Vigor

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Neuroeconomics of Movement Control

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Preface

Because of our wisdom, we will travel far for love,
As all movement is a sign of thirst,
And speaking really says
“I am hungry to know you.”
—Hafez, 14th-century Persian poet

At the airport, waiting outside the security area, you might notice a young family, mom and child, spotting the person they are waiting for: dad. There is a smile on the dad’s face as he exits the security area and finds them. They run toward each other.

At around the same time there is another man, about the same age, also coming out, but not being greeted by his family. Rather, he notices that a limo driver is holding a tablet with his name on it. Not surprisingly, he does not run toward the driver.

Why do we run toward people we love, but merely walk toward others? What brain mechanism compels us to move with more vigor towards things we value more?

To illustrate the importance of these questions, imagine that you are at a nice restaurant and the waiter rolls the dessert cart to your table. You look over the options, focusing on a couple of plates, one a chocolate cake with raspberries, the other cheesecake with sliced peaches. As you deliberate, you shift your gaze by making saccadic eye movements that go from one plate to another. After a few seconds, you make up your mind and choose the chocolate cake.

Now suppose that as you were deliberating, the restaurant had a camera that measured your eye movements. It recorded the velocity with which your eyes traveled toward each plate and noted that your saccades toward the chocolate cake had velocities that were higher than your saccades toward the peaches. From this measurement, the machine estimated the value that your brain assigned to each option, then predicted that you preferred the chocolate cake. The waiter did not need to ask you which dessert you wanted. You preferred the dessert for which your saccades had the higher velocity.

If the vigor of our movements is driven by how we value the thing we are moving toward, then our movements give away one of our big secrets: the subjective value that we assign to things and people. Notably, because velocity is a real-valued variable, one can compare velocities between two options and measure precisely how much faster we move toward one than the other.

This means that someday soon, we might be able to estimate not just which dessert you prefer by the velocity of your eyes, but how much more you prefer one dessert to the other. The restaurant would certainly be interested in using this information to set their prices.

As we like to say to our students, if you want to get a sense of how someone feels about you, you should probably pay attention to how they move toward you.

Preferences Gleaned from Vigor

If we want to know whether you prefer A or B, we proceed by presenting you with A and B and then ask you to pick the one you prefer. But suppose we wanted to measure how much more you preferred A to B. Here, the typical approach is to give you choice lotteries and ask you to make your selection from a menu of probabilities. It would go like this: you can have A with 100% probability, or choose B, for which you can get B1 or B2 with 50% probability. The result is an abstract quantity called utility. Utility is an estimate of your subjective valuation of an outcome.

Over the past decade, it has become clear that there is another way with which we might measure preference. This research has revealed that factors that affect preference, such as reward and effort, also affect movements. For example, if you prefer A to B, then you are likely to move with a shorter reaction time and greater velocity towards A. Vigor provides a real-valued scale to quantify the difference between movements toward A and B. Therefore, vigor adds a continuous dimension to the ordinal scale of choices, with the intriguing possibility that this dimension may overcome some of the limitations inherent in inferring utility from choice behavior.

The discovery that we move more vigorously toward things we prefer was serendipitous. It came about as an unexpected outcome of experiments that focused on patterns of decision-making, and used movements as a read out of choice. For instance, in studies employing eye movements as the choice-reporting method, if the subject preferred A to B, it expressed its choice by making a saccade toward A. However, it soon became clear that movements were more than just a proxy for choice. Rather, humans and other animals moved faster and with shorter reaction times toward items that they preferred. This raised the possibility that vigor could serve as a real-valued scale with which subjective value may be inferred.

The Link between Vigor and Utility

Why should the way we move be affected by how we value the item at our destination? After all, we could easily imagine a scenario in which the brain assigns values to the various stimuli, picks the one that has the greatest subjective value, and then passes on the chosen action to the motor system, which simply executes a stereotypical movement to acquire that stimulus. Indeed, many text books still separate decision-making and motor control into separate brain regions, and imagine a hierarchy in which the decision-making circuits make choices, and the motor circuits produce the action needed to acquire the chosen option.

In this book, we closely review the experimental results and arrive at a different conclusion: brain regions that were thought to be principally involved in decision-making also affect the vigor of movements, and brain regions that were thought to be principally responsible for moving a part of the body also bias patterns of decision-making.

As the promised reward increases, animals react earlier and start their movements with a shorter latency, and then move with greater velocity toward reward. In contrast, as the effort required for acquiring reward increases, subjects tend to become slower in starting their movements and take longer to complete their actions. When they arrive at their reward site, their past effort expenditure encourages them to stay longer and acquire more of the reward before moving on to the next reward opportunity.

