Behavioral and Brain Sciences

cambridge.org/bbs

Précis of *Vigor: Neuroeconomics of Movement Control*

Reza Shadmehr[a] and Alaa A. Ahmed[b]

[a]Department of Biomedical Engineering, Johns Hopkins School of Medicine, Baltimore, MD, 21205, USA and [b]Department of Mechanical Engineering and Department of Integrative Physiology, University of Colorado, Boulder, CO 80027, USA.
shadmehr@jhu.edu
alaa@colorado.edu

Précis

Cite this article: Shadmehr R, Ahmed AA. (2021) Précis of *Vigor: Neuroeconomics of Movement Control*. *Behavioral and Brain Sciences* **44**, e123: 1–42. doi:10.1017/S0140525X20000667

Target Article Accepted: 13 November 2020
Target Article Manuscript Online: 2 December 2020
Commentaries Accepted: 30 March 2021

Keywords:
basal ganglia; decision-making; dopamine; motor control; neuroeconomics; serotonin

What is Open Peer Commentary? What follows on these pages is known as a Treatment, in which a significant and controversial Target Article is published along with Commentaries (p. 5) and an Authors' Response (p. 38). See bbsonline.org for more information.

Abstract

Why do we run toward people we love, but only walk toward others? Why do people in New York seem to walk faster than other cities? Why do our eyes linger longer on things we value more? There is a link between how the brain assigns value to things, and how it controls our movements. This link is an ancient one, developed through shared neural circuits that on one hand teach us how to value things, and on the other hand control the vigor with which we move. As a result, when there is damage to systems that signal reward, like dopamine and serotonin, that damage not only affects our mood and patterns of decision-making, but how we move. In this book, we first ask why, in principle, evolution should have developed a shared system of control between valuation and vigor. We then focus on the neural basis of vigor, synthesizing results from experiments that have measured activity in various brain structures and neuromodulators, during tasks in which animals decide how patiently they should wait for reward, and how vigorously they should move to acquire it. Thus, the way we move unmasks one of our well-guarded secrets: how much we value the thing we are moving toward.

> 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

The seventeenth-century British philosopher John Locke wrote: "The actions of men are the best interpreters of their thoughts." You may have seen an example of this idea at the airport. As people come out of the security area, some run toward the ones they love, whereas others merely walk.

Is the vigor with which we express our actions a reflection of our thoughts? Is our vigor associated with the value that our brain has assigned to our destination? Although this book examines how the brain assigns vigor to actions, its real aim is to ask the deeper question of why it might be beneficial from an evolutionary standpoint to link internal variables such as subjective value and affective states, that is, how we really feel about our chosen action, and our emotions, with external variables such as speed of movement and latency of reactions. Indeed, behavioral ecologists and psychologists of social communication and emotion will guess that the vigor of action could be used as an omnibus "tell" to any observer, friend or foe, predator or prey, about the motivational strength and fundamental condition of the actor's emotional state.

1. Subjective value gleaned from vigor

The concept of subjective value is central to economics, as well as cognitive neuroscience. Economists have quantified subjective value so that governments may produce greater good via public policy. Cognitive neuroscientists have estimated subjective value to understand the neural basis of decision-making. Both have relied on a simple methodology: choice. When you select one option over another, you indicate that you value the chosen option more. However, your choice indicates your order of preference, not your degree of preference (Samuelson, 1938). For example, if I noticed that from the dessert cart you picked caramel flan, not the bowl of fruit, I would infer that you preferred the flan to the fruit. However, I could not assign a numeric scale that reflected how much more you preferred the chosen item to the one left behind. Is there a way to measure your degree of preference?

In the last decade, neuroscientists have added a new tool with which to measure subjective value: vigor. They noticed that during decision-making, as people and other animals

© The Author(s), 2020. Published by Cambridge University Press

CAMBRIDGE UNIVERSITY PRESS

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

deliberated about their options, their movements reflected not just their choice, but also the subjective value of that choice (Haith, Reppert, & Shadmehr, 2012; Reppert, Lempert, Glimcher, & Shadmehr, 2015; Reppert et al., 2018; Yoon, Geary, Ahmed, & Shadmehr, 2018; Yoon, Jaleel, Ahmed, & Shadmehr, 2020). Thus, if the restaurant used a camera to monitor your eye movements as you considered your dessert options, their analysis might reveal that when you shifted your gaze among the options, your saccadic eye movements exhibited something interesting: The velocity of the eyes was somewhat greater when you shifted your gaze from the fruit to the flan, than from the flan to the fruit (Yoon et al., 2020). That is, before you verbalized your decision to the waiter, as you deliberated and gazed back and forth between the options, your saccade vigor was greater toward the item that you eventually chose. Your choice of flan over fruit indicated your preference, but the restaurant via its measurement gained an additional piece of information: The eye velocities that shifted your gaze toward the flan or the fruit described a proxy for how much more you preferred one to the other. That would certainly be a useful bit of information for setting prices on the dessert menu.

2. The mathematical link between vigor and subjective value

Why should the way we move toward a goal be affected by how we value the destination? After all, we could imagine a scenario in which the brain assigns value 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 robotically executes a movement to acquire that stimulus. Indeed, this is the traditional framework for motor control; decision-making circuits make choices, whereas the motor circuits produce the actions needed to acquire that choice.

This robotic view of motor control, divorced from the decision-making process, is illustrated in the language that is still commonly used to describe saccadic eye movements. The relationship between saccade amplitude and velocity is imagined to be invariant in healthy people, unaffected by their affective state, or the reward at stake, and is referred to as the "main sequence," a term that motor control borrowed from astronomy (Bahill, Clark, & Stark, 1975). In astronomy, the term refers to a plot of star color versus brightness, showing that during the hydrogen burning stage of a star's lifetime, it follows a specific two-dimensional trajectory. In motor control, main sequence refers to the relationship between peak saccade velocity versus amplitude, and deviations from "normal" can be interpreted as a pathological condition. However, recent study has shown that this relationship is far from invariant. Rather, peak velocity increases when gazing toward something that the subject associates with reward (Manohar, Muhammed, Fallon, & Husain, 2019, Manohar et al., 2015; Reppert et al., 2015; Seideman, Stanford, & Salinas, 2018; Takikawa, Kawagoe, & Hikosaka, 2002; Yoon et al., 2020), decreases when the subject is fatigued (Golla et al., 2008; Straube, Fuchs, Usher, & Robinson, 1997), and is even modulated by the recent history of reward and effort experienced by the subject (Yoon et al., 2018).

In a similar vein, motor control has historically overlooked the decision-making process when considering how fast we walk and how fast we reach. For example, consider speed of walking. Unlike the invariance presumed in saccades, walking speed is thought to be determined by the energetic cost of the movement. This energetic cost is high for slow speeds of walking, and also high for fast speeds, but exhibits a minimum at an intermediate speed (Ralston, 1958). The energetically optimal speed is shifted to slower speeds on inclines and when carrying loads, and, indeed, gait speeds in animals are slower under these conditions (Wickler, Hoyt, Cogger, & Hall, 2001; Wickler, Hoyt, Cogger, & Hirschbein, 2000). Similarly, energetic cost of reaching also exhibits a minimum around an optimal speed (Shadmehr, Huang, & Ahmed, 2016), and we reach slower when the effort cost of the movement is higher (Gordon, Ghilardi, & Ghez, 1994). Thus, it has commonly been assumed that the speed with which we choose to walk or to reach is selected in such a way as to minimize the energetic cost of the movement.

However, people do not always move in the energetically optimal manner. When walking down an incline, people prefer a gait that incurs a greater energetic cost than a more relaxed gait (Hunter, Hendrix, & Dean, 2010). There is also the intriguing observation that when effort costs are higher, not only do we make slower movements, but we also take longer to start those moments, even though the reaction time has no influence on the movement's energetic cost (Reppert et al., 2018). Thus, when it comes to setting movement speed, energetic optimality is not the sole concern of the brain.

As another example, consider the curious finding that average walking speed in a city correlates the strength of a city's economy and the economic well-being of its average citizen (Levine & Norenzayan, 1999). The better off a city's residents are, the faster they walk (Shadmehr & Ahmed, 2020). Not only do people walk faster, but they also perform everyday transactions faster. This suggests that the history of an individual's experience, reflected in their well-being, influences the vigor of their movements. Similar effects have been observed in eye movements. The speed

Reza Shadmehr was born in Iran and was fortunate to be allowed by his parents and by the US consulate to immigrate to the United States when he was 14 years old. He was raised in Spokane, WA, by foster parents and attended Gonzaga University. He was subsequently mentored in robotics at the University of Southern California by Michael Arbib, and then in computational neuroscience at MIT by Emilio Bizzi. After MIT, he joined the Johns Hopkins Biomedical Engineering Department in 1995, where he has remained his entire career. He studies the problem of how the brain controls movements of the arm and the eyes, using a broad set of approaches, including behavioral and neurophysiological techniques, in both humans and monkeys. He is the author of three books and an elected Fellow of the AIMBE. His greatest accomplishment, however, has been mentoring students who have gone on to become good citizens and creative scientists.

Alaa A. Ahmed received a B.Sc. in Mechanical Engineering from the American University in Cairo and a Ph.D. in Biomedical Engineering with specialization in Biomechanics from the University of Michigan at Ann Arbor. From 2006 to 2008, she was a Whitaker International Fellow and postdoctoral researcher in sensorimotor control at the University of Cambridge. In 2008, she joined the University of Colorado Boulder, where she is now an Associate Professor and Director of the Neuromechanics Lab. Her research program uses a neuroeconomic approach that combines techniques from neuroscience, economics, biomechanics, psychology, and engineering to investigate the costs and constraints underlying human movement control, learning, and decision-making.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

with which the eyes move toward a target depends not just on the value of that target, but also the history of reward and effort experienced by the subject (Yoon et al., 2018).

The link between decision-making and motor control is illustrated by the fact that as the promised reward increases, animals are more likely to choose that option, but they also react earlier to the stimulus, and move with greater velocity toward it (Berret, Castanier, Bastide, & Deroche, 2018; Kawagoe, Takikawa, & Hikosaka, 1998; Milstein & Dorris, 2007; Sackaloo, Strouse, & Rice, 2015; Seideman et al., 2018; Summerside, Shadmehr, & Ahmed, 2018; Thura, Cos, Trung, & Cisek, 2014; Xu-Wilson, Zee, & Shadmehr, 2009). In contrast, as the effort required to acquire reward increases, animals are less likely to choose that option, but if chosen, movements take longer to start, and longer to conclude (Gordon et al., 1994; Ivry, 1986; Reppert et al., 2018; Rosenbaum, 1980; Shadmehr et al., 2016; Stelmach & Worringham, 1988; Wickler et al., 2001). These observations are true regardless of whether the action involves movements of our limbs, or movements of our eyes.

For example, when presented with a candy bar that we like, the latency to start the reach is earlier, and the reach velocity is higher. Similarly, when we are presented with a small image of that candy bar on a video screen, the saccadic eye movement toward that image tends to have a shorter latency, as well as higher peak velocity. Thus, subjective value, that elusive variable that is critical to decision-making, leaves its impression on our actions via the latency to begin movements, and the velocity with which to make that movement.

But why should the way we react (latency) and the way we move (velocity) be influenced by the subjective value that we assign to our destination? To answer this question, in this book (Shadmehr & Ahmed, 2020) we imagine the problem from the point of view of an ecologist: Is there a common currency that the brain is trying to optimize via its choices and movements?

In the natural environment, animals appear to make choices based on the desire to maximize a specific currency: the global capture rate, defined as the sum of all rewards acquired minus all efforts expended, divided by time (Bautista, Tinbergen, & Kacelnik, 2001; Richardson & Verbeek, 1986). For example, crows that live along the beaches of the pacific northwest of the United States rely on clams for their food. The clams hide in the sand, and the crows look for them, spending time and effort to dig them up. However, once a clam has been uncovered, the crow faces a critical decision: should it spend the time and energy needed to open the clam (grab it, fly over to a rocky shore, drop it a few times, etc.), or abandon this clam and look for another one? This decision depends on the size of the clam, and optimal foraging theory provides a framework to consider this decision. Once the energetic cost of searching, flying, and harvesting is considered, along with the time it takes to perform these actions, the choice of what to invest in and what to abandon becomes one of maximizing the global capture rate. Indeed, the global capture rate, which is roughly the energetic sum of reward and effort, divided by time, appears to play a fundamental role in the longevity and fecundity of animals (Lemon, 1991), suggesting that living one's life in a way that increases the capture rate has evolutionary advantages.

Until recently, optimal foraging has been viewed as a framework to consider patterns of decision-making, not patterns of movement. In this book, we extend this theory and show that it also predicts vigor modulation as a function of reward and effort. The key idea is that movements dictate expenditure of effort (which costs energy), as well as expenditure of time (Yoon et al., 2018). Moving faster gets you to the reward sooner, but requires greater energetic expenditure (Shadmehr et al., 2016). Thus, if we wish to maximize the global capture rate over the long run, then we must find policies that are informed by both the effort of making movements, and the benefit of acquiring reward.

As a result, the mathematical link between decisions and movements arises because both influence the global capture rate. To optimize this currency, we cannot simply make good choices; we must also move with vigor that is consistent with those choices.

3. Neuromodulators and their influence on decision-making and vigor

If vigor and decision-making are indeed working in alliance, then are there neural correlates to support this? A good example of the neural link between systems that assign value to stimuli, thus directing our decisions, and systems that control our movements is in Parkinson's disease. In Parkinson's disease, there is deterioration of the dopaminergic system of the basal ganglia, and its cardinal symptom is bradykinesia (slowness of movements). However, it is not the case that the patients are unable to move rapidly. Rather, it appears that the Parkinsonian brain is unwilling to expend the required effort to acquire the available reward (Manohar et al., 2015; Mazzoni, Hristova, & Krakauer, 2007). That is, the movement disorder may be a result of a dysfunction in the economic evaluation of reward and effort, which in turn is shared by the circuitry that controls movements.

This dysfunction of economic evaluation is illustrated in monkeys that do not show reward-dependent modulation of vigor (Kawagoe, Takikawa, & Hikosaka, 2004). In these subjects, there appears to be a critical problem: Dopamine release in the caudate nucleus of the basal ganglia appears insensitive to reward. Curiously, these monkeys do not exhibit lower latency and higher velocity saccades toward the more rewarding stimulus.

How does dopamine influence vigor? The magnitude of the inhibition imposed by the basal ganglia upon the superior colliculus depends on the expected reward from the stimulus (Sato & Hikosaka, 2002; Yasuda, Yamamoto, & Hikosaka, 2012). The expected reward information is transmitted from the input stage of the basal ganglia (striatum) to the output stage (substantia nigra reticulata, SNr) (Kim, Amita, & Hikosaka, 2017; Kim & Hikosaka, 2013; Lauwereyns, Watanabe, Coe, & Hikosaka, 2002). The striatal cells receive excitatory inputs from the cerebral cortex, but their output to the SNr via the direct and indirect pathways depends on the amount of dopamine that is present in the striatum. That is, dopamine influences how the striatal cells respond to their cortical inputs, impeding or encouraging a transition to an active state, a state in which the striatal cells are more responsive to their excitatory cortical inputs. Dopamine activity, in turn, is influenced by serotonin. Together, dopamine and serotonin, these ancient neurotransmitters, influence both the decision-making process, and its vigor. As a result, dopamine release before movement onset is sufficient to increase vigor of that movement (da Silva, Tecuapetla, Paixao, & Costa, 2018).

Although dopamine neurons fire in response to stimuli that promise reward, acting as a teacher for learning subjective value, dopamine concentration in the striatum is modulated by

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

the effort required to acquire that reward (Schelp et al., 2017, p. 2017; Syed et al., 2016). That is, dopamine spiking activity at the time of stimulus presentation appears to encode reward prediction error, whereas during production of effort, dopamine concentrations appear to support production of vigorous movements. Indeed, reward prediction error, and not reward alone, is the dominant modulator of vigor (Sedaghat-Nejad, Herzfeld, & Shadmehr, 2019). In this way, dopamine plays the role of Janus the Roman god: one face looking forward to reward, the other looking toward the effort needed to acquire that reward.

However, dopamine firing rates appear insensitive to one of the critical variables necessary to control vigor: the global capture rate (i.e., history of reward and effort) (Cohen, Amoroso, & Uchida, 2015). If firing rates of dopamine neurons do not provide a signal that reflects the global capture rate, then how is it that the brain controls vigor as a function of reward history? (Yoon et al., 2018). One possible answer is serotonin (Cohen et al., 2015), which is sensitive to reward history, and in many ways appears to act as an antagonist to dopamine, modulating the willingness to wait (Eagle, Bari, & Robbins, 2008; Miyazaki et al., 2014), increasing the harvest duration (Lottem et al., 2018), and encouraging sloth (Correia et al., 2017).

The elevated presence of serotonin in the brain under normal conditions coincides with reduced movement vigor, and a reluctance to produce effort in exchange for reward (Bailey et al., 2018). In addition, serotonin increases the tendency to linger and harvest for a longer period, encouraging persistence. In some of these cases, the effect of serotonin on behavior is mediated via modulation of dopamine.

4. Moving forward

An exciting implication of the research on vigor is that movements can provide a proxy for subjective value. This may be of importance to two disparate fields: economics and neuroscience. Although economists have strived for decades to estimate subjective value based on preferences that people have expressed via their choices, vigor may provide an implicit measure of this elusive variable. On the contrary, because neurobiology of vigor is based on many of the same neurotransmitters that malfunction in disease, such as Parkinson's disease and depression, tracking vigor may provide a real-time proxy for the state of these chemicals, thus aiding administration of interventions and providing an objective measure of treatment efficacy.

Overall, the book *Vigor* attempts to synthesize the mathematical, behavioral, and neurophysiological results gathered in the past decade regarding the link between control of movements, and control of decisions. From a scientific perspective, the results imply 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 value. 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, machines may measure our movements and gather vigor-based estimates of our personal preferences, even when we are not overtly making a choice, thereby unwittingly revealing one of our secrets; how much we value the thing we are moving toward.

Financial support. This study was supported by grants from the Office of Naval Research (N00014-15-1-2312), the National Institutes of Health (R01-NS078311 and R01-NS096083), and the National Science Foundation (CNS-1714623).

Conflict of interest. None.

References

Bahill, A. T., Clark, M. R., & Stark, L. (1975). The main sequence: A tool for studying human eye movements. *Mathematical Biosciences*, *24*, 191–204.

Bailey, M. R., Goldman, O., Bello, E. P., Chohan, M. O., Jeong, N., Winiger, V., … Simpson, E. H. (2018). An interaction between serotonin receptor signaling and dopamine enhances goal-directed vigor and persistence in mice. *Journal of Neuroscience*, *38*, 2149–2162. https://doi.org/10.1523/JNEUROSCI.2088-17.2018.

Bautista, L. M., Tinbergen, J., & Kacelnik, A. (2001). To walk or to fly? How birds choose among foraging modes. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 1089–1094. https://doi.org/10.1073/pnas.98.3.1089.

Berret, B., Castanier, C., Bastide, S., & Deroche, T. (2018). Vigour of self-paced reaching movement: Cost of time and individual traits. *Scientific Reports*, *8*, 10655. https://doi.org/10.1038/s41598-018-28979-6.

Cohen, J. Y., Amoroso, M. W., & Uchida, N. (2015). Serotonergic neurons signal reward and punishment on multiple timescales. *eLife*, *4*, e06346. https://doi.org/10.7554/eLife.06346.

Correia, P. A., Lottem, E., Banerjee, D., Machado, A. S., Carey, M. R., & Mainen, Z. F. (2017). Transient inhibition and long-term facilitation of locomotion by phasic optogenetic activation of serotonin neurons. *eLife*, *6*, e20975. https://doi.org/10.7554/eLife.20975.

da Silva, J. A., Tecuapetla, F., Paixao, V., & Costa, R. M. (2018). Dopamine neuron activity before action initiation gates and invigorates future movements. *Nature*, *554*, 244–248. https://doi.org/10.1038/nature25457.

