the optimal effort to invest in reward-seeking behaviors?

In a recent issue of *Current Biology*, Ahmed and colleagues [4] propose that the brain uses metabolic energy cost to determine the speed with which an organism moves toward a reward. For many tasks, such as walking, the metabolic energy (i.e., calories) expended per distance traveled is a function of speed; moving faster requires more energy per meter. A reward's value can be a function of speed as well. Under a temporal discounting model, a reward's value decreases the longer it takes to obtain it; food might decay or be lost to competitors, the comfortable seats on the rush-hour train might be taken. Given the cost:speed function for a given task and the value:time function for a given reward, one can solve for the speed that maximizes net return for a given action.

Ahmed and colleagues tested their model in a series of reaching tasks with human subjects and found strong support for it. Subjects were seated at a desk and instructed to reach with their arms and touch different targets on a screen. Before these tasks, they used a set of respirometry trials to determine the speed:cost function of reaching for each subject. They then had subjects perform different reaching tasks while varying the reward structure across conditions. Consistent with their model, subjects consistently chose to reach faster, and exert more energy, when the reward was greater or discounted more steeply. Importantly, Ahmed and colleagues are able to show that their metabolic model, with its specific discounting functions, predicts reaching speeds more accurately than other models.

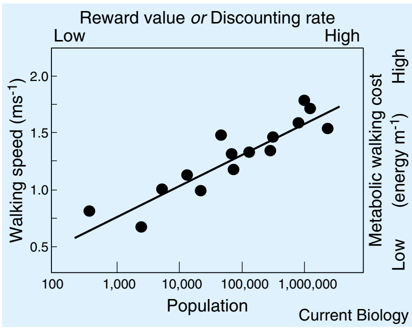

Figure 1. Walking speed and population size for a range of cities and towns across Europe, the United States, and Israel.
People in larger cities habitually walk faster, which increases the energy cost per meter traveled. Following the model proposed by Ahmed and colleagues [4], the decision to walk faster and incur a greater energy cost reflects a greater perceived value or a steeper perceived temporal discounting function for the reward being sought. (Figure adapted from [1].)

Impressively, despite its simplicity the model makes reliable predictions across a variety of different tasks and even across species. Analyzing the behavior of finches reported in an experimental study of foraging behavior [5], Ahmed and colleagues showed that their model correctly predicts whether the birds chose to walk (which is slow but metabolically inexpensive) or fly (fast but costly) to acquire food. When the time to acquire the food increased, its value as estimated by the discounting model decreased, and as predicted the birds chose to walk. In a separate analysis of isometric force production in human subjects, their model correctly predicted subjects' decreasing sensitivity to task duration as the force exerted decreased.

For all of the obvious anatomical differences, the neurological development and metabolic physiology of vertebrates are largely conserved. That the model's predictions work well across species suggests it may reflect a common, evolved neurobiological mechanism that is shared across species. Ahmed and colleagues suggest, for example, that the neural circuits involved in generating actions should be strongly coupled to the circuits involved in deciding between actions. Such shared, evolved neurological mechanisms are powerful tools for research, as they present a common framework for comparing behavioral strategies across species, tasks, and environments. For example, the model might enable researchers to compare the perceived value of a given reward (e.g., an apple) across different species or populations by measuring changes in the speed of pursuit as the time to acquire the item is varied. Similarly, the relative perceived value of different rewards (e.g., apples and oranges) might be assessed by comparing the speed of pursuit when the time to acquire the items is identical.

Another important feature of the model is that it predicts when, and to what degree, organisms should sacrifice energy efficiency to obtain a reward. More work is needed, however, to assess the model's predictions across a wider range of species and environments, especially outside of the lab. Can the model predict travel speeds for humans and other animals in complex environments where reward is probabilistic and uncertain? Do tasks with flat cost:speed relationships, where discounting of energy cost is negligible, adhere to model predictions? Current approaches to studying foraging behaviors, travel speeds, and ranging decisions in humans [2] and other species [6] provide the precision needed to begin testing these and other predictions in real world conditions.

For my fellow New Yorkers, Ahmed and colleagues' model suggests two, mutually compatible reasons that we habitually walk faster [1], and less efficiently, than our relaxed, rural comrades (Figure 1). We may perceive greater rewards are at stake, and given the remarkable sums of money exchanged each day in the city, that assessment may well be accurate for some. Alternatively, with over 8 million fellow primates foraging for the same resources, we may sense that the rewards we seek are slipping away more quickly — something to ponder next time you're running for the train.

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