That is, reward and effort, factors that were thought to be the domain of decision-making, have a clear effect on vigor. Furthermore, these same factors also affect what we do when we get to our destination: harvest duration depends on the effort we have spent to get there. We linger longer at the restaurant if we had to spend effort securing a reservation.

Now why should the way we move be influenced by the same factors that influence our decisions? That is, why should you not only prefer to spend time with your best friend rather than your school teacher, but also walk faster to meet your friend? To answer this question, we imagine the problem from the point of view of an ecologist: what is the currency that the brain is trying to optimize via its choices and movements?

In their natural environment, animals make choices on the basis of a desire to maximize a specific currency: the global capture rate, which is defined as the sum of all rewards acquired minus all efforts expended, divided by total time. This currency plays a fundamental role in the longevity and fecundity of animals, suggesting that living one's life in a way that increases the capture rate has evolutionary advantages.

Because movements require expenditure of effort, and utility-based decisions affect reward accumulation, if we wish to maximize the capture rate, then we must find policies that are informed by both the effort of making movements and the joy of acquiring reward.

Thus, the link between movements and decisions arises because both are elements of behavior that the brain must control to maximize a single currency: the capture rate. To optimize this currency, you cannot simply make good choices; you must also move with vigor that is consistent with those choices. When rewards are low, it is not cost effective to pay for time with expenditure effort. However, when rewards are larger, it is worthwhile to move faster because the time that is saved in acquiring that reward increases the capture rate. Effectively, by moving faster, you are buying time through expenditure of effort, thereby raising your capture rate when you get the reward.

Neural Basis of Vigor

A good example of the neural link between systems that assign value to things and systems that control our movements is illustrated in Parkinson's disease.

Patient C1 was a 62-year-old retired florist who had suffered from Parkinson's disease for about 14 years. He exhibited severe tremor and rigidity, and he was totally dependent on his wife. She started her day by dressing him, laying out his breakfast, and making his lunch. She went to work, then came back in the afternoon to make his dinner and finally got him undressed and ready for bed. One evening, she had severe abdominal pain and had to be taken to the hospital by ambulance for emergency surgery. The next day she woke at the hospital worried about her husband. However, the nurse informed her that he had come to visit her. He had dressed himself, made his own breakfast, and then walked to the hospital. At the hospital his neurologist noticed him and upon examination found that he walked considerably faster than in past examinations. In his case report (Schwab and Zieper, 1965), the neurologist wrote the following: "All his motor tests were improved in spite of the presence of the same amount of rigidity and tremor that had been present before."

It was clear that this patient could, under increased urgency, dress himself, make his own breakfast, and move fairly normally. But why wasn't this potential available to him until he was put in the extraordinary circumstance of having his wife taken to the hospital? Pietro Mazzoni, Anna Hristova, and John Krakauer (2007) were among the first neuroscientists to examine this question. They named the phenomenon motor motivation and suggested that movement slowness in Parkinson's disease was not due to a loss of ability to make normal movements, but rather an altered economic evaluation of movements that resulted in reduced vigor.

Indeed, research in the past decade has demonstrated that control of vigor is influenced by release of dopamine. Dopamine is like the two faced god Janus. On the one hand, when the brain experiences more reward than expected, there is a burst of dopamine, and the dopamine release teaches us to increase the value that we assigned this stimulus: it was better than expected. On the other hand, just before a movement starts, dopamine levels rise and stay higher if we are spending effort. For example, if an animal has to press a lever to get a pellet of food, the levels of dopamine in the basal ganglia are greater than if the same animal has to simply stay still and be given that pellet of food. Thus, on the one hand, dopamine teaches us about the value of things, and on the other hand it supports expenditure of effort. As we will see, this bridge that dopamine builds between reward and effort has much to do with the fact that we place greater value on things that we have worked for.

Arrival of dopamine affects the excitability of neurons, particularly those in the striatum, which constitutes the input stage of the basal ganglia. The striatal neurons react to dopamine by altering how they respond to cortical inputs, eventually affecting how much inhibition the output structures of the basal ganglia produce upon downstream motor structures. When an act is expected to be more rewarding, the inhibition produced by the basal ganglia output structures upon the motor system is reduced. This modulation of inhibition is one of the principal ways with which our perception of reward affects the vigor of our movements.

A second principal factor is the excitation that the motor structures receive from cortical neurons that are involved in computing utility. Utility is a complicated quantity that reflects how we subjectively evaluate reward and effort. Many cortical regions participate in evaluating utility of each option, and then compete to produce a choice, which is followed by a movement that expresses that choice. The most valuable option produces neural activity that rises quickly, and reaches threshold earlier, thereby triggering a movement. The rate at which this activity builds influences reaction time of the movement that follows.