Eagle, D. M., Bari, A., & Robbins, T. W. (2008). The neuropsychopharmacology of action inhibition: Cross-species translation of the stop-signal and go/no-go tasks. *Psychopharmacology (Berlin)*, *199*, 439–456. https://doi.org/10.1007/s00213-008-1127-6.

Golla, H., Tziridis, K., Haarmeier, T., Catz, N., Barash, S., & Thier, P. (2008). Reduced saccadic resilience and impaired saccadic adaptation due to cerebellar disease. *European Journal of Neuroscience*, *27*, 132–144.

Gordon, J., Ghilardi, M. F., & Ghez, C. (1994). Accuracy of planar reaching movements. I. Independence of direction and extent variability. *Experimental Brain Research*, *99*, 97–111.

Haith, A. M., Reppert, T. R., & Shadmehr, R. (2012). Evidence for hyperbolic temporal discounting of reward in control of movements. *Journal of Neuroscience*, *32*, 11727–11736. https://doi.org/10.1523/JNEUROSCI.0424-12.2012.

Hunter, L. C., Hendrix, E. C., & Dean, J. C. (2010). The cost of walking downhill: Is the preferred gait energetically optimal? *Journal of Biomechanics*, *43*, 1910–1915. https://doi.org/10.1016/j.jbiomech.2010.03.030.

Ivry, R. B. (1986). Force and timing components of the motor program. *Journal of Motor Behavior*, *18*, 449–474.

Kawagoe, R., Takikawa, Y., & Hikosaka, O. (1998). Expectation of reward modulates cognitive signals in the basal ganglia. *Nature Neuroscience*, *1*, 411–416.

Kawagoe, R., Takikawa, Y., & Hikosaka, O. (2004). Reward-predicting activity of dopamine and caudate neurons – A possible mechanism of motivational control of saccadic eye movement. *Journal of Neurophysiology*, *91*, 1013–1024. https://doi.org/10.1152/jn.00721.2003.

Kim, H. F., Amita, H., & Hikosaka, O. (2017). Indirect pathway of caudal basal ganglia for rejection of valueless visual objects. *Neuron*, *94*, 920–930. https://doi.org/10.1016/j.neuron.2017.04.033.

Kim, H. F., & Hikosaka, O. (2013). Distinct basal ganglia circuits controlling behaviors guided by flexible and stable values. *Neuron*, *79*, 1001–1010. https://doi.org/10.1016/j.neuron.2013.06.044.

Lauwereyns, J., Watanabe, K., Coe, B., & Hikosaka, O. (2002). A neural correlate of response bias in monkey caudate nucleus. *Nature*, *418*, 413–417.

Lemon, W. C. (1991). Fitness consequences of foraging behaviour in the zebra finch. *Nature*, *352*, 153–155.

Levine, R. V., & Norenzayan, A. (1999). The pace of life in 31 countries. *Journal of Cross-Cultural Psychology*, *30*, 178–205.

Lottem, E., Banerjee, D., Vertechi, P., Sarra, D., Lohuis, M. O., & Mainen, Z. F. (2018). Activation of serotonin neurons promotes active persistence in a probabilistic foraging task. *Nature Communications*, *9*, 1000. https://doi.org/10.1038/s41467-018-03438-y.

Manohar, S. G., Chong, T. T., Apps, M. A., Batla, A., Stamelou, M., Jarman, P. R., … Husain, M. (2015). Reward pays the cost of noise reduction in motor and cognitive control. *Current Biology*, *25*, 1707–1716. https://doi.org/10.1016/j.cub.2015.05.038.

Manohar, S. G., Muhammed, K., Fallon, S. J., & Husain, M. (2019). Motivation dynamically increases noise resistance by internal feedback during movement. *Neuropsychologia, Cognitive Effort*, *123*, 19–29. https://doi.org/10.1016/j.neuropsychologia.2018.07.011.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

Mazzoni, P., Hristova, A., & Krakauer, J. W. (2007). Why don't we move faster? Parkinson's disease, movement vigor, and implicit motivation. *Journal of Neuroscience*, *27*, 7105–7116.

Milstein, D. M., & Dorris, M. C. (2007). The influence of expected value on saccadic preparation. *Journal of Neuroscience*, *27*, 4810–4818.

Miyazaki, K. W., Miyazaki, K., Tanaka, K. F., Yamanaka, A., Takahashi, A., Tabuchi, S., & Doya, K. (2014). Optogenetic activation of dorsal raphe serotonin neurons enhances patience for future rewards. *Current Biology*, *24*, 2033–2040. https://doi.org/10.1016/j.cub.2014.07.041.

Ralston, H. J. (1958). Energy-speed relation and optimal speed during level walking. *Internationale Zeitschrift fur Angewandte Physiologie, Einschliesslich Arbeitsphysiologie*, *17*, 277–283.

Reppert, T. R., Lempert, K. M., Glimcher, P. W., & Shadmehr, R. (2015). Modulation of saccade vigor during value-based decision making. *Journal of Neuroscience*, *35*, 15369–15378. https://doi.org/10.1523/JNEUROSCI.2621-15.2015.

Reppert, T. R., Rigas, I., Herzfeld, D., Sedaghat-Nejad, E., Komogortsev, O., & Shadmehr, R. (2018). Movement vigor as a trait-like attribute of individuality. *Journal of Neurophysiology*, *120*, 741–757. https://doi.org/10.1152/jn.00033.2018.

Richardson, H., & Verbeek, N. A. M. (1986). Diet selection and optimization by northwestern crows feeding on Japanese littleneck clams. *Ecology*, *67*, 1219–1226.

Rosenbaum, D. A. (1980). Human movement initiation: Specification of arm, direction, and extent. *Journal of Experimental Psychology General*, *109*, 444–474.

Sackaloo, K., Strouse, E., & Rice, M. S. (2015). Degree of preference and its influence on motor control when reaching for most preferred, neutrally preferred, and least preferred candy. *OTJR Occupation, Participation and Health*, *35*, 81–88.

Samuelson, P. A. (1938). A note on the pure theory of consumer's behaviour. *Economica*, *51*, 61–72.

Sato, M., & Hikosaka, O. (2002). Role of primate substantia nigra pars reticulata in reward-oriented saccadic eye movement. *Journal of Neuroscience*, *22*, 2363–2373.

Schelp, S. A., Pultorak, K. J., Rakowski, D. R., Gomez, D. M., Krzystyniak, G., Das, R., & Oleson, E. B. (2017). A transient dopamine signal encodes subjective value and causally influences demand in an economic context. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, E11303–E11312. https://doi.org/10.1073/pnas.1706969114.

Sedaghat-Nejad, E., Herzfeld, D. J., & Shadmehr, R. (2019). Reward prediction error modulates saccade vigor. *Journal of Neuroscience*, *39*, 5010–5017.

Seideman, J. A., Stanford, T. R., & Salinas, E. (2018). Saccade metrics reflect decision-making dynamics during urgent choices. *Nature Communications*, *9*, 2907. https://doi.org/10.1038/s41467-018-05319-w.

Shadmehr, R., & Ahmed, A. A. (2020). *Vigor: Neuroeconomics of movement control*. MIT Press.

Shadmehr, R., Huang, H. J., & Ahmed, A. A. (2016). A representation of effort in decision-making and motor control. *Current Biology*, *26*, 1929–1934.

Stelmach, G. E., & Worringham, C. J. (1988). The preparation and production of isometric force in Parkinson's disease. *Neuropsychologia*, *26*, 93–103.

Straube, A., Fuchs, A. F., Usher, S., & Robinson, F. R. (1997). Characteristics of saccadic gain adaptation in rhesus macaques. *Journal of Neurophysiology*, *77*, 874–895.

Summerside, E. M., Shadmehr, R., & Ahmed, A. A. (2018). Vigor of reaching movements: Reward discounts the cost of effort. *Journal of Neurophysiology*, *119*, 2347–2357.

Syed, E. C., Grima, L. L., Magill, P. J., Bogacz, R., Brown, P., & Walton, M. E. (2016). Action initiation shapes mesolimbic dopamine encoding of future rewards. *Nature Neuroscience*, *19*, 34–36. https://doi.org/10.1038/nn.4187.

Takikawa, Y., Kawagoe, R., & Hikosaka, O. (2002). Reward-dependent spatial selectivity of anticipatory activity in monkey caudate neurons. *Journal of Neurophysiology*, *87*, 508–515.

Thura, D., Cos, I., Trung, J., & Cisek, P. (2014). Context-dependent urgency influences speed-accuracy trade-offs in decision-making and movement execution. *Journal of Neuroscience*, *34*, 16442–16454. https://doi.org/10.1523/JNEUROSCI.0162-14.2014.

Wickler, S. J., Hoyt, D. F., Cogger, E. A., & Hall, K. M. (2001). Effect of load on preferred speed and cost of transport. *Journal of Applied Physiology*, *90*, 1548–1551. https://doi.org/10.1152/jappl.2001.90.4.1548.

Wickler, S. J., Hoyt, D. F., Cogger, E. A., & Hirschbein, M. H. (2000). Preferred speed and cost of transport: The effect of incline. *Journal of Experimental Biology*, *203*, 2195–2200.

Xu-Wilson, M., Zee, D. S., & Shadmehr, R. (2009). The intrinsic value of visual information affects saccade velocities. *Experimental Brain Research*, *196*, 475–481.

Yasuda, M., Yamamoto, S., & Hikosaka, O. (2012). Robust representation of stable object values in the oculomotor Basal Ganglia. *Journal of Neuroscience*, *32*, 16917–16932. https://doi.org/10.1523/JNEUROSCI.3438-12.2012.

Yoon, T., Geary, R. B., Ahmed, A. A., & Shadmehr, R. (2018). Control of movement vigor and decision making during foraging. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, E10476–E10485.

Yoon, T., Jaleel, A., Ahmed, A. A., & Shadmehr, R. (2020). Saccade vigor and the subjective economic value of visual stimuli. *Journal of Neurophysiology*, *123*, 2161–2172. https://doi.org/10.1152/jn.00700.2019.

Open Peer Commentary

Costs and benefits of communicating vigor

Cristina Becchio[a], Kiri Pullar[a,b] and Stefano Panzeri[b]

[a]Cognition, Motion & Neuroscience, Center for Human Technologies, Istituto Italiano di Tecnologia, 16152 Genoa, Italy and [b]Neural Computation Laboratory, Center for Human Technologies, Istituto Italiano di Tecnologia, 16152 Genoa, Italy.
cristina.becchio@iit.it; https://www.iit.it/people/cristina-becchio; kiri.pullar@iit.it; https://www.iit.it/people/kiri-pullar; stefano.panzeri@iit.it; https://www.iit.it/people/stefano-panzeri

doi:10.1017/S0140525X21000200, e124

Abstract

Why do we run toward people we love, but only walk toward others? One reason is to let them know we love them. In this commentary, we elaborate on how subjective utility information encoded in vigor is read out by others. We consider the potential implications for understanding and modeling the link between movements and decisions in social environments.

Shadmehr and Ahmed propose that movement vigor can provide an easily measured proxy for hidden variables such as subjective value. The authors state that, with the increasing power of smart phones and presence of surveillance cameras, they "would not be surprised if someday soon the results of this research encourage the invention of machines that measure our movements and gather vigor-based estimates of our personal preferences." An alternative perspective is that such machines already exist; human brains are such machines.

Human observers are remarkably good at estimating hidden variables from movement parameters (Becchio, Koul, Ansuini, Bertone, & Cavallo, 2018). For example, they can easily discern the emotion of a person walking toward them (Chouchourelou, Matsuka, Harber, & Shiffrar, 2006). Studies have shown that subtle variations in movement kinematics are sufficient for observers to infer other people's intentions (Cavallo, Koul, Ansuini, Capozzi, & Becchio, 2016), attitudes (Manera, Becchio, Cavallo, Sartori, & Castiello, 2011), expectations (Grezes, Frith, & Passingham, 2004; Runeson & Frykholm, 1983), and beliefs (van der Wel, Sebanz, & Knoblich, 2014). A recent study from our laboratories demonstrates that naïve observers are sensitive to intention information encoded in less than 3% of the total variance of the movements (Patri et al., 2020).

Such studies raise the intriguing possibility that subjective utility information is not only *encoded* in movement vigor – as Shadmehr and Ahmed convincingly demonstrate – but can also be *read out* from movement vigor. In what follows, we briefly consider some of the implications of this idea within the conceptual framework of intersection information (Panzeri, Harvey, Piasini, Latham, & Fellin, 2017; Pica et al., 2017). This framework was initially proposed to quantify how sensory information encoded in a neural population is read out to inform single-trial behavioral choices (Panzeri et al., 2017; Pica et al., 2017). It has,

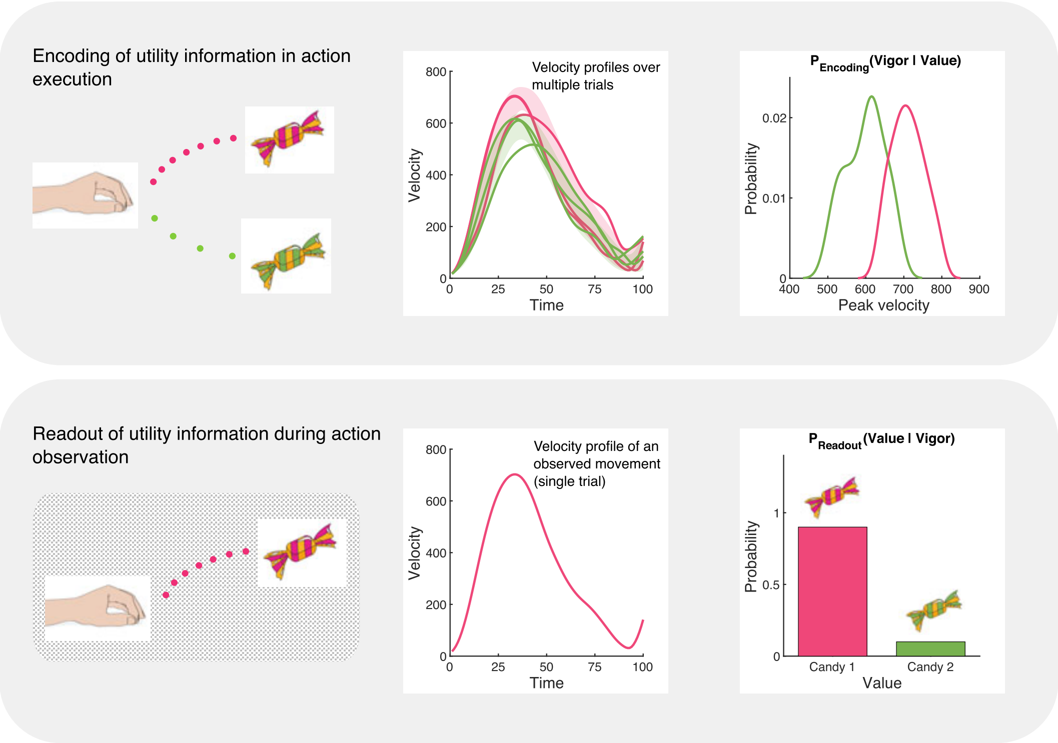

Figure 1 (Becchio et al.). *Analyzing vigor as a proxy for utility within the intersection information framework*. Consider the example of a person reaching toward a preferred versus non-preferred candy. Top row: Encoding. The subjective utility assigned to each candy subtly changes the vigor (velocity) of the reaching movement. By conducting multiple trials, we can isolate the variance that reflects utility information from motor variability contributed from other sources and develop an *encoding model* (P_{Encoding}), which maps utility to vigor. Bottom row: Readout. We can then examine if observers are able to use these subtle variations in movement vigor to unmask subjective views. By showing the recorded set of movements and asking observers to judge, on each trial, whether the hand grasped for the preferred versus the non-preferred candy a *readout model* (P_{Readout}) can be developed, which maps vigor to utility choice. The intersection between encoding and readout allows us to examine the flow of utility information communicated between individuals through movement vigor.

subsequently, been extended to quantify how information about intentions encoded in movement kinematics is read out by observers (Patri et al., 2020). Here, we adapt the intersection information framework to elaborate on how subjective utility information *encoded* in movement vigor can be *read out* (Fig. 1). We then discuss the potential implications for understanding and modeling the link between movements and decisions in social environments.

The logic of our proposal is straightforward. If humans and other animals tend to move faster (with increased vigor) toward things that they value more, then the value they assign to things can be inferred from the vigor with which they move. Importantly, the intersection information framework does not assume (or require) that the subjective utility information encoded in movement vigor is optimally read out. For example, an observer may read some features encoding utility information but ignore other informative features. Determining how (and how well) utility information is read out requires, first, measuring how it is encoded in movement parameters. Consider reaching for one of two candies, a candy with a preferred flavor versus a candy with a non-preferred flavor, as in (Sackaloo, Strouse, & Rice, 2015). Operationally, encoding of utility information can be computed by asking human volunteers to reach for each candy. With the assumption that the physical constraints of reaching are identical (e.g., initial arm configuration, size, shape, weight, and position of the candy), variations in vigor (e.g., the onset latency and the velocity) of movements made toward different candies can be taken to reflect utility (Summerside, Shadmehr, & Ahmed, 2018). One difficulty here is related to the motor variability across individual trials. By having each volunteer perform multiple repetitions of each movement, however, it is possible to isolate the variance that reflects utility from the trial-to-trial variance unrelated to utility. A statistical model (the encoding model) can be used to identify the specific movement features that carry utility information (Patri et al., 2020).

Having determined how utility information is encoded in movement parameters, one can proceed to investigate how it is read out. A simple way of doing this is to show naïve observers the recorded set of movements and ask them to judge, on each trial, whether the hand grasped for the preferred versus the non-preferred candy. Using the same logic as for encoding, a statistical readout model can be used to determine how observers combine information from different features to infer utility.

Readout is optimal (and intersection information maximal) when all available utility information is correctly read out. Human readout rarely achieves this absolute level of optimality. Real observers often ignore some of the features that encode information (Patri et al., 2020). Additionally, they may read features that do not encode utility information. Because such features do not carry information, they will add noise to the inference computation (Panzeri et al., 2017).

Suboptimality of readout may at first appear to be a glitch of evolution. However, an alternative view is that suboptimality of

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

readout represents a rich opportunity for communication. For any given motor task or behavior, there is generally a large number of "motor-equivalent" solutions that can produce similar or functionally equivalent behaviors (Latash, 2012). If not all the information encoded in vigor is read out, actors can exploit variance in the space of parameters that has no effect on the overall performance (so-called "good variance"; Latash, 2012) to manipulate readout. In the reaching for a candy situation, for example, an actor trying to deceive the observer about the preferred candy may favor the vigor-equivalent solution that carries little utility information along the dimensions that are read out. Conversely, a combination of parameters that maximizes readout may be selected by an actor wanting to communicate their preference.

Evidence that action planning is influenced by readout consideration exists in primate studies using the informed forager paradigm. In this paradigm, the subordinate primate sees the location of hidden food, but the dominant does not. Using this paradigm, Hall et al. (2017) found that subordinate chimpanzees alter their gaze direction not only to withhold information about the location of the highly preferred banana, but also to mislead the dominant competitor toward the less preferred cucumber. It remains to be verified whether chimpanzees (and other primates) are also capable of tactfully manipulating vigor. Anecdotally, it certainly feels that we move with less or more vigor depending on the subjective value we want to communicate to others.

Shadmehr and Ahmed investigate the link between how the brain assigns value to things and how it controls our movements from the perspective of a solitary forager. In this commentary, we approach vigor research from the complementary perspective of a group forager (Stephens, Brown, & Ydenberg, 2007). Viewed from this perspective, the latency with which we react and the speed with which we move become sources of information about subjective utility, that can, in turn, be read by other individuals. The intersection information framework provides a useful starting point for developing new experimental paradigms and mathematical tools for measuring how utility information is encoded and read out. Integrated with information about the neural basis of vigor, these measures could be used not only to achieve a better qualitative understanding of the social effect of communicating vigor, but also to help producing actual equations that quantify how the utility information flow between individuals shapes the behavior of a group.

In sum, the intersection information framework can be instrumental to the ambitious goal of incorporating the social dimensions into quantitative models of vigor. After all, one reason we run toward people we love is to let them know that we love them.

Acknowledgments. We are grateful to Laura Taverna for Figure 1.

Funding statement. This study was supported by INAIL (PR19-PAS-P1 – iHannes).

Conflict of interest. None.

References

Becchio, C., Koul, A., Ansuini, C., Bertone, C., & Cavallo, A. (2018). Seeing mental states: An experimental strategy for measuring the observability of other minds. *Physics of Life Reviews*, *24*, 67–80. doi: 10.1016/j.plrev.2017.10.002.

Cavallo, A., Koul, A., Ansuini, C., Capozzi, F., & Becchio, C. (2016). Decoding intentions from movement kinematics. *Science Reports*, *6*, 37036. doi: 10.1038/srep37036.

Chouchourelou, A., Matsuka, T., Harber, K., & Shiffrar, M. (2006). The visual analysis of emotional actions. *Social Neuroscience*, *1*(1), 63–74. doi: 10.1080/17470910600630599.

Grezes, J., Frith, C., & Passingham, R. E. (2004). Brain mechanisms for inferring deceit in the actions of others. *Journal of Neuroscience*, *24*(24), 5500–5505. doi: 10.1523/jneurosci.0219-04.2004.

Hall, K., Oram, M. W., Campbell, M. W., Eppley, T. M., Byrne, R. W., & de Waal, F. B. M. (2017). Chimpanzee uses manipulative gaze cues to conceal and reveal information to foraging competitor. *American Journal of Primatology*, *79*(3), 1–11. https://doi.org/10.1002/ajp.22622.

Latash, M. L. (2012). The bliss (not the problem) of motor abundance (not redundancy). *Experimental Brain Research*, *217*(1), 1–5. doi: 10.1007/s00221-012-3000-4.

Manera, V., Becchio, C., Cavallo, A., Sartori, L., & Castiello, U. (2011). Cooperation or competition? Discriminating between social intentions by observing prehensile movements. *Experimental Brain Research*, *211*(3–4), 547–556. doi: 10.1007/s00221-011-2649-4.

Panzeri, S., Harvey, C. D., Piasini, E., Latham, P. E., & Fellin, T. (2017). Cracking the neural code for sensory perception by combining statistics, intervention, and behavior. *Neuron*, *93*(3), 491–507. doi: 10.1016/j.neuron.2016.12.036.

Patri, J.-F., Cavallo, A., Pullar, K., Soriano, M., Valente, M., Koul, A., … Becchio, C. (2020). Transient disruption of the inferior parietal lobule impairs the ability to attribute intention to action. *Current Biology*, *30*, 4594–4605. doi: 10.1016/j.cub.2020.08.104.

Pica, G., Piasini, E., Safaai, H., Runyan, C. A., Diamond, M. E., Fellin, T., … Panzeri, S. (2017). Quantifying how much sensory information in a neural code is relevant for behavior. *Advances in Neural Information Processing Systems 30* (Nips 2017), 3686–3696.

Runeson, S., & Frykholm, G. (1983). Kinematic specification of dynamics as an informational basis for person-and-action perception: Expectation, gender recognition, and deceptive intention. *Journal of Experimental Psychology: General*, *112*(4), 585–615. doi: 10.1037/0096-3445.112.4.585.v

Sackaloo, K., Strouse, E., & Rice, M. S. (2015). Degree of preference and its influence on motor control when reaching for most preferred, neutrally preferred, and least preferred candy. *OTJR: Occupation, Participation and Health*, *35*(2), 81–88. doi: 10.1177/1539449214561763.

Stephens, D. W., Brown, J. S., & Ydenberg, R. C. (2007). *Foraging: Behavior and ecology*. Chicago: University of Chicago Press.

Summerside, E. M., Shadmehr, R., & Ahmed, A. A. (2018). Vigor of reaching movements: Reward discounts the cost of effort. *Journal of Neurophysiology*, *119*(6), 2347–2357. doi: 10.1152/jn.00872.2017.

van der Wel, R. P. R. D., Sebanz, N., & Knoblich, G. (2014). Do people automatically track others' beliefs? Evidence from a continuous measure. *Cognition*, *130*(1), 128–133. doi: 10.1016/j.cognition.2013.10.004.

How not to answer interdisciplinary "Why?" questions

Fred L. Bookstein

Department of Statistics, University of Washington, Seattle, WA 98195, USA.
flb@stat.washington.edu

doi:10.1017/S0140525X21000066, e125

Abstract

The book under review tries to link the economic concept of "reward," or, more accurately, "capture rate," to the experimental literature of various neuroscientific quantities dealing with motor control. But this reviewer argues that such a linkage requires a richer language of quantification than the book actually affords: a language not just of "greater" or "less," but of *how much* greater or less. Without such a methodology, the arguments here cannot be persuasive.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

> "When I use a word," Humpty Dumpty said, in rather a scornful tone, "it means just what I choose it to mean – neither more nor less."
> — Lewis Carroll, *Alice in Wonderland*

> The theorizing mind tends always to the oversimplification of its materials.
> — William James, *The Varieties of Religious Experience*

The seventh sentence of the book under review (opening of the Preface, p. vii) is a question: "Why do we run toward people we love, but merely walk toward others?" The sentence is copied 332 pages later to launch the book's Conclusion, p. 323. A reader might expect, then, that that embedded proposition, that "we run toward people we love … but only walk toward others," is pertinent to *Vigor*'s actual empirical content. But a word-by-word scan of the book's electronic version uncovers only eight appearances of the word "love" (also three of "loved one," but that is a different concept) of which four are from Shakespeare, one is from a fourteenth-century poet named Hafez, and two others are from the duplicate sentence I've already quoted. Only one of the eight actually deals with the notion of "love" at all: "when we are walking to meet someone we love, … reward is computed via its neural proxy, dopamine" (p. 15), and that is another proposition for which no evidence is offered.

The grammar of embedded sentences such as those lulls us into glossing them as factual, but they could as easily be myth or exaggeration as generalization. Noting the lack of discussion, a skeptical reader might well conclude that the book won't answer that "why" opening teaser, inasmuch as it has no intention of answering the simpler embedded question: *Do* we move faster toward people we love? On this specific point, the book offers no discussion at all. The answer would, of course, have been "Well, it depends" – countless other factors affect speed of ambulation: stature, altitude, rate of climb or descent, age, social context, crowding, health, weather, footwear, category of love, and so on, and the answer to that "Why" query would depend on all those other factors. Although the book refers to the opening statement as "our airport example," p. 14, it presents no data relevant to this fable, from airports or anywhere else. Therefore, the authors' initial Why question is incoherent: there is not yet any phenomenon to be explained.

The critique instigated by this casual aspect of the book's introduction applies across all the domains of "neuroeconomics of movement control" that its authors purport to consider. Let me illustrate lexicometrically. The word "vigor" itself, title of the book, appears 521 times; "dopamine," that proxy for "reward," 468 times; "capture rate," a general term from "optimal foraging theory" defined as "the sum of all rewards acquired minus all efforts expended, divided by total time" (p. 331), 285 times; "utility," the unobservable core of economic theory, 431 times. But then explore the glossary of inference. The words "prove," "proof," "disprove," and so on never appear here at all! Evidently the authors do not claim to have actually settled any scientific debate. The word "proxy" itself, which surely is relevant to any interdisciplinary argument as complicated as theirs, appears 24 times but is never defined: apparently this is a term of art. The trope of "consistent," as in "being consistent with," appears 46 times, and "correspond," 40 times; but the total number of correlation coefficients printed here is a mere three, and the concept of "regression" arises only in connection with two of the figures, 5.16 and 5.19. The appearances of the word "suggest," a vestige of the weakest form of scientific inference, total 118, but the number of inferences, or rather the count of appearances of the word "infer" and its derivatives, is only 19, less than one-sixth as many.

Now let us dig more deeply into the methodology of this volume. The Preface summarizes its purpose on p. xi: "In this book, our goal is to consider a simple question: why do we move faster toward things we value more?" A quick retort would be "Who says?" or "Oh, do we?" A more reasoned response would note that no such "Why?" question can be answered until there are quantifications of *how much* – how much faster, how much more valued. Therefore, a book like this cannot validly persuade unless its methodology is explicitly written out – how every discussion like "why greater values of A sometimes accompany greater values of B" is to be pursued in a logically rigorous way that convinces readers not already indoctrinated into its esoterica. *Vigor*, alas, eschews any such prolegomenon. The phrase "how much" appears 17 times in this book, but the usage is always merely qualitative: The probe is never responded to with an actual quantity, let alone a regression slope, as on p. viii, where the phrase "how much more you prefer one dessert to the other" is simply left hanging. Although every chapter ends with a discussion under a heading of "Limitations," the roster of these taps not the logic of interdisciplinary inference but instead diverse aspects of experimental design. In these commentaries, too, all comparisons are of the purely qualitative semantics I've been criticizing.

How ought one to carry out a study bridging economics to other disciplines? A good example comes from the classic topic of how environmental tobacco smoke (ETS, passive smoking) affects health, as uncovered by a research consensus in the late 1990s reviewed on pp. 253–262 of my textbook on quantitative reasoning (Bookstein, 2014). The study precised there demonstrated the truth of the proposition that ETS *causes* excess cases of ischemic heart disease (Law, Morris, & Wald, 1997) or lung cancer (Hackshaw, Law, & Law, 1997) by finding that the increased rates of prevalence among nonsmoking wives of smokers match known direct causal analyses *numerically* – dose–response models from other studies – and are stable against challenge by a great variety of competing explanations, such as diet (which is where aspects of economics come in, namely, home economics). The basic logic of inferring causation from extended chains of mixed-modality quantitative data is by now a well-established branch of applied statistics where the fundamental notion linking data to theory is a particularly fruitful diagram style, the *directed acyclic graph* (cf. Pearl, 2009). Hyphen-economics fields themselves have celebrated this same basic logic, as reviewed, for instance, in Wold and Jöreskog (1982) and polished in the method of *structural equations analysis*. In this mature methodology, causation, measurement proxies, and competing inferences are all handled at once.

These rules of interdisciplinary causal reasoning lie nowadays at the core of every graduate curriculum in statistics or biostatistics; but they make no appearance in *Vigor*. The word "effect" appears 150 times, and "affect" (as a verb) another 133; but the technical term "effect size," which is universally acknowledged the currency according to which magnitudes should be exported across disciplines, never appears here at all. (In linear models, effect size is a standardized path coefficient; in grouped or experimental data, it is the ratio of a group difference to the pooled within-group standard deviation. It has hardly anything to do with statistical significance or p-values.)

The authors of *Vigor* have ignored these and many other tenets of interdisciplinary quantitative method. This is in spite of the massive menu of quantitative diagrams on offer – the book's 134 figures span a total of 331 named panels, many of which themselves involve multiple parts (alternative experimental

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

conditions or measures). But no tables present any roster of alternative *explanations* compared among themselves for the power with which they manage to explain the same empirical pattern ("strong inference," Platt, 1964). The comparisons reported from experimental data all come in the form of one average being "greater" than another, or one movement "faster," or one chemical titre "higher," all these comparisons "consistent with" or "corresponding to" the capture-rate theory, but never is there any more convincing language of agreement. Theory is never called upon to predict *how much* higher or faster or greater the one empirically grounded quantity should be than the other. But *all* the great examples of interdisciplinary quantitative inference take the form of agreement of such quantities across multidisciplinary testing, the methodology Wilson (1998) famously reminded us is called *consilience* (see my review in Ch. 3 of Bookstein, 2014).

"Because the neurobiology of vigor is based on many of the same neurotransmitters that malfunction in diseases such as Parkinson's and depression," the authors say on p. 327, "tracking vigor may provide a real-time proxy for the state of these chemicals. Thus, vigor assessment could aid in the administration of interventions and provide an objective measure of treatment efficacy." Here, the casual informality with which this book tosses around the undefined concept of proxy is worse than unconvincing – attributing any credibility to so untested a claim of proxy outcomes would actually be dangerous. In any context of medical intervention it is unethical simply to *declare* one quantity to be a proxy of another. Enormous additional effort needs to be invested *first* in all the factors that link the proxy to the variable it is supposedly proxy for. (This is a main theme of today's evidence-based medicine: see e.g., Higgins & Green, 2008.) No such effort is evident in any of *Vigor*'s examples, and so any talk of applications to Parkinson's disease is vastly premature; similarly, the promise of other payoffs such as the various erosions of privacy suggested as future marketing applications on pp. xii–xiii. For an opposite example, one where this methodological mandate for interdisciplinary inference has been accepted, see Atwater et al. (2005) on the causal analysis of a tsunami following the great Seattle earthquake of 1700.

In closing, I return to my critique of the factoid about when we run that both opens and closes this book, along with the tacit assumption that it can be embedded inside a "why" query without fallacy. A treatise claiming to bridge multiple disciplines of mismatched intellectual impedance (from EEG voltages to "love" is indeed quite a range of observation styles!) requires sustained methodological clarity, particularly in respect of its ultimate component, the conversion of a quantitative comparison into an explanation. A rhetoric of "how much more" is mandatory for any methodology that claims to be explaining "more" across disciplines. One must not settle for the purely qualitative polarity, "more" versus "less," that is encountered throughout this book.

What emerges from *Vigor*'s failure to constructively critique its own methodology or even to set it out in propositions is a book only for the True Believer, or maybe someone worried about Parkinson's. You can't build an interdisciplinary theme grounded in laboratory-derived data (as were all the data in nearly all the figures of this book) if your only arguments are about the signs of differences or slopes from a roster of experimental measurements untethered to any quantitative theory, any metrological chain. But the book's "Conclusions" chapter, pp. 323–327, in spite of its dozens of qualitative terms ("greater," "lower," "faster," "shorter," "biased," etc.) per page, presents the reader not a single decimal quantity at all. Incomprehensibly, the book under review neither explicitly sets down nor implicitly acknowledges any methodology for quantitative inference from instrument readings to human actions, and its absence severely (in my view, fatally) impugns the authority of its narrative. The concern about love with which the book begins and ends is itself no model of inquiry – it brackets neither valid inferences about causal chains in neuroeconomics nor valid explanations of human action from laboratory evidence. The rest of the purported "explanations" here are lost in the fog of proxy measurement, a domain the authors never subjected to any formal discipline. "Proxy" here is a Humpty Dumpty word, meaning whatever the authors choose it to mean; but one cannot persuasively disseminate an interdisciplinary claim when crucial concepts such as this are left undefined, which is to say, unconstrained by method.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

References

Atwater, B. F., Musumi-Rokkaku, S., Satake, K., Tsuji, Y., Ueba, K., & Yamaguchi, D. K. (2005). *The Orphan Tsunami of 1700: Japanese clues to a parent earthquake in North America*. United States Geological Survey and University of Washington Press.
Bookstein, F. L. (2014). *Measuring and reasoning: Numerical inference in the sciences*. Cambridge University Press.
Hackshaw, A. K., Law, M. R., & Law, N. J. (1997). The accumulated evidence on lung cancer and environmental tobacco smoke. *British Medical Journal*, *315*, 980–988.
Higgins, J. P. T., & Green, S., eds. (2008). *Cochrane handbook for systematic reviews of interventions*. Wiley-Blackwell.
Law, M. R., Morris, J. K., & Wald, N. J. (1997). Environmental tobacco smoke exposure and ischaemic heart disease: an evaluation of the evidence. *British Medical Journal*, *315*, 973–980.
Pearl, J. (2009). *Causality: Reasoning, models, and inference* (2nd ed.). Cambridge University Press.
Platt, J. R. (1964). Strong inference. *Science*, *146*, 347–353.
Wilson, E. O. (1998). *Consilience: The unity of knowledge*. Knopf.
Wold, H., & Jöreskog, K. eds. (1982). *Systems under indirect observation: Causality, structure, prediction* (Vol. *2*). North-Holland.

Movement vigor: Frameworks, exceptions, and nomenclature

Rory John Bufacchi[a,b] and Gian Domenico Iannetti[a,b]

[a]Center for Life Nano- & Neuro-Science, Italian Institute of Technology (IIT), 00161 Rome, Italy and [b]Department of Neuroscience, Physiology and Pharmacology, University College London (UCL), London WC1E 6BT, UK.
rory.bufacchi@iit.it, giandomenico.iannetti@iit.it
www.iannettilab.net

doi:10.1017/S0140525X21000315, e126

Abstract

Shadmehr and Ahmed cogently argue that vigor of appetitive movements is positively correlated with their value, and that value can therefore be inferred by measuring vigor. Here, we highlight three points to consider when interpreting this account: (1) The correlation between vigor and value is not obligatory, (2) the vigor effect also arises in frameworks other than optimal foraging, and (3) the term vigor can be misinterpreted, thereby affecting rigor.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

1. Vigor is not an obligatory readout of value

The optimal foraging framework states that organisms maximize utility. Maximizing utility brings about a correlation between vigor of movement toward a target, and the reward offered by that target. On the basis of this correlation, Shadmehr and Ahmed suggest using vigor as a readout of value. However, one must be cautious when drawing such a conclusion, because it relies on reverse inference; it overlooks the basic tenet that correlation does not necessarily imply causation. We feel this is particularly important, because there are many exceptions to the vigor-value correlation. An armchair ethologist might say that neither the leopard stalking its prey, nor the poker player bluffing a hand, show the target's value through vigorous actions. Indeed, the vigor-value relationship is only obligatory when comparing two identical situations that only differ in the value of an object. There are many other reasons for vigor of a movement to change even if the target's value is constant. This weakens Shadmehr and Ahmed's claim that vigor can be used to reliably infer value.

Although the authors do discuss some other factors that modulate vigor, such as reward history and stimulus uncertainty, they provide such a compelling account of the correlation between vigor and value that it is easy to forget that there is no obligatory one-to-one mapping between the two. To clarify this point, we will consider cases where the usual positive correlation between *expected* value and movement vigor is reversed. These examples serve to highlight that care must be taken when using vigor to infer value.

An inverse relationship between vigor and expected reward: Vanishing expected reward. Shadmehr and Ahmed emphasize that smaller expected reward results in lower vigor. This is not necessarily the case when the reward is only obtainable for a limited amount of time.

Consider a situation where a reward is likely to disappear within a short time-window (e.g., multiple dogs trying to eat from the same bowl with limited food). Here, a fast appetitive movement has a higher probability of obtaining the reward than a slow movement. If the reward is expected to be available for a shorter time, the agent should move faster, but is less likely to obtain the reward; the *expected reward* is smaller. Therefore, in such situations, one sees higher vigor for smaller expected reward (Kue, Avgar, & Fryxell, 2013). The early bird gets the worm.