Thus, movement vigor is a result of the combined excitation and inhibition from disparate neural structures that converge upon the motor system, compelling it to not only move toward a particular reward, but do so with a vigor that depends on the subjective value of reward. When the reward system is affected because of disease, or because of a history of low rewards, as in depression, our movements become slowed, and vigor drops.

Organization of the Book

In this book, our goal is to consider a simple question: why do we move faster toward things we value more? The first part of the book considers (chapters 1–3) this question from a behavioral and mathematical perspective, while the second part (chapters 4–7) considers it by looking at the neural mechanisms that control our choices and movements.

To formulate a rationale for why subjective value of an option should affect vigor, we consider the mathematical framework of optimal foraging theory. This theory was designed to provide an understanding of the various factors that animals consider as they choose between their options, and was motivated by the observation that animals sometimes behave unexpectedly: as they search for food, they sometimes pass on an inferior piece, even though they have already spent effort trying to find it.

An example of this is behavior of crows as they search for clams on the beaches of the Pacific Northwest of the United States. They spend effort digging up a clam, but if it is small, they abandon it and go try to find another clam. Optimal foraging accounts for this decision by suggesting that the option that the animal prefers often accords with a desire to maximize their capture rate. By passing up the small reward, thereby not spending additional time in trying to open the clam, the crows make a series of decisions that in the long run increases their global capture rate.

When we move fast, we are expending greater effort. It turns out that moving vigorously, and thereby spending more energy, makes sense in the framework of optimal foraging. If we use the energy that it takes to perform a movement as a proxy for effort expenditure, then there is a natural link between movements and decisions: moving faster is a good policy because it improves the capture rate, even though it also requires greater effort expenditure. Effectively, by moving faster toward more valuable options we are spending energy to buy time (and thus get the reward sooner). This is a worthwhile purchase because it improves our capture rate currency.

Animals that achieve increased capture rates tend to have an evolutionary advantage through greater longevity and fecundity. Therefore, this evolutionary benefit links control of movements with control of decisions.

The resulting framework provides a way to consider many fascinating observations, including the data that show that people in certain cities tend to walk faster than those that live elsewhere, and data that show that after a period of low reward rates, we not only tend to move more slowly but also linger longer at the next reward site.

In the second part of the book we consider the neural link between control of movements and subjective valuation of options. There, we focus on the simplest of voluntary movements: saccades. There are two reasons for focusing on saccades. First, we make about 100,000 saccades during each day, directing our fovea so that we acquire information from various items in our visual space. Each saccade takes around 50 ms, during which time we are effectively blind. As a result, we are blind for a total of 1.5 hours during each waking day, making it particularly important for the brain to optimize duration of each saccade.

With each movement of our eyes, we express what we value in our visual scene, and how much we value it. If the image that we are making a saccade toward is valuable, the brain generates that saccade with greater velocity, reducing saccade duration by a few milliseconds. The sensitivity of saccades makes them a particularly useful behavior with which to test the links between variables that affect choice and variables that affect vigor.

The second reason that this book delves deeply into control of saccades is because the entire neural system of saccades is within the cranium, affording neurophysiologists the ability to study the neurons that control eye movements. In comparison, arm movements and walking partly rely on neural structures within the spinal cord, making it more difficult to study vigor of these behaviors by using standard techniques.

Our analysis of the neural basis of vigor will begin with the superior colliculus. We will incorporate contributions of the frontal eye field and other cortical regions, then shift to the basal ganglia, where we will focus on dopamine and the neural basis of reward evaluation and vigor modulation. We will conclude our journey with serotonin, a neurotransmitter that in many ways functions to oppose dopamine: whereas dopamine signals the rewarding value of the stimulus and encourages vigor, serotonin signals the punishing value of the stimulus and encourages sloth.

Overall, the results suggest that the neural circuits that determine our choices are deeply influenced by the circuits that control our movements. From a scientific perspective, this implies that by studying vigor, we may discover a new way with which to measure individual preferences and thus provide economists a behavioral tool that can objectively estimate subjective utility. From a clinical perspective, vigor may act as a proxy for our current affective state. And from a technological perspective, with the increasing power of smart phones and presence of surveillance cameras, we would not be surprised if someday soon, the results of this research encourage invention of machines that measure our movements and gather vigor-based estimates of our personal preferences. These machines would gather these data even when we are not overtly making a choice, thereby unwittingly revealing one of our secrets: how much we value the thing we are looking at or moving toward.