This scenario reverses the usual relationship between expected reward and vigor, while it remains entirely consistent with optimal foraging theory. To demonstrate this, assume that the probability P that the reward is present decreases linearly over time T (Fig. 1A):

$$P(T) = \begin{cases} 0 & \text{for} \quad T < 0 \\ 1 - \dfrac{T}{T_{\text{end}}} & \text{for} \quad 0 \le T \le T_{\text{end}} \\ 0 & \text{for} \quad T > T_{\text{end}} \end{cases} \tag{1}$$

Therefore, the expected reward $E[r]$ *decreases* as a function of time:

$$E[r] = \begin{cases} \alpha(1 - cT) & \text{for} \;\; 0 \le T \le \dfrac{1}{c} \\ 0 & \text{for} \;\; T > \dfrac{1}{c} \end{cases} \tag{2}$$

where $c = 1/T_{\text{end}}$, and α is the magnitude of the reward *if it is obtained*. We now demonstrate that a *decrease* in expected reward can lead to an *increase* in vigor. Following the authors' convention, we write utility J as the temporally discounted sum of the expected reward $E[r]$ and the effort $e = -AT - B/T$:

$$J(T) = \begin{cases} \dfrac{\alpha(1 - cT) - AT - B/T}{(1 + \gamma T)} & \text{for} \;\; 0 \le T \le \dfrac{1}{c} \\ \dfrac{0 - AT - B/T}{(1 + \gamma T)} & \text{for} \;\; T > \dfrac{1}{c} \end{cases} \tag{3}$$

where A specifies base metabolic rate and B movement cost. γ is the time-discount factor. We can find the optimal movement duration T^* by setting $\mathrm{d}J(T)/\mathrm{d}T = 0$:

$$T^* = \frac{B\gamma + \sqrt{\alpha Bc + \alpha B\gamma + AB + B^2\gamma^2}}{\alpha c + \alpha\gamma + A} \tag{4}$$

This shows that as the reward vanishes sooner (i.e., c increases), the utility J decreases, but the optimum movement speed $V^* = 1/T^*$ increases (Fig. 1B). In other words, when the expected reward is smaller, movement speed is faster.

This effect is ubiquitous in marketing: make a product available for a short period and watch your sales soar. Individuals are faster and more likely to choose a product they think might go out of stock, even if its value is less than its alternatives (Byun & Sternquist, 2012; Inman, Peter, & Raghubir, 1997; Maimaran & Salant, 2019). Thus, the *positive* vigor-expected value correlation is not obligatory, and vigor cannot be easily exploited as an indirect measure of an expected reward as Shadmehr and Ahmed affirm.

Another example: defensive escape behavior. Most of the examples in the book relate to appetitive behavior, which leads to obtaining a reward. But another example of disruption of the positive correlation between vigor and value is that of defensive and avoidance behaviors, in which the increased *negative* valence of a state often results in increased vigor.

Consider a situation in which a given area of space comes with a non-zero *probability* of punishment per unit time (e.g., a room with a cat for a mouse). The mouse will be more incentivized to exit the area if the *probability of harm per unit time* P_h is greater. Assuming P_h is constant, the expected harm from predation is then:

$$E[h] = \int_0^{T_{\text{esc}}} \beta P_h \, \mathrm{d}T = \beta P_h T_{\text{esc}} \tag{5}$$

where β is the harm done if the agent is harmed. Utility of the escape can be written as:

$$J(T) = -\beta P_h T - AT - B/T \tag{6}$$

Thus, the optimal escape duration T^* decreases as P_h increases (Fig. 2):

$$T^* = \frac{B\gamma + \sqrt{B(A + \beta P + B\gamma^2)}}{A + \beta P} \tag{7}$$

Therefore, the more threatening the environment, the more vigorous the escape, even though the absolute utility is always negative. This emphasizes that vigor does not depend on absolute utility *per se*, but rather on differential utility between the current state and

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

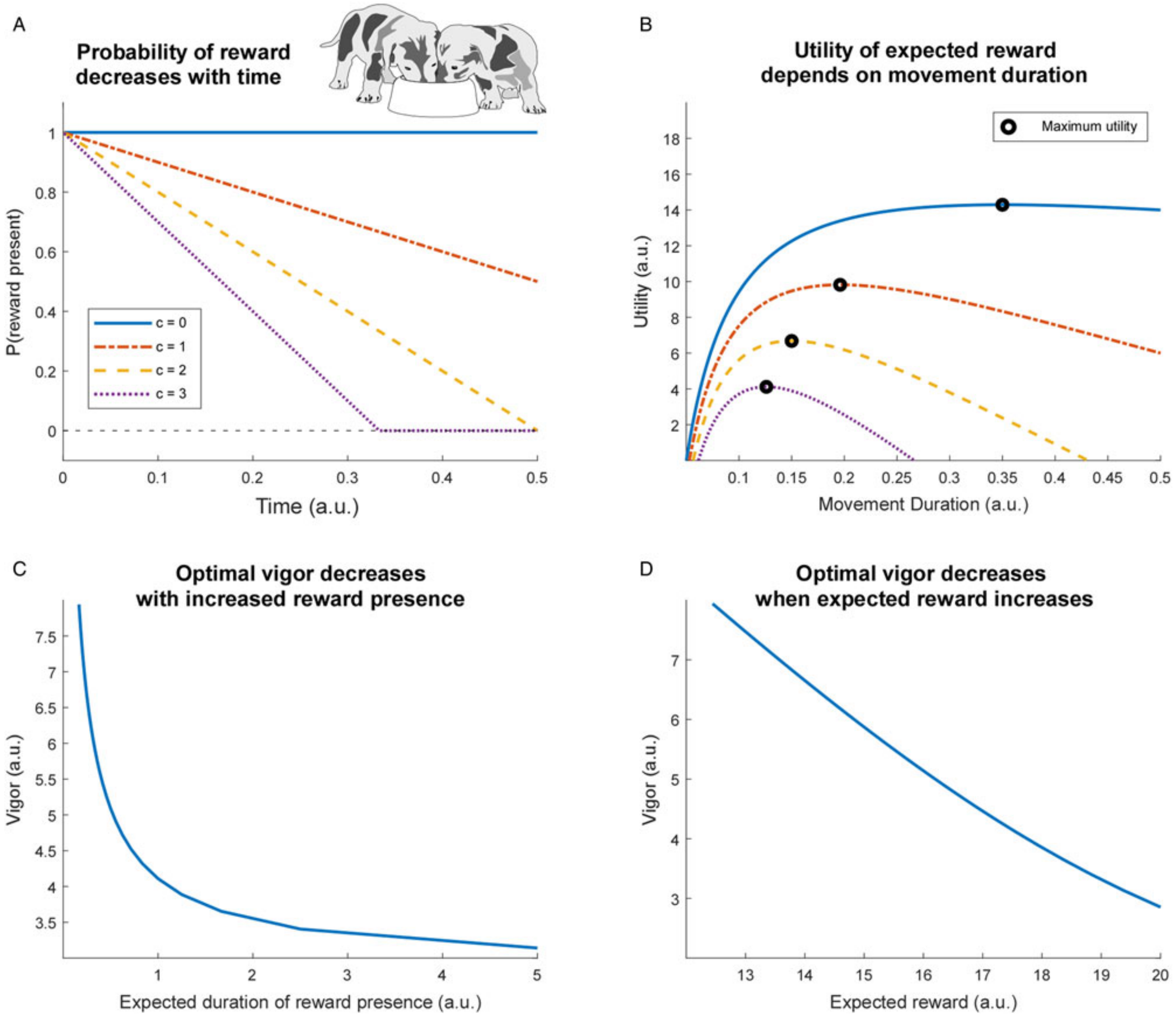

Figure 1 (Bufacchi and Iannetti). Decreasing expected reward can also enhance vigor. (A) We consider a situation in which the probability that a reward is still present decreases linearly with time, proportionally to a constant *c* (e.g., when many dogs try to eat a limited amount of food from the same bowl). (B) The utility of an appetitive movement toward a reward depends on the movement duration. For each value of *c*, the optimum duration is different (the actual reward is a constant value, here set to 20). An expectation that the reward vanishes more quickly (i.e., with higher *c*), corresponds to a shorter optimal movement time (black circles). (C) Therefore, when the reward is expected to be present for a longer time, vigor is lower. (D) Analogously, when expected reward is lowered by time-limiting its availability, movement vigor increases.

the state after the action (Friston et al., 2013; Jocham, Hunt, Near, & Behrens, 2012).

To better appreciate the difference in the effect of cost and reward on vigor, we should start thinking about vigor as a velocity (i.e., a vector) rather than a speed (i.e., a positive scalar). A threatening situation can increase the velocity of a movement, but only of a movement in the direction that decreases cost. Therefore, when attempting to interpret vigor as a readout of value, one should be conscious of the effect of that movement.

Role of dopamine and serotonin in modulating vigor. The authors explain beautifully how dopamine levels in SNr rise in rewarding environments and increase vigor. Serotonin produced in the dorsal raphe nucleus contributes to this effect by tracking reward history and acting as an antagonist to dopamine: it promotes sloth. Highly-rewarding environments thereby increase vigor, whereas low-reward environments produce sloth. However, this account is incompatible with the effect of a threatening environment on vigor that we just demonstrated. Perhaps the solution lies again in not considering vigor to be an absolute (i.e., only positive) scalar variable, but by always bearing in mind its direction. This can resolve the seemingly confusing effect of serotonin, which promotes vigor in stressful environments (Seo et al., 2019). Where dopamine could be seen as promoting attraction, and therefore vigor in appetitive movements, serotonin might be seen as promoting avoidance, slowing appetitive behavior when the threat-level is low, and promoting escape behavior when the threat-level is high.

2. The vigor effect also arises in frameworks other than optimal foraging

Shadmehr and Ahmed explain *why* the vigor effect exists through the ethological optimal foraging framework. Other frameworks such as *reinforcement learning* and *active inference* can equally

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

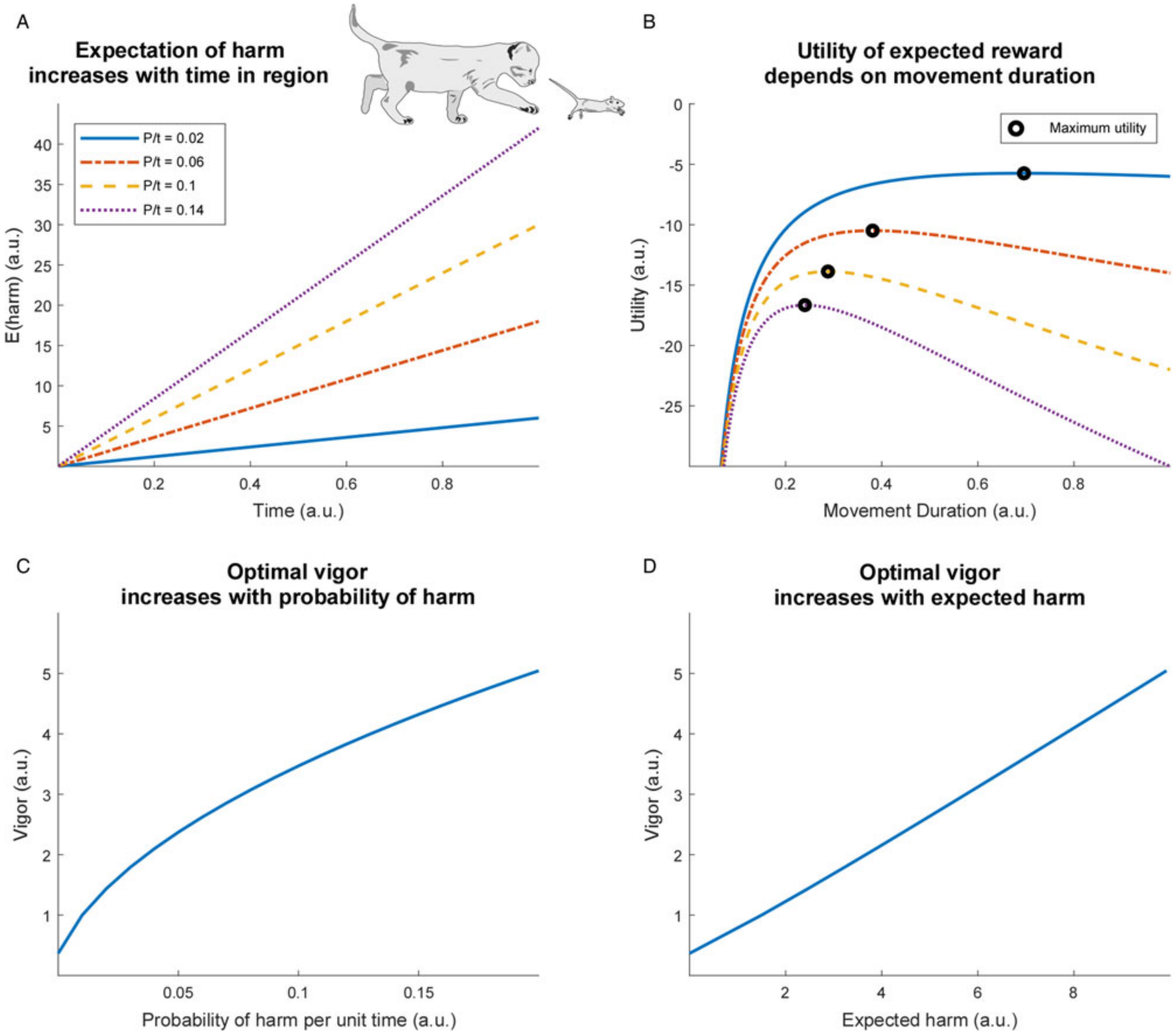

Figure 2 (Bufacchi and Iannetti). Increasing expected harm can enhance vigor. (A) We consider an environment with a fixed probability per unit time (*P*/*t*) that an agent will be harmed (e.g., a room with a cat, for a mouse). As such, the expectation of harm increases linearly with time (the harm that the agent would experience if the dangerous event occurs is a constant value set at −300). (B) The utility of escaping from the dangerous region depends on the movement duration. For each value of *P*/*t*, this optimum duration is different, because moving also entails a cost. Here, greater probability of harm leads to a shorter optimal movement time. (C) Therefore, when probability of harm increases, vigor increases. (D) Analogously, expected harm correlates positively with the vigor of a harm-reducing movement.

provide a *why*, while also having more explanatory power. However, they are more complex, difficult to understand, and thus make it harder to gain clear behavioral insights.

Reinforcement learning (RL). Like in the optimal foraging framework, movements in RL are selected to maximize utility. As a consequence, RL also shows that, all things being equal, more valuable stimuli can result in more vigorous movements (Niv, 2009; Niv, Daw, Joel, & Dayan, 2007). In RL an agent is given the goal to maximize cumulative discounted future reward R by interacting through actions A with its environment. The value Q of performing an action a in a state s_t at time t under a policy π is the expectation E of the discounted cumulative reward R:

$$Q^{\pi}(s_t, a) = E^{\pi}\left[\sum_{i=t}^{\infty} \gamma_{\mathrm{RL}}^{j} R_{t+i} \mid s_t, a\right] \tag{8}$$

where $\gamma_{\mathrm{RL}}^{j} < 1$ is the standard RL discount factor.

This means that RL can result in formulae of utility of action (or value of actions, in RL terminology) very similar to those of optimal foraging. For example, Eq. (3) – an expression of utility under optimal foraging – is the first term of RL Eq. (8), in an RL scenario under the following circumstances:

1) Time steps i of variable length T_i represent one reaching movement
2) Action a_i specifies T_i
3) We define $\gamma_{\mathrm{RL}}^{j} = 1/(1 + \gamma T_i)$
4) We define $R_i = \alpha(1 - cT_i) - AT_i - B/T_i$

Therefore, as Shadmehr and Ahmed themselves mention, "a reinforcement learning framework […] allows for a more dynamic model of learned reward and punishment values in changing environments. For example, in a reinforcement learning framework, one can consider more realistic scenarios in which the

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

value of states in the future depends on the current action." On the other hand, optimal foraging is useful exactly because it simplifies situations to a point where they can be manipulated intuitively, and with more tractable maths.

Active inference. Both RL and optimal foraging can be understood as part of wider frameworks postulating that biological entities aim to keep themselves alive and pass their genes to future generations. Such frameworks state that agents keep certain variables within specific bounds, such as heart rate, temperature, and bodily integrity (Ashby, 1952). Selecting actions to maximize utility is an important part of this story, but not the whole of it. Instead, such wider frameworks show that an agent trying to stay alive will act to maximize utility (like in RL and optimal foraging) but also to explore its environment (Clark, 2013). For example, in *active inference* a direct consequence of staying alive is that "agents should sample […] the parts of the sensory environment that resolve most uncertainty about the causes of their sensations" (Parr & Friston, 2017).

Shadmehr and Ahmed show a strong relationship between certain features of a visual stimulus and the vigor of saccading toward it. They explain this effect through image reward: people prefer looking at faces over white noise. However, saccades contribute strongly to *exploring* the environment, and outside a laboratory they don't often lead directly to a reward. Furthermore, saccade vigor to aversive/threatening images is higher than to neutral stimuli (Schmidt, Belopolsky, & Theeuwes, 2015), and there is little difference in saccade vigor when pleasant and unpleasant scenes are matched (Nummenmaa, Hyönä, & Calvo, 2009). Should one then conclude that aversive and disgusting scenes are also rewarding to the viewer?

This question highlights an issue with the central tenet of the authors' perspective – in some instances, forcing observations to fit a framework not designed to accommodate them becomes detrimental (Chomsky, 1959). Unlike escapes and vanishing rewards, we feel that the vigor of saccades, and especially fast saccades to aversive stimuli, is not easily understood under the optimal foraging framework. Frameworks that do not solely rely on utility to explain actions might be more useful in this case. Notably, active inference provides a strong framework for modeling saccades (Friston, Adams, Perrinet, & Breakspear, 2012; Parr & Friston, 2018).

3. On the use of the term vigor

Throughout the book, the authors give different meaning to the word "vigor." At the beginning, vigor is defined as the inverse of the sum of reaction and movement times. Although this seems to be the running definition, at some point (between-subject) vigor is defined as "the relationship between the velocity-amplitude function for movements of one individual with respect to those of the mean of the population" – a definition clearly excluding reaction times. Elsewhere, it is stated that "manipulating the activity of fovea-related cells in the colliculus alters the reaction time and vigor of the macrosaccade," and "an increase in the effort expenditure […] should dampen changes in vigor and reaction time." In these instances, the authors use vigor as a direct synonym of rotational speed, separately from reaction time.

Besides the definitional inconsistencies in the book, the term "vigor" is commonly understood as denoting strength or liveliness (as shown in the Oxford dictionary, reflecting the Latin etymology). In scientific writing the rationale for choosing a word should be clear. One must be careful of introducing new terms on literary merit. An epistemological perspective could contribute to this discourse: The incontrovertibility of terms rule (Gardiner & Java, 1993) states that within a field of science there should be a one-to-one mapping between terms and meanings. The occasional many-to-many mapping of the word "vigor" in this book might lead to confusion.

Given that there is currently no term that succinctly summarizes reaction and movement time in the way that vigor does, vigor defined as "the inverse of reaction time plus movement time" can be a novel addition to the scientific lexicon of motor control, provided one considers the caveats we have discussed. However, any empirical study demonstrating a correlation between vigor and a given experimental variable would not be complete without dissecting whether the effect of that variable is on either reaction time, movement time, or both. Therefore, we feel that the use of "vigor" as a scientific, rather than an evocative, term is up for debate.

Financial support. This study is supported by the Wellcome Trust Strategic Award (GDI, grant number COLL JLARAXR) and by the ERC Consolidator Grant (GDI, grant number PAINSTRAT).

Conflict of interest. None.

References

Ashby, W. R. (1952). *Design for a brain an introduction to cybernetics*. Chapman & Hall LTD.

Byun, S. E., & Sternquist, B. (2012). Here today, gone tomorrow: Consumer reactions to perceived limited availability. *Journal of Marketing Theory and Practice*, *20*(2), 223–234. https://doi.org/10.2753/MTP1069-6679200207

Chomsky, N. (1959). A review of B. F. Skinner's verbal behavior. *Language*, *35*(1), 26–58.

Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behavioral and Brain Sciences*, *36*(3), 181–204. https://doi.org/10.1017/S0140525X12000477

Friston, K., Adams, R. A., Perrinet, L., & Breakspear, M. (2012). Perceptions as hypotheses: Saccades as experiments. *Frontiers in Psychology*, *3*(MAY), 1–20. https://doi.org/10.3389/fpsyg.2012.00151

Friston, K., Schwartenbeck, P., FitzGerald, T., Moutoussis, M., Behrens, T., & Dolan, R. J. (2013). The anatomy of choice: Active inference and agency. *Frontiers in Human Neuroscience*, *7*(SEP), 1–18. https://doi.org/10.3389/fnhum.2013.00598

Gardiner, J. M., & Java, R. I. (1993). *Recognising and remembering*. Theories of Memory. https://doi.org/10.4324/9781315782119-6

Inman, J. J., Peter, A. C., & Raghubir, P. (1997). Framing the deal: The role of restrictions in accentuating deal value. *Journal of Consumer Research*, *24*(1), 68–79. https://doi.org/10.1086/209494

Jocham, G., Hunt, L. T., Near, J., & Behrens, T. E. J. (2012). A mechanism for value-guided choice based on the excitation-inhibition balance in prefrontal cortex. *Nature Neuroscience*, *15*(7), 960–961. https://doi.org/10.1038/nn.3140

Kue, D., Avgar, T., & Fryxell, J. M. (2013). Density- and resource-dependent movement characteristics in a rotifer. *Functional Ecology*, *27*, 323–328. https://doi.org/10.1111/1365-2435.12065

Maimaran, M., & Salant, Y. (2019). The effect of limited availability on children's consumption, engagement, and choice behavior. *Judgment and Decision Making*, *14*(1), 72–79.

Niv, Y. (2009). Reinforcement learning in the brain. *Journal of Mathematical Psychology*, *53*, 139–154.

Niv, Y., Daw, N. D., Joel, D., & Dayan, P. (2007). Tonic dopamine: Opportunity costs and the control of response vigor. *Psychopharmacology*, *191*(3), 507–520. https://doi.org/10.1007/s00213-006-0502-4

Nummenmaa, L., Hyönä, J., & Calvo, M. G. (2009). Emotional scene content drives the saccade generation system reflexively. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(2), 305–323. https://doi.org/10.1037/a0013626

Parr, T., & Friston, K. J. (2017). The active construction of the visual world. *Neuropsychologia*, *104*(July), 92–101. https://doi.org/10.1016/j.neuropsychologia.2017.08.003

Parr, T., & Friston, K. J. (2018). Active inference and the anatomy of oculomotion. *Neuropsychologia*, *111*(October 2017), 334–343. https://doi.org/10.1016/j.neuropsychologia.2018.01.041

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

Schmidt, L. J., Belopolsky, A. V., & Theeuwes, J. (2015). Potential threat attracts attention and interferes with voluntary saccades. *Emotion (Washington, D.C.)*, *15*(3), 329–338. https://doi.org/10.1037/emo0000041

Seo, C., Guru, A., Jin, M., Ito, B., Sleezer, B. J., Ho, Y. Y., … Warden, M. R. (2019). Intense threat switches dorsal raphe serotonin neurons to a paradoxical operational mode. *Science (New York, N.Y.)*, *363*(6426), 539–542. https://doi.org/10.1126/science.aau8722

Quantum decision corrections for the neuroeconomics of irrational movement control and goal attainment

Kevin B. Clark[a,b,c,d,e,f,g,h]

[a]Felidae Conservation Fund, Mill Valley, CA 94941, USA; [b]Campus and Domain Champions, Extreme Science and Engineering Discovery Environment (XSEDE), National Center for Supercomputing Applications, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA; [c]Expert Network, Penn Center for Innovation, University of Pennsylvania, Philadelphia, PA 19104, USA; [d]Network for Life Detection (NfoLD), NASA Astrobiology Program, NASA Ames Research Center, Mountain View, CA 94035, USA; [e]SETI Institute, Mountain View, CA 94043, USA; [f]Peace Innovation Institute, The Hague 2511, Netherlands and Peace Innovation Institute, Stanford University, Palo Alto, CA 94305, USA; [g]Shared Interest Group for Natural and Artificial Intelligence (sigNAI), Max Planck Alumni Association, 14057 Berlin, Germany and [h]Biometrics and Nanotechnology Councils, Institute for Electrical and Electronics Engineers (IEEE), New York, NY 10016-5997, USA.
kbclarkphd@yahoo.com; www.linkedin.com/pub/kevin-clark/58/67/19a

doi:10.1017/S0140525X21000078, e127

Abstract

Quantum decision theory corrects categorical and propositional logic pathologies common to classic statistical goal-oriented reasoning, such as rational neuroeconomics-based optimal foraging. Within this ecosalient framework, motivation, perception, learning, deliberation, brain computation, and conjunctive risk-order errors may be understood for subjective utility judgments underlying either rational or irrational canonical decisions-actions used to choose, procure, and consume rewarding nutrition with variable fitness.

Through a neuroeconomics lens of optimal foraging, expected utility, brain computation, and central aminergic reward systems, Shadmehr and Ahmed deconstruct classic decision-theory explanations for observed animal and human choice behavior in a badly needed effort to re-synthesize a more convincing adaptationist view of the origins, evolution, and nature of movement control. This root-source analysis leads the authors to justifiably reject outdated automaton traditions that champion the ill-reasoned partitioning of executive decision-making substrate and processes from those of all-or-none stereotypical action-making sequences. For Shadmehr and Ahmed, movement control relies on well integrated, if not entirely reciprocal, functional relationships between decision, motor, and modulator neurocircuits to determine subjective valuation of choice as embodied in modifiable fitness or utility, salience, and vigor of action to execute some goal-oriented plan. Vigor, proportional to the inverse function of time required to complete target-attaining motions, is a more-or-less recently accepted indirect measure of desire or demand in behavioral economics (Haith, Reppert, & Shadmehr, 2012; Niv, Daw, Joel, & Dayan, 2007; Reppert, Lempert, Glimcher, & Shadmehr, 2015; Todorov & Jordan, 2002; Yoon, Jaleel, Ahmed, & Shadmehr, 2020). As a natural proclivity and empirical metric, vigor helps behaviorally contextualize motivation and target worth associated with nonlinear relative fitness or utility of past acquired and new forecasted outcomes, further implying motor control emerged from multilevel ecoevolutionary pressures driving rationality and affect across organism lifespans, generations, and phyla (cf. Clark, 2018).

These broad assertions are narrowly and uniquely epitomized for the authors in one established mathematical framework – classic optimal foraging theory (Stephens & Krebs, 1986). Optimal foraging theory derives from prospect and nonexpected utility theories (Bautista, Tinbergen, & Kacelnik, 2001; Kahneman & Tversky, 1979; Lemon, 1991; Stott, 2006; Tversky & Kahneman, 1992), where utility or specific currency is quantified in global capture rates of optional goods, such as net energetic intake of niche-dispersed variable nutrition over time. Shadmehr and Ahmed use the theory to equate subjective purposefulness of utility with merits of cortical computation, cognitive effort, and weighted experience-dependent selection of movement energetics, precision, patterns or trajectories, magnitudes, latencies, and durations or periods to obtain reward. Optimal foraging theory improves upon the rigid absoluteness of standard utility theory and its psychological constructs of rational selfishness, objective value, and perfect or invariant agent choice of maximized final-state or one-trial utility under risk and uncertainty (Gollier, 2004; Von Neumann & Morgenstern, 1953). Indeed, the theory accounts for both rationality and particular irrational cognitive biases, such as the Allais paradox, by introducing a value function taken from a relative or neutral gains-losses reference point (Kahneman & Tversky, 1979; Stott, 2006), so (mis) perceived wealth variations may be affixed to expected utility to effect rule-of-thumb, strategy, or policy goodness appraisals governed by local and global parameters. When ecological tradeoffs favor local parameters, the marginal value theorem renders policies for nontrivial rational solutions, termed marginal or local returns, which maximize foraging success with spatiotemporal independence. That is, foragers prefer to pick best options with local capture rates backed by accurate knowledge of the status of current food availability and effort expenditures rather than running-average historical values distributed over time and space. Rational preferences at global capture rates may be determined by foragers when global parameters prevail in accurately giving best solutions, termed optimal or global returns, via spatiotemporally aggregate details. Decisions to stay or switch between these two extreme classes of foraging policies, and amounts of movement vigor exerted to minimize opportunity costs in procuring and consuming nutrients, depend on minimax equilibria or stability points between local and global returns in the universal utility probability density matrix or vector space and the thermodynamic-sensitive direction and magnitude of utility-symmetry breaking that produces suboptimal to optimal choice alternatives.

Classic decision theories based on classical probability theory, such as that formalizing popular Bayesian probability, often yield fair approximations of choice behavior and Shadmehr and Ahmed express their belief in the power, internal and external validity, and novel application of optimal foraging theory for better data-fitted descriptions of movement control. The authors, nonetheless, warn complexities in representing risk from subjective values of foraging reward, effort, and time limit the theory's

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

predictive power, as do inconsistencies in estimating time spent collecting food from separate geographical patches or in wasting accessible abundant food sources. Although they attribute rational prediction failures to missing or poorly conceived model parameters, Shadmehr and Ahmed sadly neglect to address major experimentally identified paradoxes linked with stochastic error and other aspects of classic decision theories, damaging their attempt to create a foundational vigor-centered neuroeconomics interpretation of canonical decision and action making. Paradoxes that plaque classic decision theories, including disjunction and conjunction fallacies, Allais paradox, and Ellsberg or planning paradox (Allais, 1953; Shafir & Tversky, 1992; Tversky & Kahneman, 1983; Yukalov & Sornette, 2009), transfer to movement control (Clark & Hassert, 2013) and, therefore, violate classical probability axioms of normative movement-control risk and uncertainty within an optimal foraging approach. Gödelian completeness theorems (1931; Clark & Hassert, 2013) importantly hinder possible development of any practical paradox-free complete and consistent classical neuroeconomics definition of movement control. Perhaps, the top neuroeconomics prescription for categorical and propositional logic paradoxes involves use of quantum cognition or decision theory, a mathematical method regrettably overlooked by Shadmehr and Ahmed. Quite successful in cognitive modeling, quantum decision theory is supported by quantum probability theory, a legitimate mathematics for formally assigning probabilities to events from quantum mechanics without physical constraints (Aerts, 2009; Aerts & Aerts, 1995; Ashtiani & Azgomi, 2015; Beck, 2016; Busemeyer & Bruza, 2011; Busemeyer, Pothos, Franco, & Trueblood, 2011; Chater, 2015; Clark, 2011, 2012a, 2012b, 2014a, 2014b, 2015, 2017, 2020; Favre, Wittwer, Heinimann, Yukalov, & Sornette, 2016; Hu & Loo, 2014; Pothos & Busemeyer, 2013; Yukalov & Sornette, 2014). The axioms of quantum probability theory vary and might result in predictions that diverge, similar to the consequences of classical and relativistic probability axioms (Jumarie, 1980, 1984, 1990; Nielson & Chuang, 2000). However, they also provide necessary degrees of freedom – an infinite Hilbert space of known and hidden vectors representing cognitive-emotional-motor substrate, processes, states, and factors – to accommodate or correct many persistently troublesome pathologies common to prospect or nonexpected optimal foraging, including subjective bias inconsistencies which may irrationally affect accuracy of payoff, work, or time inferences and magnitude of corresponding movement vigor for individual and group decision makers (cf. Clark, 2019; Pothos & Busemeyer, 2009; Yukalov & Sornette, 2010).

Subjective bias inconsistencies in utility judgments are inherent in the complexities of risk representation and may manifest themselves as risk-order deliberation effects caused by conjunctive or disjunctive errors accompanying movement selection and execution, especially for unfamiliar and/or complex goal contexts. Shadmehr and Ahmed, as do other scientists, regard deliberation as a decision parameter bounded by classical probability density matrices that define distributions of rates for neurally integrating stimulus/reward traits and of latency thresholds for inducing behavioral performance. Theoretical models that employ variable rates with constant thresholds predict skewed reaction-time distributions, whereas models employing constant rates with variable thresholds predict normal reaction-time distributions, a poorer match to observed data on reaction time and vigor. Actual and forecasted reward and effort, which confer dissociable value to action utility, proportionately modulate vigor through the same sorts of deterministic and random variables and constants underlying movement deliberation, imbuing instantaneous (e.g., single reward-acquisition trial) or summated (e.g., serial reward-acquisition trials) utility with capacities to bias perception, memory, and deliberation during decision making. But classical probability theory notably cannot fully clarify psychological order effects, such as significant differential judgment values due only to order of perceived, recollected, and/or deliberated information, because all events are represented as probability submatrices of a respective universal matrix with commutative mathematical properties. For instance, the classical joint probability $P(A \cap B) \neq 0$ of event A, with probability submatrix $P_A = \{p_{A1}, \ldots, p_{An}\}$, intersecting event B, with probability submatrix $P_B = \{p_{B1}, \ldots, p_{Bn}\}$, is equivalent for ordered event pairs (A, B) and (B, A). Accordingly, if decision-action A, with risk probability submatrix P_A to not receive payoffs (i.e., opportunity costs), and decision-action B, with risk probability submatrix P_B to not receive payoffs (i.e., opportunity costs), intersect with joint probability $P(A \cap B) \neq 0$, then the joint risk probability or uncertainty of decisions-actions remains identical regardless of the ordered series of movement deliberations. Violation of the commutativity law for equally weighted risks and corresponding utilities and movement vigor for separate, probabilistically joint canonical decisions and actions constitutes a conjunctive error with irrational behavior unexplainable by classic optimal foraging theory. In contrast, quantum probability theory represents events as vectors or closed subspaces of Hilbert space, a universal vector space where conjunction of two such events or decisions-actions A and B may or may not exist (Atmanspacher & Römer, 2012; Wang & Busemeyer, 2015). Conjunction between events or decisions-actions is absent when events or decisions-actions are noncommutative and complementary or mutually exclusive, allowing for random or nonrandom order effects to influence definite deliberation by foragers unable to perform simultaneous or compatible perceptual, attentional, emotive, motivational, pneumonic, and decisional assessments, among other psychological processes necessary for rational motor control.

Conjunctive errors and resultant irrational decision-action risk evaluations resemble other risk-order superstitious behaviors, including the Gambler's Fallacy, where learned increases in behavior frequency, such as riding-out strings of statistically independent losing choices in hope of turning bad luck into prosperity, are caused by accidental or random pairings of reinforcement with behavior and by an inability to logically perceive, calculate, assign, and/or understand real outcome probabilities. Each type of choice bias may become evident when foraging scenarios force actual local and global returns into equilibrium, whether or not both returns are suboptimal, near optimal, or optimal. At equilibrium, a forager earns the same utility at the same elemental and same joint probabilities, despite possible intermittent or continued use of a (naturally or artificially elicited) favorite order policy distinguishing subjective bias and irrationality (i.e., local-before-global vs. global-before-local returns selection). Irrational order effects may be explained with standard learning and cognitive (computation) theory, such as primacy and recency effects due to resource-allocation limitations, priming, or higher-order instrumental learning. Quantum decision theory agrees with classic decision theories on this matter. Quantum decision theory takes a black-box approach, sometimes called cognitive completeness (Tressoldi, Maier, Buechner, & Khrennikov, 2015; Yearsley & Pothos, 2014), which isolates any evaluated cognitive system from the formidable measurement problem of quantum mechanics and information theory. Scientists believe the scalable neurophysiological contents of this black box map onto cognitive states relevant to

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

particular sets of judgments and their corresponding outcome probabilities. Such theoretical elegance in describing complex choice behavior pushes quantum aspects of brain structure and function beyond most current modeling endeavors, although defining computational features of brain areas, cells, and macromolecules, such as those noted by Shadmehr and Ahmed, may be tractable under certain conditions. Evidence from decades of analytical and experimental research continues to oppose the conventional tenet that quantum mechanical phenomena exert, at most, trivial influences over bioprocesses (Davies, 2004). Criticisms still concentrate on the likelihood of biological systems cohering into a quantum regime long enough to accomplish quantum computation. However, issues regarding quantum decoherence, the collapse of the Schrödinger wave function into a single classical or macroscopic state because of thermodynamic processes involving a system and its environment, are less problematic for cellular enzymatic processes reliant on small, thermally-shielded protein reaction sites and/or on local temperature gradients which drive cellular substrate from decoherent to coherent activity.

Considering these points, substrates essential for neuronal computations are connected with quantum operation characteristics, such as cytoskeletal lattices, the citric acid cycle and metabolism, molecule folding, synaptic boutons and vesicles, and autocatalytic second-messenger cascades (Clark, 2012b, 2015, 2017). Quantum effects at both informational and physical degrees of freedom thus seem to appear at every key level of brain structure and function, with activity maintaining capacities to benefit signal coincidence detection and integration, bidirectional synaptic plasticity, and other vital cell functions by rapidly selecting, ordering, and/or counting optional cellular processes (Clark, 2014b). Scaling quantum effects between microscopic and macroscopic physical states, such as that associated with entire brains and probabilistic cognitive events, including perception, recollection, and deliberation, fills the black box of cognitive completeness and affirms a quantum neuroeconomics of rational and irrational movement control and goal attainment.

Conflict of interest. None.

References

Aerts, D. (2009). Quantum structure in cognition. *Journal of Mathematical Psychology*, *53*, 314–348.

Aerts, D., & Aerts, S. (1995). Applications of quantum statistics in psychological studies of decision processes. *Foundations of Science*, *1*, 85–97.

Allais, M. (1953). Le comportement de l'homme rationnel devant le risque, critique des postulats et axiomes de l'eÂcole AmeÂ ricaine. *Econometrica*, *21*, 503–546.

Ashtiani, M., & Azgomi, M. A. (2015). A survey of quantum-like approaches to decision making and cognition. *Mathematical Social Sciences*, *75*, 49–80.

Atmanspacher, H., & Römer, H. (2012). Order effects in sequential measurements of non-commuting psychological observables. *Journal of Mathematical Psychology*, *56*, 274–280.

Bautista, L. M., Tinbergen, J., & Kacelnik, A. (2001). To walk or to fly? How birds choose among foraging modes. *Proceedings of the National Academy of Sciences USA*, *98*, 1089–1094.

Beck, N. (2016). The spontaneous market order and evolution. *Studies on the History and Philosophy of Biological and Biomedical Sciences*, *58*, 49–55.

Busemeyer, J. R., & Bruza, P. (2011). *Quantum models of cognition and decision making*. Cambridge: Cambridge University Press. ISBN-13 978–1107419889.

Busemeyer, J. R., Pothos, E., Franco, R., & Trueblood, J. S. (2011). A quantum theoretical explanation for probability judgment "errors." *Psychological Reviews*, *118*, 193–218.

Chater, N. (2015). Can cognitive science create a cognitive economics? *Cognition*, *35*, 52–55.

Clark, K. B. (2011). Live soft-matter quantum computing. In E. C. Salander (Ed.), *Computer search algorithms* (pp. 1–24). Nova Science Publishers, Inc. ISBN 978-1-61122-527-3.

Clark, K. B. (2012a). A statistical mechanics definition of insight. In A. G. Floares (Ed.), *Computational intelligence* (pp. 139–162). Nova Science Publishers, Inc. ISBN 978-1-62081-901-2.

Clark, K. B. (2012b). Bioreaction quantum computing without quantum diffusion. *NeuroQuantology*, *10*(4), 646–654.

Clark, K. B. (2014a). Evolution of affective and linguistic disambiguation under social eavesdropping pressures. *Behavioral and Brain Sciences*, *37*(6), 551–552.

Clark, K. B. (2014b). Basis for a neuronal version of Grover's quantum algorithm. *Frontiers in Molecular Neuroscience*, *7*, 29.

Clark, K. B. (2015). Insight and analysis problem solving in microbes to machines. *Progress in Biophysics and Molecular Biology*, *119*, 183–193.

Clark, K. B. (2017). Cognitive completeness of quantum teleportation and superdense coding in neuronal response regulation and plasticity. *Proceedings of the Royal Society B: Biological Sciences*. eLetter: https://royalsocietypublishing.org/doi/suppl/10.1098/rspb.2013.3056.

Clark, K. B. (2018). Possible origins of consciousness in simple control over "involuntary" neuroimmunological action. *Consciousness and Cognition*, *61*, 76–78.

Clark, K. B. (2019). Unpredictable homeodynamic and ambient constraints on irrational decision making of aneural and neural foragers. *Behavioral and Brain Sciences*, *42*, e40.

Clark, K. B. (2020). Digital life, a theory of minds, and mapping human and machine cultural universals. *Behavioral and Brain Sciences*, *43*, e98.

Clark, K. B., & Hassert, D. L. (2013). Undecidability and opacity of metacognition in animals and humans. *Frontiers in Psychology*, *4*, 171.

Davies, P. C. W. (2004). Does quantum mechanics play a non-trivial role in life? *BioSystems*, *78*, 69–79.

Favre, M., Wittwer, A., Heinimann, H. R., Yukalov, V. I., & Sornette, D. (2016). Quantum decision theory in simple risky choices. *PLoS ONE*, *11*(12), e0168045.

Gödel, K. (1931). Über formal unentscheidbare Säze der Principia Mathematica und verwandter Systeme I. *Monatshefte für Mathematik und Physik*, *38*, 173–198.

Gollier, C. (2004). *The economics of risk and time*. Cambridge: The MIT Press.

Haith, A. M., Reppert, T. R., & Shadmehr, R. (2012). Evidence for hyperbolic temporal discounting of reward in control of movements. *Journal of Neuroscience*, *32*, 11727–11736.

Hu, Y., & Loo, C. K. (2014). A generalized quantum-inspired decision making model for intelligent agent. *The Scientific World Journal*, *2014*, 240983.

Jumarie, G. (1980). An approach to encoding in the presence of subjectivity. *Journal of Information and Optimization Sciences*, *1*(2), 166–186.

Jumarie, G. (1984). On the consistency between thermodynamic entropy, information entropy, and relativistic information. *Cybernetica*, *27*(2), 93–105.

Jumarie, G. (1990). *Relative information: Theories and applications. Springer Series in Synergetics*. Berlin: Springer-Verlag. ISBN 978–3642840197.

Kahneman, D., & Tversky, A. (1979). An analysis of decision under risk. *Econometrica*, *47* (2), 263–292.

Lemon, W. C. (1991). Fitness consequences of foraging behaviour in the zebra finch. *Nature*, *352*, 153–155.

Nielson, M. A., & Chuang, I. L. (2000). *Quantum computation and quantum information*. Cambridge: Cambridge University Press. ISBN 0-521-63503-9.

Niv, Y., Daw, N. D., Joel, D., & Dayan, P. (2007). Tonic dopamine: Opportunity costs and the control of response vigor. *Psychopharmacology (Berl)*, *191*, 507–520.

Pothos, E. M., & Busemeyer, J. R. (2009). A quantum probability explanation for violations of "rational" decision theory. *Proceedings of Biological Sciences*, *276*, 2171–2178.

Pothos, E. M., & Busemeyer, J. R. (2013). Can quantum probability provide a new direction for cognitive modeling? *Behavioral and Brain Sciences*, *36*, 255–327.

Reppert, T. R., Lempert, K. M., Glimcher, P. W., & Shadmehr, R. (2015). Modulation of saccade vigor during value-based decision making. *Journal of Neuroscience*, *35*, 15369–15378.

Shafir, E., & Tversky, A. (1992). Thinking through uncertainty: Nonconsequential reasoning and choice. *Cognitive Psychology*, *24*, 449–474.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton University Press.

Stott, H. P. (2006). Cumulative prospect theory's functional menagerie. *Journal of Risk and Uncertainty*, *32*, 101–130.

Todorov, E., & Jordan, M. I. (2002). Optimal feedback control as a theory of motor coordination. *Nature Neuroscience*, *5*, 1226–1235.

Tressoldi, P. E., Maier, M. A., Buechner, V. L., & Khrennikov, A. (2015). A macroscopic violation of no-signaling in time inequalities? How to test temporal entanglement with behavioral observables. *Frontiers in Psychology*, *6*, 1061.

Tversky, A., & Kahneman, D. (1983). Extensional versus intuitive reasoning: The conjunctive fallacy in probability judgment. *Psychological Reviews*, *90*, 293–315.

Tversky, A., & Kahneman, D. (1992). Advances in prospect theory: Cumulative representation of uncertainty. *Journal of Risk and Uncertainty*, *5*, 297–323.

Von Neumann, J., & Morgenstern, O. (1953). *Theory of games and economic behavior*. Princeton University.

Wang, Z., & Busemeyer, J. (2015). Reintroducing the concept of complementarity to psychology. *Frontiers in Psychology*, *6*, 1822.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

Yearsley, J. M., & Pothos, E. M. (2014). Challenging the classical notion of time in cognition: A quantum perspective. *Proceedings of the Royal Society London B: Biological Sciences*, *281*, 20133056.

Yoon, T., Jaleel, A., Ahmed, A. A., & Shadmehr, R. (2020). Saccade vigor and the subjective economic value of visual stimuli. *Journal of Neurophysiology*, *123*, 2161–2172.

Yukalov, V. I., & Sornette, D. (2009). Processing information in quantum decision theory. *Entropy*, *11*, 1073–1120.

Yukalov, V. I., & Sornette, D. (2010). Entanglement production in quantum decision making. *Physics of Atomic Nuclei*, *73*, 559–562.

Yukalov, V. I., & Sornette, D. (2014). Conditions for quantum interference in cognitive sciences. *Topics in Cognitive Science*, *6*, 79–90.

Thoughts on vigor in the motor and cognitive domains

Takashi Hanakawa

Integrated Neuroanatomy and Neuroimaging, Kyoto University Graduate School of Medicine, Yoshidakonoe-cho, Sakyo-ku, Kyoto 606-8501, Japan.
hanakawa.takashi.2s@kyoto-u.ac.jp;
https://www.brainteg.med.kyoto-u.ac.jp/

doi:10.1017/S0140525X21000133, e128

Abstract

We feel exhausted after working mentally hard even while just sitting on a chair, suggesting the concept of cognitive vigor. Do movement vigor and cognitive vigor share control mechanisms? Functions of the basal ganglia-cortical circuits, which are regulated by the midbrain dopaminergic system, appear to underlie both movement vigor and cognitive vigor.

In *Vigor: Neuroeconomics of Movement Control*, Shadmehr and Ahmed convince us that the vigor of movements can be measured through movement speeds. It was especially interesting to know preference to stimuli can be inferred from eye movements, that is, speeds of saccade to a preferred target. An appetizing example is something like this. In front of the dessert cart with a couple of plates, if my saccade speed to a plate with a chocolate cake is faster than saccades to the other plates, then I would pick the chocolate cake. This observation will have utility in the real-world situation. I really look forward to visiting a restaurant of the future where an artificial intelligent waitstaff, who monitors my saccades through eye cameras, serves the dessert of my choice before I verbalize.

By Shadmehr and Ahmed, movement vigor is a function of the value of stimulus/contingent behavior and the cost of the movement. The midbrain dopaminergic system, which is widely accepted as the key mechanism of valuation and motivation, seems to play a key role in regulating movement vigor. In humans, progressive loss of dopamine neurons is the central pathology of Parkinson's disease. People with Parkinson's disease are slow in movement (bradykinesia), which likely reflects the loss of movement vigor (Albin & Leventhal, 2017). In genetically engineered mice, progressive loss of dopamine neurons changes firing properties of neurons in the striatum, which receives dopaminergic projections from the midbrain (Panigrahi et al., 2015). Movement vigor is reduced in these mice with dysfunctional striatal neurons. The administration of dopamine precursor restores dopamine tone, recovers the firing patterns of the striatal neurons, and revives movement vigor in these mice.

In the dictionary of the motor domain, vigor is defined as the speed or strength of actions. But, in another dictionary (COBUILD Advanced English Dictionary), vigor is defined as "physical or mental energy and enthusiasm." Therefore, the concept of vigor may be applied to *mental vigor* as well as physical vigor. Indeed, we feel exhausted not only after hard physical exercise but also after intense mental working even while just sitting on a chair physically. This experience especially holds when we need to do the job in rush. A school kid may finish homework of one's favorite subject much quicker than the same homework burden of a compelling yet unfavorite subject. Then, a question arises if the cost–benefit computation of mental energy consumption follows the same rule with that of physical energy consumption. Does mental vigor have similar control mechanisms and neural correlates with motor vigor?

Moving and thinking seem to be distinct. Parkinson's disease has long been considered a pure movement disorder as originally denoted by James Parkinson himself (Parkinson, 1817): "Involuntary tremulous motion, with lessened muscular power, in parts not in action and even when supported; with a propensity to bend the trunk forwards, and to pass from a walking to a running pace: the senses and intellects being uninjured." Hence, the loss of dopamine has long been considered to affect the motor domain only, including the reduction of movement speeds or the loss of motor vigor. Consistently, recent experimental evidence shows that a valuation-related dopaminergic neural population distinctly responds to a stimulus, depending on if the stimulus is going to trigger a motor behavior or not in order to get the same reward (Syed et al., 2016). Dopamine release in the nucleus accumbens is increased in response to a cue for a "Go" task triggering movement but not to a cue for a "NoGo" task requiring a certain period of staying still. These old and new lines of evidence seem to suggest that the loss of dopamine affects motor vigor only.

However, the advent of Parkinson's disease research has expanded of the concept of the disease. Parkinson's disease is now known to present many non-motor symptoms even at an early stage of the disease. One of the possible non-motor symptoms is slowing in thinking (bradyphrenia), which makes sense because it conceptually parallels slowing in movement. But it has been difficult to prove mental slowing in Parkinson's disease (Berardelli, Rothwell, Thompson, & Hallett, 2001). This problem stems, in part, from technical difficulty in measuring cognitive speed especially in people who are slow in movement. Traditional cognitive tasks require motor responses using hand, mouth, or eyes as effector in each trial for behavioral reports. To measure cognitive speeds, past studies measured reaction times, assuming that the processes from cognitive decision to motor responses remain intact. However, people with Parkinson's disease are slow in eye movements (Shaikh & Ghasia, 2019) and speech (Cantiniaux et al., 2010) as well, indicative of generalized reduction of movement vigor following dopamine loss. This makes the reaction time measurement less reliable in Parkinson's disease. An idea is to measure movement time as a control task. Yet, it is likely that people with Parkinson's disease are also slow in motor planning and preparation before motor execution (Berardelli et al., 2001). The prolonged process of motor planning and preparation would make reaction time long, and thus the prolonged reaction time does not necessarily mean lagged cognitive processing even after controlling for movement time.

To detour the problem of reaction time measurements, Sawamoto, Honda, Hanakawa, Fukuyama, and Shibasaki (2002)

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

assessed the accuracy of, rather than the speed of, reports from serial mental operation tasks. The serial mental operation tasks require cognitive operations of working memory contents in response to serially presented visual cues. The behavioral reports were required only at the end of a trial with 10 serial cognitive operations. To measure processing speed through accuracy, the rate of visual cue presentation was manipulated, so that trials with faster rates forced faster cognitive processing than trials with slower rates. As expected, accuracy was declined as a function of the stimulus rate in both healthy elderlies and adults with Parkinson's disease. Of note, the adults with Parkinson's disease showed a steeper decline of rate-dependent accuracy than the healthy elderly controls, supporting the presence of cognitive slowing or bradyphrenia. Moreover, the degree of cognitive slowing was correlated with the bradykinesia subscale of the Unified Parkinson's Disease Raring Scale. This study indicates the correlated reduction of motor vigor and cognitive vigor in people with Parkinson's disease.

The reduction of motor vigor and cognitive vigor in Parkinson's disease suggests that the effects of dopamine loss on vigor extend from the motor domain to the cognitive domain. Hanakawa, Goldfine, and Hallett (2017) extended the serial mental operation tasks used by Sawamoto et al. (2002) back into the motor domain, so that motor vigor and cognitive vigor can be measured with the same method. Study participants included healthy people with various age range and adults with Parkinson's disease. The participants were asked to perform the execution and imagery of finger tapping and mental calculation in response to visually presented cues. The rate of cues was manipulated so that the trials with faster rates forced faster movement, motor imagery and mental calculation than trials with slower rates. Accuracy was decreased as a function of the stimulus rate in all the three tasks, yielding a measure of vigor for the movement, motor imagery, and calculation tasks. A score of agility (a surrogate measure of vigor) was computed through curve fitting of the rate-accuracy function, supporting that adults with Parkinson's disease were slow in movement, motor imagery, and mental calculation. This finding is consistent with the idea that dopamine loss negatively affects motor vigor as well as cognitive vigor. The reduction of motor imagery speed suggests slowing of motor planning in Parkinson's disease, raising further doubt about the assessment with reaction time task to measure cognitive vigor in Parkinson's disease.

To explore the correlates of the reduction of motor vigor and cognitive vigor, Hanakawa, Goldfine, and Hallett (2017) performed a functional magnetic resonance imaging (MRI) experiment using the same paradigm. In healthy participants, activity in the basal ganglia-thalamo-cortical circuits was linearly increased as a function of the stimulus rate in the three tasks. The movement rate was correlated with activity in the motor cortex, and motor sector of the striatum and the thalamus, as revealed by diffusion MRI tractography. The calculation rate was correlated with activity in the cortical language area, and the language sector of the striatum and thalamus. The imagery rate was correlated with activity in the premotor cortex, and the premotor sector of the striatum and thalamus, which underlie motor planning. These three basal ganglia-cortical sub-circuits are largely organized in a parallel manner. Adults with Parkinson's disease, in whom both motor vigor and cognitive vigor were reduced, showed reduction of the activity in the corresponding basal ganglia-cortical sub-circuits, especially in the cortex and the striatum. Thus, the motor and cognitive basal ganglia-cortical circuits appear to underlie the vigor of both movement and cognition.

In conclusion, the converging evidence discussed above provides further support for the relationship between the movement vigor and the striatum receiving dopaminergic projections from the midbrain as claimed by Shadmehr and Ahmed. Furthermore, my claim here is that the concept of vigor may be extended into the non-motor cognitive domains, and cognitive vigor is also likely supported by the midbrain dopaminergic system.

Financial support. This study was supported by the Japan Agency for Medical Research and Development (Brain/MINDS, grant number 19dm0207070s0101; Brain/MINDS Beyond, grant number 19dm0307003h0002); and Japan Society for the Promotion of Science (KAKENHI grant numbers 19H03536 and 18H04960).

Conflict of interest. None.

References

Albin, R. L., & Leventhal, D. K. (2017). The missing, the short, and the long: Levodopa responses and dopamine actions. *Annals of Neurology*, *82*(1), 4–19.

Berardelli, A., Rothwell, J. C., Thompson, P. D., & Hallett, M. (2001). Pathophysiology of bradykinesia in Parkinson's disease. *Brain*, *124*(Pt 11), 2131–2146.

Cantiniaux, S., Vaugoyeau, M., Robert, D., Horrelou-Pitek, C., Mancini, J., Witjas, T., & Azulay, J. P. (2010). Comparative analysis of gait and speech in Parkinson's disease: Hypokinetic or dysrhythmic disorders? *Journal of Neurology Neurosurgery & Psychiatry*, *81*(2), 177–184.

COBUILD Advanced English Dictionary: https://www.collinsdictionary.com/dictionary/english.

Hanakawa, T., & Goldfine, A. M., & Hallett M. (2017). A common function of basal ganglia-cortical circuits subserving speed in both motor and cognitive domains. *eNeuro*, *4*(6), e0200–e0217.

Panigrahi, B., Martin, K. A., Li, Y., Graves, A. R., Vollmer, A., Olson, L., … Dudman, J. T. (2015). Dopamine is required for the neural representation and control of movement vigor. *Cell*, *162*(6), 1418–1430.

Parkinson, J. (1817) *An essay on the shaking palsy*. Sherwood, Neely, and Jones.

Sawamoto, N., Honda, M., Hanakawa, T., Fukuyama, H., & Shibasaki, H. (2002). Cognitive slowing in Parkinson's disease. *Journal of Neuroscience*, *22*(12), 5198–5203.

Shaikh, A. G., & Ghasia, F. F. (2019). Saccades in Parkinson's disease: Hypometric, slow, and maladaptive. *Progress in Brain Research*, *249*, 81–94.

Syed, E. C., Grima, L. L., Magill, P. J., Bogacz, R., Brown, P., & Walton, M. E. (2016). Action initiation shapes mesolimbic dopamine encoding of future rewards. *Nature Neuroscience*, *19*(1), 34–6.

Vigor and aspiration levels in neuroeconomics

Antonio Mastrogiorgio

Laboratory for the Analysis of Complex Economic Systems (AXES), IMT School for Advanced Studies Lucca (Italy), Scuola IMT Alti Studi Lucca, 55100, Lucca, Lu, Italy.
a.mastrogiorgio@imtlucca.it; www.imtlucca.it

doi:10.1017/S0140525X21000182, e129

Abstract

In this contribution, we criticize the demanding assumption of vigor that economic agents are maximizers. We discuss the link between vigor and subjective value through the alternative notion of aspiration levels, arguing that vigor can help articulate the ecological balance – central in bounded and ecological rationality – between minimum expected reward (aspiration level) and the efforts made for its attainment.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

Vigor represents a novel theoretical framework able to shed new light on the economic notion of individual preference. According to Shadmehr and Ahmed (hereafter, the authors), vigor can be used to quantify individual preferences, which, in standard economic theory, do not admit a cardinal representation but only an ordinal one. Indeed, although, in standard economic theory, agents are only able to compare and rank alternatives (so as to indirectly "reveal" their optimum, i.e., Samuelson, 1948), vigor can provide a continuous scale for a direct measurement of subjective value, according to the general hypothesis that the vigor of movements toward things is a proxy of how we value them.

The hypothesized isomorphism between vigor and subjective value is a powerful idea. As such, it should be scrutinized through the arguments of one of the most heated debates in the economics of this past century: precisely, the debate about the nature of subjective value and individual preferences. A significant innovation, dialectical in this debate, was carried out by Herbert A. Simon through the notion of bounded rationality (foundational for behavioral economics), as an alternative to perfect rationality of *homo oeconomicus* (assumed in standard economic theory). Simon's critique relies on the argument that human beings are not maximizers, but *satisficers*, where satisficing is a portmanteau of "satisfice" and "suffice": Economic agents do not compare choice options so as to select their optimum, they simply choose the first available alternative that meets their *aspiration level* (Gigerenzer & Selten, 2002; Simon, 1956). For instance, when we look for a restaurant in a new city, we plausibly choose the first one that is acceptable to us – it reaches the threshold of our own aspiration level – instead of comparing (all) the restaurants of the city. We are aware that, probably, there are better restaurants we are not considering (and, *a fortiori*, we are not comparing), nevertheless this rule works.

If we look at individual preferences through the lens of bounded rationality, we realize that conflating vigor and subjective value is not a neutral idea, as standard economic theory could suggest, and as the authors hypothesize. The central intuition of vigor, according to which (in the authors' own words, p. xi, emphasis added) "*we move faster toward the things that we value more*," takes on a different meaning if aspiration levels come into play. *More than what*? we could ask. We can posit, as the authors do, that we move faster toward the things we value more in absolute terms (upper bound), but, more conservatively, we could hypothesize that we move faster toward the things that surpass our aspiration level (lower threshold). Very importantly, the demarcation between an upper bound (assumed in standard economic theory) and a lower threshold (assumed in bounded rationality) is not a matter of degree on a continuous scale. As vehemently remarked by H. A. Simon on several occasions, aspirational levels do not require a theoretical consistency with sub-optimality, being the notion of satisficing a *tout-court* alternative to both optimality and sub-optimality (e.g., Simon, 1996).

The authors explicitly ascribe the theoretical scope of vigor to standard economic theory stating that "choices are determined by the computation of a utility, a logical process of deliberation that results in the maximization of the gain ascribed to the utility" (p. 69). Indeed, in standard economic theory, choices require the perfect rationality of economic agents, which is instantiated in an omnibus comparison of alternatives based on monotonic preferences. Actually, such instantiation is problematic, considering that transitivity of preferences is often violated (Tversky, 1969; see also Regenwetter, Dana & Davis-Stober, 2011). The existence of an omnibus comparison of alternatives based on monotonic preferences is a demanding assumption – axiomatically postulated in standard economic theory – that the authors embrace as vigorously as uncritically. And this assumption is precisely the one that bounded rationality tries to overcome with a more realistic (where "realistic" is the equivalent of cognitively plausible) explanation of how choices are made *de facto* in ecological settings.

But, if we think that bounded rationality and aspiration levels jeopardize the theoretical scope of vigor as a proxy of subjective value, we could be wrong. Far from playing only the role of *pars destruens*, the notion of aspiration levels is surprisingly consistent with vigor, although the authors do not explore this theoretical link. The idea of utility proposed by the authors – "Utility of an action may be defined as the *reward* expected when the action is completed minus the *effort* required to complete the action, divided by time to acquire the reward" (p. 13, emphasis added) – articulates a fundamental facet of aspiration levels: economic agents conjointly evaluate the expected reward and the costs related to its attainment. Put differently, economic agents seek a satisficing balance between "what they can get" and "to what effort," where the effort is affected by the limited endowment of time, information, and computational capabilities (as postulated in bounded rationality, Simon 1955, 1987). Although in standard economic theory, efforts are ruled out (or, they are modeled as monetary costs, expressed in terms of budget constraints), in bounded rationality and its articulation of ecological rationality (e.g., Gigerenzer & Selten, 2002; Todd & Gigerenzer, 2012), efforts are theoretically central, being related to the procedural dimension of rationality (Simon, 1976) and, in particular, to *search*: efforts signal how much an available alternative is still not worth – the lower threshold is not reached – so that (the action of) search must continue. Using again the restaurant example, we easily realize that in a new city we will keep on searching for a restaurant until we find one that meets our aspiration level.

Although the authors speculate on individual preferences, sitting in the realm of standard economic theory, we believe that bounded and ecological rationality represent the theoretical domains of behavioral economics, on which vigor could have a significant impact for future research. Indeed, a core argument of vigor – the effort of making movements and the benefit of acquiring rewards are conceived within a unitary theoretical framework – is able to articulate the nature of ecological balance (central in bounded and ecological rationality) between aspiration level (the minimum expected reward) and cost of search (the effort made). Using again our previous example about the restaurant, we realize that the rule of choosing the first restaurant that meets our aspiration level, works precisely because it is based on an acceptable balance between efforts and reward. Speculatively, efforts could be considered the "psychophysiological" price to pay for a specific reward. Note that, in bounded and ecological rationality, the ecological balance between efforts and reward is achieved *de facto* through the use of heuristics, which represent adaptive tools able overcome the limited endowment of time, information and computational capabilities of the economic agents (Gigerenzer, 2008). Again with the restaurant example: asking local people or looking at parked cars are common "rules of thumb" used to make inferences about restaurants.

Studying economic choice in ecological settings is a pillar of bounded and ecological rationality, but it is not a mark of standard economic theory. Strangely, despite the authors' consideration of how ecological dimension enters economic choice (in

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

particular, they discuss modal representations of the environment, looking at salience as an alternative to utility maximization, in sect. 2.7) they do not explore this aspect further. If we discard the demanding assumptions of omnibus comparison and maximization (connoting standard economic theory, endorsed by the authors) and, more conservatively, we contemplate the existence of aspiration levels – where subjective value is situated in the neighborhoods of an ecologically salient lower threshold – we will mitigate the Panglossian risk of conflating the adaptive scope of vigor into the teleological need for optimality.

Acknowledgment. A special thanks goes to Enrico Petracca for our discussions on embodied rationality.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

References

Gigerenzer, G. (2008). Why heuristics work. *Perspectives on Psychological Science*, *3*(1), 20–29.
Gigerenzer, G., & Selten, R. (Eds.) (2002). *Bounded rationality: The adaptive toolbox*. MIT Press.
Regenwetter, M., Dana, J., & Davis-Stober, C. P. (2011). Transitivity of preferences. *Psychological Review*, *118*(1), 42.
Samuelson, P. A. (1948). Consumption theory in terms of revealed preference. *Economica*, *15*(60), 243–253.
Simon, H. A. (1955). A behavioral model of rational choice. *The Quarterly Journal of Economics*, *69*(1), 99–118.
Simon, H. A. (1956). Rational choice and the structure of the environment. *Psychological Review*, *63*(2), 129–138.
Simon, H. A. (1976). From substantive to procedural rationality. In T. J. Kastelein, S. K. Kuipers, W. A. Nijenhuis & G. R. Wagenaar (Eds.), *25 Years of economic theory* (pp. 65–86). Springer.
Simon, H. A. (1987). Bounded rationality. In J. Eatwell, M. Milgate & P. Newman (Eds.), *The New Palgrave dictionary of economics* (pp. 266–268). Macmillan.
Simon, H. A. (1996). *The sciences of the artificial* (3rd ed.). Cambridge, MA: MIT Press.
Todd, P. M., & Gigerenzer, G. E. (2012). *Ecological rationality: Intelligence in the world*. Oxford University Press.
Tversky, A. (1969). Intransitivity of preferences. *Psychological Review*, *76*(1), 31.

Construction of Roman roads toward neuroeconomics

Toshiya Matsushima[a,b], Ai Kawamori[c]
and Yukiko Ogura[d]

[a]Faculty of Science, Hokkaido University, Sapporo 060-0810, Japan; [b]Animal Cognition and Neuroscience Laboratory, Center for Mind/Brain, University of Trento, Rovereto 38068, Italy; [c]Risk Analysis Research Center, The Institute of Statistical Mathematics, Tokyo 190-8562 and [d]Graduate School of Information Science and Technology, The University of Tokyo, Tokyo 113-8656, Japan
matusima@sci.hokudai.ac.jp, kawamoriai@gmail.com,
ykk.ogr@gmail.com,
https://www.sci.hokudai.ac.jp/~matusima/chinou3/Matsushima_english.html

doi:10.1017/S0140525X21000303, e130

Abstract

Neuroeconomics is still "under construction." To be a leading discipline, it needs firm ecological rationale and neurobiological bases. "*Vigor*" supplies this infrastructure through the mathematics of the foraging theory and system-neuroscience evidence on utility and motor control. It will prepare us for the future neuroeconomics, if studied appropriately in the light of evolution.

Roman roads represented the core infrastructure of the empire constructed for political and economic unification of the nations. Archeological studies revealed that the roads were constructed with a consistent design while people made the best use of locally available materials. The heavy cost invested in their construction contributed to their exceptional longevity because their design was reasonable. The "construction" of scientific disciplines also ought to be like this.

The science of neuroeconomics, first coined by Glimcher (2003), owes a lot to the concept of optimal foraging in behavioral ecology (Stephens & Krebs, 1986). The patch use model, particularly the marginal value theorem (MVT) introduced by Charnov (1976), had a huge impact on this field because of the transparency of its graphical explanation and applicability to a wide range of animals such as great tits (Cowie, 1977), paper wasps (Kasuya, 1982), starlings (Kacelnik, 1984), and humans (as for information foraging) (Pirolli, 2007). System neuroscientists have designed several behavioral tasks intended to reflect the ecological considerations in their neurophysiological studies.

MVT itself has left room for further sophistication of its mathematical aspects, while system neuroscientists have produced a flood of data ranging from single unit neurophysiology to functional magnetic resonance imaging (fMRI). Unfortunately, the data on the behavior of neurons often lose its relevance to ecological reality. We, therefore, need a good set of both mathematical and ecological theories. In this concise but dense book, the authors revive the classical MVT by adopting canonical mathematical analysis. The authors are also successful in digesting ample neurophysiological data on their mathematical platform, and they formulate clear links between foraging behavior and neuroscience.

In this commentary, we would like to draw attention to several issues that remain unaddressed in this book of "*Vigor*." In chapter 4, the authors focus on superior colliculus (SC), and introduce readers to the two competing systems of SC, namely, one for holding still (fixation) and another for moving (saccade to targets). They construct a clear model of "build-up to threshold" neurons that account for the reaction time. Here arise two questions: (1) How and where is the associated utility computed? (2) What dynamics underlie the choice at the level of the SC and downstream? The authors return to the first question in chapters 5 and 6, but they leave the second question partially addressed.

In recent decades, we have witnessed huge advances in our understanding of the representation of utility in cortical structures such as frontal eye field, lateral intraparietal sulcus, orbitofrontal cortex, and dorsal anterior cingulate cortex (dACC). Of particular importance is the study by Hayden, Pearson, and Platt (2011), which revealed stay-time related neural activities in dACC in a task that mimicked patch-use behavior. The idea of "build-up to threshold for decision making" proved central to understanding the machinery of foraging control. However, a question arises: What determines this threshold? To find the answer, research efforts must be directed toward the sub-SC control in the brainstem.

We may assume that the decision to move occurs in a single step at some higher level of the brain. But we can also consider multiple decision steps distributed along the entire brain/spinal cord network. A study by one of the commentators addresses

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

the control of swimming direction in lamprey spinal cord, which is composed of coupled segmental neural oscillators for locomotor pattern generation. The lamprey instantaneously transitions from forward to backward swimming, and the reversal of the swim direction was reproduced when the caudal segment received stronger excitation than the rostral (Matsushima & Grillner, 1992). A commonly accepted idea is that the brain sends descending signals that change the direction by biased excitation to the caudal spinal cord segments. We may otherwise assume that the brain is informed of the change in swim direction *post-hoc*, only after the spinal network has decided it via inter-segmental interactions. If this is the case, it is implied that the brain center can only predict the swimming direction with uncertainty.

The possibility of multiple decision steps and the involvement of lower brain mechanisms in decision-making lead us to question the evolutionary origin of optimal behaviors. The authors emphasize the role of the cerebral cortex in the computation of utilities (Ch. 5), which probably applies to us humans and most mammals with developed cortical structures. But what about fishes, amphibians, and birds? Lower vertebrates also have layered cortex (Suryanarayana, Robertson, Wallén, & Grillner, 2017), but these are underdeveloped when compared with mammals. Birds have a big cerebrum comparable to that of primates (Olkowicz et al., 2016), but it is not layered and the architecture of telencephalic pallia is different from the mammalian cortex (Shanahan, Bingman, Shimizu, Wild, & Güntürkün, 2013). Do these non-mammalians put up with sub-optimal decisions based on awkward payoff computation because they lack the mammalian-like cerebral cortex? Certainly, they do not.

The book of "*Vigor*" concludes by tentatively assigning serotonin to effort (Ch. 7), and two cited papers are particularly important in this argument. The first paper by Lottem et al. (2018) examined the effects of optogenetic activation of raphe nuclei (serotonergic cells) on foraging tasks. Contrary to the widely accepted idea that serotonin tames animals (i.e., inhibitory control), the study suggests that serotonin promotes resource exploitation and suppresses exploration of new patches; this is in concert with our pharmacological study using serotonin-selective reuptake inhibitor (Matsunami et al., 2012). The second paper is by Cohen, Amoroso, and Uchida (2015), who carefully studied activities of serotonergic neurons and found that (1) tonic activities could represent the global capture rate, whereas (2) transient activities the local capture rate.

The evolutionarily conserved lower brainstem could, therefore, be sufficient for behavioral variables necessary for the control of vigor. If so, how do these serotonergic neurons compute the signals? Do cortical networks instruct the lower brainstem? Or do they uniquely compute the capture rate at the level of the lower brainstem and allow the higher center to be informed of it subsequently? Evolutionary considerations teach us that animals usually make the best use of available "construction materials" to adapt to environmental changes, and rarely innovate new machinery to introduce novel behaviors. The stories of dopamine and serotonin are linked to the phylogenic origins of human neuroeconomics of vigor.

The control of vigor in social setting is another challenging topic that needs to be addressed in the future. When competing for limited resources such as food and mates, animals and humans often invest more efforts; this is known as "social facilitation" (Zajonc, 1965). When foraging together, animals pay more physical effort without an increase in the capture rate (Amita & Matsushima, 2011; in domestic chicks; Ogura, Masamoto, & Kameda, 2020 in humans; Ogura & Matsushima, 2011), therefore they apparently deviate from optimality. Competition also causes impulsive choices, encouraging animals choose small-but-immediate reward more frequently even though the alternative delayed option is larger (Amita, Kawamori, & Matsushima, 2010; also see Ogura, Amita, & Matsushima, 2018 for an adaptive value of impulsiveness). Notably, the social facilitation of effort investment was not impaired by selective depletion of mesolimbic dopamine (Ogura, Izumi, Yoshioka, & Matsushima, 2015). We may have to consider variables other than the local/global capture rates when animals interact.

The field of neuroeconomics is still "under construction." To develop this novel science, we require a lot of "locally available materials" (understanding of foraging behaviors in a variety of animals with different evolutionary and ecological backgrounds) and "a consistent design concept" (common mathematical frameworks). In this book, a gap exists between the concept of metabolic optimization of human locomotion and the mathematical formulations for optimal foraging behaviors (Chs. 1 and 2). Another gap is found between the discussion on the ecology of foraging behavior and the eye movement studies in monkeys, the cortical representations of utility, and the aspects of neuromodulation in mice (Chs. 3, 4, and 5). Despite these few uncomfortable gaps, readers will find the proposed design concept highly valuable, inspiring novel approaches for the unification of different but highly related scientific disciplines of ecology, evolution, economics, and neuroscience in the coming decades.

Financial support. T.M. is supported by Kakenhi from Japan Society for Promotion of Science (JSPS); Grant-in-aid for scientific research (C) JP18K07351 and Promotion of Joint International Research (B) JP19KK0211. A.K. is supported by JSPS Kakenhi; Grant-in-Aid for JSPS Fellows JP19J40208 and Grant-in-Aid for Challenging Research (Exploratory) JP17K18718. Y.O. is supported by JSPS Kakenhi; Grant-in-Aid for Early-Career Scientists JP18K13267.

Conflict of interest. None.

References

Amita, H., Kawamori, A., & Matsushima, T. (2010). Social influences of competition on impulsive choices in domestic chicks. *Biology Letters*, *6*, 183–186. https://doi.org/10.1098/rsbl.2009.0748

Amita, H., & Matsushima, T. (2011). Instantaneous and cumulative influences of competition on impulsive choices in domestic chicks. *Frontiers in Neuroscience*, *5*, 101. https://doi.org/doi: 10.3389/fnins.2011.00101

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*, 129–136.

Cohen, J. Y., Amoroso, M. W., & Uchida, N. (2015). Serotonergic neurons signal reward and punishment on multiple timescales. *eLife*, *4*, e06346. https://doi.org/10.7554/eLife.06346

Cowie, R. J. (1977). Optimal foraging in great tits (*Parus major*). *Nature*, *268*, 137–139. https://doi.org/10.1038/268137a0

Glimcher, P. W. (2003). *Decisions, uncertainty, and the brain, the science of neuroeconomics*. MIT Press.

Hayden, B. Y., Pearson, J. M., & Platt, M. L. (2011). Neuronal basis of sequential foraging decisions in a patchy environment. *Nature Neuroscience*, *14*, 933–939. https://doi.org/10.1038/nn.2856

Kacelnik, A. (1984). Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence time. *Journal of Animal Ecology*, *53*, 283–299. https://doi.org/10.2307/4357

Kasuya, E. (1982). Central place water collection in a Japanese paper wasp, *Polistes Chinensis antennalis*. *Animal Behaviour*, *30*, 1010–1014. https://doi.org/10.1016/S0003-3472(82)80189-9

Lottem, E., Banerjee, D., Vertechi, P., Sarra D., Lohuis, M. O., & Mainen, Z. F. (2018). Activation of serotonin neurons promotes active persistence in a probabilistic foraging task. *Nature Communications*, *9*, 1000. https://doi.org/10.1038/s41467-018-03438-y

Matsunami, S., Ogura, Y., Amita, H., Izumi, T., Yoshioka, M., & Matsushima, T. (2012). Behavioral and pharmacological effects of fluvoxamine on decision-making in food patches and the inter-temporal choices of domestic chicks. *Behavioural Brain Research*, *233*, 577–586. http://dx.doi.org/10.1016/j.bbr.2012.05.045

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

Matsushima, T., & Grillner, S. (1992). Neural mechanisms of intersegmental coordination in lamprey – Local excitability changes modify the phase coupling along the spinal cord. *Journal of Neurophysiology*, *67*, 373–388. https://doi.org/10.1152/jn.1992.67.2.373

Ogura, Y., Amita, H., & Matsushima, T. (2018). Ecological validity of impulsive choice: Consequences of profitability-based short-sighted evaluation in the producer-scrounger game. *Frontiers in Applied Mathematics and Statistics*, *4*, 49. http://dx.doi.org/10.3389/fams.2018.00049

Ogura, Y., Izumi, T., Yoshioka, M., & Matsushima, T. (2015). Dissociation of the neural substrates of foraging effort and its social facilitation in the domestic chick. *Behavioural Brain Research*, *294*, 162–176. https://doi.org/10.1016/j.bbr.2015.07.052

Ogura, Y., Masamoto, T., & Kameda, T. (2020). Mere presence of co-eater automatically shifts foraging tactics toward "Fast and Easy" food in humans. *Royal Society Open Science*, *7*, 200044. http://dx.doi.org/10.1098/rsos.200044

Ogura, Y., & Matsushima, T. (2011). Social facilitation revisited: Increase in foraging efforts and synchronization of running in domestic chicks. *Frontiers in Neuroscience*, *5*, 91. https://doi.org/10.3389/fnins.2011.00091

Olkowicz, S., Kocourek, M., Lučan, R. K., Porteš, M., Fitch, W. T., Herculano-Houzel, S., & Němec, P. (2016). Birds have primate-like numbers of neurons in the forebrain. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 7255–7260. https://doi.org/10.1073/pnas.1517131113

Pirolli, P. (2007). *Information foraging theory, adaptive interaction with information*. Oxford University Press.

Shanahan, M., Bingman, V. P., Shimizu, T., Wild, M., & Güntürkün, O. (2013). Large-scale network organization in the avian forebrain: A connectivity matrix and theoretical analysis. *Frontiers in Computational Neuroscience*, *7*, 89. https://doi.org/10.3389/fncom.2013.00089

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton University Press.

Suryanarayana, S. M., Robertson, B., Wallén, P., & Grillner, S. (2017). The lamprey pallium provides a blueprint of the mammalian layered cortex. *Current Biology*, *27*, 3264–3277. https://doi.org/10.1016/j.cub.2017.09.034

Zajonc, R. B. (1965). Social facilitation. *Science (New York, N.Y.)*, *149*, 269–274. https://doi.org/10.1126/science.149.3681.269

Moving fast and seeing slow? The visual consequences of vigorous movement

Martin Rolfs[a,b] and Sven Ohl[a]

[a]Department of Psychology, Humboldt-Universität zu Berlin, Berlin 10099, Germany and [b]Bernstein Center for Computational Neuroscience Berlin, Berlin 10115, Germany
martin.rolfs@hu-berlin.de; sven.ohl@hu-berlin.de; http://www.rolfslab.de

doi:10.1017/S0140525X2100025X, e131

Abstract

In active agents, sensory and motor processes form an inevitable bond. This wedding is particularly striking for saccadic eye movements – the prime target of Shadmehr and Ahmed's thesis – which impose frequent changes on the retinal image. Changes in movement vigor (latency and speed), therefore, will need to be accompanied by changes in visual and attentional processes. We argue that the mechanisms that control movement vigor may also enable vision to attune to changes in movement kinematics.

In their book *Vigor*, Shadmehr and Ahmed synthesize the vast literature on movement and reward to compose an intriguing thesis: that the kinematics of our movements betray how much we value the goal we move toward. Their core argument is that – at the expense of more effort – we increase movement speed and decrease movement latency to more quickly reach goals that are valuable to us. With a pen for poetry, they craft beautiful examples of vigor and sloth in movements that could fill the pages of a popular science book. But the authors take the reader on a different route, deeper into the material, meticulously building a coherent case for their thesis. This is a scientific *magnum opus* of the kind that is rarely seen these days, by two outstanding scientists in neuroscience and biomechanics, taking a passionate look at the relation between movement and reward through the spectacles of economics. In the first part of their book, they introduce optimal foraging theory as a mathematical framework for their argument, and review the evidence for its quantitative, empirically testable predictions regarding the link between reward and vigor. In the second part of the book, they focus on eye movements, in particular – the motor system that has been studied the most – recasting the classic literature of the neural control of saccades from a neuroeconomic perspective. Weaving together different fields of investigation, their analysis makes a strong case for the proposed link between reward and movement vigor, geared toward maximizing what is known as the global capture rate (i.e., the rewards gained less the efforts spent, in a given time). This link inspires behavioral, electrophysiological, and neurochemical research questions and, more often than not, the authors' predictions across these various levels of analysis are met.

Here, we consider a fundamental consequence of Shadmehr and Ahmed's thesis that remained unexplored throughout their book. In an active agent, movement is wedded to perception more than to any other function of the brain. Saccadic eye movements – the type of movement that the authors focus on throughout the bulk of their book – are a prime example of this bond. Small, fixational eye movements allow the visual system to code space by time (Rucci, Ahissar, & Burr, 2018). Saccades bring the fovea to different parts of the visual scene (Rayner, 2009). And large-scale gaze shifts, involving movement of the head and the trunk, bring new parts of the world into view (Land, 2004). These movements do not only change what we look at, they impose rapid global displacements of the visual scene on the retina that require keeping track of where things are in space (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Wurtz, 2008). Every degree of change in movement vigor, thus, entails an equal degree of change in the perceptual consequences of these movements. Shadmehr and Ahmed briefly allude to this idea, arguing that "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" (p. xii). They calculate that higher movement speeds (as those observed in response to high reward) could reduce this time by 10 min a day, which would yield a gain of many months of seeing over a human lifetime. Although these numbers are flabbergasting, this argument might not age well. We now know that the processing of visual information acquired strictly during a saccade is intact and functional, serving object continuity across saccades and facilitating gaze correction upon saccade landing (Schweitzer & Rolfs, 2020, in press). Thus, reducing the duration of saccade-induced blindness might not be a top priority of this sensorimotor system.

Our point, therefore, is a different one. Imagine you would get a chip implanted that optimized your movement skills – including what is commonly called "muscle memory" and the reward-based mechanisms maintaining speed and accuracy. You would be gifted, say, with the nimble movements of a Parkour master, the rapid dexterity of an E-sports champion, or a professional dancer's finesse in combining intricate body movements. Would you instantly run, play, or dance at their level of skill? We argue that you would not. Just like tuning the engine of a car for higher

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

speed would impose stress on other key parts of the machine (say, the steering, the suspension, or the brakes), an isolated update of the motor and reward system might leave the other core systems of the brain incapable to catch up. This point is most evident for perception – when we alter the way we move, new sensory information arrives at a different rate. More vigorous (i.e., high-speed and low-latency) eye movements, for instance, would require more efficient visual processing, as the sensory consequences of saccades hit the visual system at a quicker pace. Although the speed of looking at a desirable object – such as the candy bar spotlighted by the authors – may reveal its subjective value, the fast movement does not achieve its goal if the visual system is not prepared to apprehend the next part of the scene.

Thus, the efficiency of a sensory system must match the vigor of the movement system that alters its input. To achieve and maintain an appropriate, systemic balance, there appears to be a need for plasticity in perceptual and attentional processes in response to changes in movement vigor. In spelling out this argument, the focus can remain on saccadic eye movements, as they showcase our point prominently. Saccades are visual actions that are inextricably linked to their sensory consequences – every movement of the eyes across the visual scene yields an immediate, equal and opposite movement of the scene across the retina. The perceptual consequences of saccades depend on saccadic peak velocity (Ostendorf, Fischer, Finke, & Ploner, 2007) and the timing of post-saccadic visual information (Balsdon, Schweitzer, Watson, & Rolfs, 2018; Castet, Jeanjean, & Masson, 2002). In addition, even though pre- and intra-saccadic stimuli are routinely omitted from conscious perception (Campbell & Wurtz, 1978; Duyck, Collins, & Wexler, 2016), visual processing remains effective during omission (Watson & Krekelberg, 2009) and serves fundamental visuomotor functions (Schweitzer & Rolfs, 2020, in press). Changes in vigor should thus have immediate consequences for visual processing during and around the time of saccades. Is the visual system prepared to deal with these consequences?

Next to nothing is known about the plasticity of intra-saccadic visual processes (for a first exception, see Scholes, McGraw, & Roach, 2021), so we will focus on another key player in the active visual system – attentional selection. Predictive attentional processes support vision across saccades (Rolfs, 2015). Some 100 ms before the eyes move to a new location, the part of the scene that the saccade aims for stands out from the background (Rolfs & Carrasco, 2012) and can be more easily discerned than other locations in the scene (Deubel & Schneider, 1996; Ohl, Kuper, & Rolfs, 2017). As a consequence of the saccade, objects that have a fixed place in the world rapidly shift to new positions on the retina (e.g., the target of a saccade shifts to the fovea). Pre-saccadic attention enhances performance in a broad range of spatial frequencies, with an emphasis on the highest spatial frequencies that can be resolved (at a given eccentricity), presumably to prepare for foveal processing (Kroell & Rolfs, 2021). At the same time, sensory tuning toward features of the target object sharpens as movement preparation progresses (Li, Barbot, & Carrasco, 2016; Ohl et al., 2017). To keep track of attended objects' changing locations, visual processing relies on the predictive updating of this pre-saccadic attention (Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011), and we have argued that it is this concert of attentional processes that gives rise to perceptual continuity across saccades (Cavanagh et al., 2010; Rolfs, 2015; Rolfs & Szinte, 2016). To maintain perceptual continuity in the face of changes in saccadic vigor, therefore, we need to understand how differences in movement latency and velocity could alter the dynamics of these predictive attentional processes.

We suggest that the pace of information arriving in volleys on the retina itself would allow the visual system to sharpen its attentional priorities in time and space, and increase sensitivity to the features of objects it is going to look at next. One way to achieve that would rely on the same quantity that, in Shadmehr and Ahmed's view, controls movement vigor – reward, harvested at each new fixation. Although the direct impact of reward on pre-saccadic attention (as to our knowledge) has never been investigated, reward does alter visual processing in a way similar to pre-saccadic attention. For instance, reward history strongly shapes attentional selection in favor of high-reward stimuli with corresponding advantages in visual processing (Failing & Theeuwes, 2018). Higher reward improves orientation discrimination by sharpening behavioral orientation tuning functions (Baldassi & Simoncini, 2011), and increases visual sensitivity in response to exogenous spatial cueing (Engelmann & Pessoa, 2007). Correspondingly, stimuli associated with high reward elicit stronger responses in visual cortex and in the attentional control network than low-reward stimuli do (Serences, 2008). Indeed, selection based on reward history as opposed to selective attention seems to be hard to dissociate at a neural level. Curiously, the basal ganglia – a key player in the modulation of vigor according to Shadmehr and Ahmed – are involved in the control of visual attention (Arcizet & Krauzlis, 2018). They may thus constitute a shared origin of simultaneous changes in reward-related priorities for action as well as attentional influences on perception.

The similarities between the consequences of reward and pre-saccadic attention for visual processing suggest that the mechanisms to prepare the visual system for faster (or slower) movements are in place, in that reward serves both the motor and the visual system at the same time. Although the relation between vigor and visual processing remains largely unexplored, some evidence suggests that pursuing a research program in this direction could be fruitful.

First, there is at least one hint that pre-saccadic attention shifts are malleable, and that this plasticity occurs as a consequence of implicit reward. White, Rolfs, and Carrasco (2013) had observers saccade to one of six patches of moving dots. The target location, and the motion direction of each patch, were randomly chosen on each trial. Observers were asked to execute the saccade and discriminate a brief luminance pulse (the probe) displayed some time before movement onset at an unpredictable location. They showed that, just before saccade onset, performance in the luminance discrimination task (their proxy for the deployment of selective attention) was tied specifically to the saccade target location. Interestingly, this spatial specificity was reduced when the probe had appeared at a non-target location on the previous trial. Another way to put this result is that observers paid more attention to non-target locations when they had just made the experience that the perceptual task was spatially dissociated from the saccade target. Along the same vein, if on the previous trial, the motion direction at the probed location matched that of the saccade target, then the current target's motion direction improved performance across all locations. Thus, the recent history of utility of the feature and location of the saccade target was associated with adaptive changes in pre-saccadic attention.

Second, Jonikaitis and colleagues showed that attention shifts more vigorously to the target of a saccade when the imminent movement has a shorter as compared to a longer latency (Jonikaitis & Deubel, 2011). This pattern of results was consistent

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

across many data sets (Jonikaitis & Theeuwes, 2013) and suggests that attention is coupled to movement onset, not to the onset of the instruction to move. A more intriguing aspect of this result, however, is that the dynamics of predictive attentional processes may covary with the vigor of our movements.

Such links between movement and attention provide a rare glimpse at how visual processing covaries with the kinematics of movement control (for another striking example in the domain of perception, see van Heusden, Rolfs, Cavanagh, & Hogendoorn, 2018). Future research should address directly how changes in movement vigor accelerate or decelerate perceptual processes, and how, at the same time, the needs of the visual system may impose constraints on the variability and plasticity of movement vigor.

Financial support. This study was supported by the Deutsche Forschungsgemeinschaft (MR, grant number RO3579/12-1), (SO, grant number OH274/2-2), and the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (MR, Grant agreement number 865715).

Conflict of interest. None.

References

Arcizet, F., & Krauzlis, R. J. (2018). Covert spatial selection in primate basal ganglia. *PLoS Biology*, *16*(10), e2005930.

Baldassi, S., & Simoncini, C. (2011). Reward sharpens orientation coding independently of attention. *Frontiers in Neuroscience*, *5*, 13.

Balsdon, T., Schweitzer, R., Watson, T. L., & Rolfs, M. (2018). All is not lost: Post-saccadic contributions to the perceptual omission of intra-saccadic streaks. *Consciousness and Cognition*, *64*, 19–31.

Campbell, F. W., & Wurtz, R. H. (1978). Saccadic omission: Why we do not see a grey-out during a saccadic eye movement. *Vision Research*, *18*(10), 1297–1303.

Castet, E., Jeanjean, S., & Masson, G. S. (2002). Motion perception of saccade-induced retinal translation. *Proceedings of the National Academy of Sciences*, *99*(23), 15159–15163.

Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences*, *14*(4), 147–153.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837.

Duyck, M., Collins, T., & Wexler, M. (2016). Masking the saccadic smear. *Journal of Vision*, *16*(10), 1–13.

Engelmann, J. B., & Pessoa, L. (2007). Motivation sharpens exogenous spatial attention. *Emotion (Washington, D.C.)*, *7*(3), 668–674.

Failing, M., & Theeuwes, J. (2018). Selection history: How reward modulates selectivity of visual attention. *Psychonomic Bulletin & Review*, *25*(2), 514–538.

Jonikaitis, D., & Deubel, H. (2011). Independent allocation of attention to eye and hand targets in coordinated eye-hand movements. *Psychological Science*, *22*(3), 339–347.

Jonikaitis, D., & Theeuwes, J. (2013). Dissociating oculomotor contributions to spatial and feature-based selection. *Journal of Neurophysiology*, *110*(7), 1525–1534.

Kroell, L. M., & Rolfs, M. (2021). The peripheral sensitivity profile at the saccade target reshapes during saccade preparation, *Cortex*, *139*, 12–26. https://doi.org/10.1016/j.cortex.2021.02.021.

Land, M. F. (2004). The coordination of rotations of the eyes, head and trunk in saccadic turns produced in natural situations. *Experimental Brain Research*, *159*(2), 151–160.

Li, H. H., Barbot, A., & Carrasco, M. (2016). Saccade preparation reshapes sensory tuning. *Current Biology*, *26*(12), 1564–1570.

Ohl, S., Kuper, C., & Rolfs, M. (2017). Selective enhancement of orientation tuning before saccades. *Journal of Vision*, *17*(13), 1–11.

Ostendorf, F., Fischer, C., Finke, C., & Ploner, C. J. (2007). Perisaccadic compression correlates with saccadic peak velocity: Differential association of eye movement dynamics with perceptual mislocalization patterns. *Journal of Neuroscience*, *27*(28), 7559–7563.

Rayner, K. (2009). The 35th Sir Frederick Bartlett Lecture: Eye movements and attention in reading, scene perception, and visual search. *Quarterly Journal of Experimental Psychology*, *62*(8), 1457–1506.

Rolfs, M. (2015). Attention in active vision: A perspective on perceptual continuity across saccades. *Perception*, *44*(8–9), 900–919.

Rolfs, M., & Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. *Journal of Neuroscience*, *32*(40), 13744–13752a.

Rolfs, M., Jonikaitis, D., Deubel, H., & Cavanagh, P. (2011). Predictive remapping of attention across eye movements. *Nature Neuroscience*, *14*(2), 252–256.

Rolfs, M., & Szinte, M. (2016). Remapping attention pointers: Linking physiology and behavior. *Trends in Cognitive Sciences*, *20*(6), 399–401.

Rucci, M., Ahissar, E., & Burr, D. (2018). Temporal coding of visual space. *Trends in Cognitive Sciences*, *22*(10), 883–895.

Scholes, C., McGraw, P. V., & Roach, N. W. (2021). Learning to silence saccadic suppression. *Proceedings of the National Academy of Sciences*, *118*(6), e2012937118.

Schweitzer, R., & Rolfs, M. (2020). Intra-saccadic motion streaks as cues to linking object locations across saccades. *Journal of Vision*, *20*(4):17, 1–24.

Schweitzer, R., & Rolfs, M. (in press). Intra-saccadic motion streaks jump-start gaze correction. *bioRxiv*. https://doi.org/10.1101/2020.04.30.070094.

Serences, J. T. (2008). Value-based modulations in human visual cortex. *Neuron*, *60*(6), 1169–1181.

van Heusden, E., Rolfs, M., Cavanagh, P., & Hogendoorn, H. (2018). Motion extrapolation for eye movements predicts perceived motion-induced position shifts. *Journal of Neuroscience*, *38*, 8243–8250.

Watson, T. L., & Krekelberg, B. (2009). The relationship between saccadic suppression and perceptual stability. *Current Biology*, *19*(12), 1040–1043.

White, A. L., Rolfs, M., & Carrasco, M. (2013). Adaptive deployment of spatial and feature-based attention before saccades. *Vision Research*, *85*, 26–35.

Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, *48*(20), 2070–2089.

Why we don't move: The importance of somatic maintenance and resting

Joshua M. Schrock

Department of Anthropology and Institute for Sexual and Gender Minority Health and Wellbeing, Northwestern University, Chicago, IL 60611, USA.
joshua.schrock@northwestern.edu; jmschrock.com

doi:10.1017/S0140525X21000248, e132

Abstract

A compelling ecological theory of movement and vigor must explain why humans and other animals spend so much time not moving. When we rest, our somatic maintenance systems continue to work. When our somatic maintenance requirements increase, we place greater subjective value on resting. To explain variation in movement and vigor, we must account for the subjective value of resting.

This book is an important contribution to the study of movement. Shadmehr and Ahmed propose that humans and other animals move in ways that maximize the rate of net utility acquired over time. Moving with greater vigor to obtain a reward costs more energy but secures the reward sooner. Thus, vigor is a mechanism that helps us navigate tradeoffs between time and energy costs. An individual's degree of vigor in pursuit of a given reward offers a window into how much subjective value the individual places on that reward.

But a compelling ecological theory of movement and vigor must also explain why humans and other animals spend so much time not moving. As it turns out, the relative utility of resting may explain a lot about when and how much we choose to move.

Resting (i.e., abstaining from effortful movement) is not a reward-neutral behavior. Much like a motivation to feed generates feelings of hunger; a motivation to rest generates feelings of fatigue (Hockey, 2013). The motivation to rest appears to track both internal information (e.g., nutritional status and illness) and external information (e.g., ambient light and environmental

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

hazards) (Hubbard, Ruppert, Gropp, & Bourgin, 2013; Lima, 2005; Schrock, Snodgrass, & Sugiyama, 2019; Spurr, 1983).

When we are at rest, our somatic maintenance systems continue to work – identifying and neutralizing toxins and pathogens, repairing tissue damage, digesting food, and synthesizing proteins for a range of other functions (Snodgrass, 2012). Resting is a behavior that maximizes the metabolic resources available for somatic maintenance. Energy that would otherwise have been spent on movement can instead be spent on somatic maintenance when we are at rest (Westerterp, 2017).

Rest also has other benefits. For example, resting in a safe place may, on average, reduce the risk of predation or pathogen exposure (Hart, 1990; Lima, 2005). Resting is so central to our behavioral repertoires that most humans dedicate at least 6 hours of each 24-hour period to obligate rest, in the form of sleep (Nunn & Samson, 2018). In addition to extended periods of rest at night, human daytime activities are also interspersed with frequent bouts of resting (Munroe et al., 1983).

An individual who moves forfeits the benefits of rest. A motivational system that optimally regulates movement must account for the opportunity costs of giving up rest. For movement to be worthwhile, its net payoff must outweigh the benefits of resting.

The motivation to rest, or at least to minimize movement, is surprisingly strong (Lieberman, 2015). The high subjective value of resting, in the absence of a compelling reason to move, is illustrated by the fact that many of us find it difficult to maintain minimum levels of physical activity recommended by medical experts (Guthold, Stevens, Riley, & Bull, 2018), despite the well-known health benefits and social desirability of being physically active.

Human motivational systems that regulate movement evolved in environments where subsistence required relatively demanding physical work and calorie-dense foods were relatively scarce (Eaton, Konner, & Shostak, 1988; Lieberman, 2015). The evolutionarily novel energetic conditions of many contemporary environments may lead to patterns of movement regulation that are not optimal for long-term cardiometabolic health (Eaton & Eaton, 2003).

The average utility of resting, relative to other behaviors, appears to vary widely across species. For example, a comparative study of time allocation budgets in primates, based on direct behavioral observation of free-living populations, reported that the proportion of observed time spent resting varies from 70.3% in Columbian red howler monkeys to 10.9% in common squirrel monkeys (Pollard & Blumstein, 2008). Differences between primate species in resting time are associated with other key determinants of the energy budget, including brain size, body size, and caloric density of the diet (Schrock, 2020).

Changes in the subjective value of resting can have a profound influence on movement and vigor. For example, humans and other animals typically place a greater subjective value on rest when they are sick compared to when they are healthy (Shattuck & Muehlenbein, 2015). Greater lethargy during sickness has been reported in multiple taxa, including humans (Lasselin et al., 2020a), nonhuman primates (Friedman, Reyes, & Coe, 1996), rodents (Engeland, Nielsen, Kavaliers, & Ossenkopp, 2001), birds (Owen-Ashley & Wingfield, 2007), and amphibians (Llewellyn, Brown, Thompson, & Shine, 2011), suggesting that increased resting when sick is a phylogenetically ancient response. This likely reflects, in part, the high energy costs of activating the immune system to fight infection and repair somatic damage (Horan, Little, Rothwell, & Strijbos, 1989; Muehlenbein, Hirschtick, Bonner, & Swartz, 2010). During illness, calories that are saved by not moving can instead be used to fund the elevated somatic maintenance costs incurred by immune activation (Schrock et al., 2019).

Somatic maintenance costs can be manipulated via administration of lipopolysaccharide (LPS) (Lasselin et al., 2020b). LPS is a molecule found on Gram-negative bacteria. Many of our cells have receptors that detect LPS circulating in the blood supply and in other tissues. When these receptors detect LPS, it triggers a calorically costly inflammatory immune response aimed at fighting bacterial infection (Horan et al., 1989). This inflammatory immune response triggers the classic features of sickness, including lethargy, social withdrawal, reduced appetite, and increased body temperature (Shattuck & Muehlenbein, 2015). The administration of LPS (without causing actual infection) is a commonly used paradigm to study the behavioral and motivation changes that occur during sickness.

One study found that male zebra finches who were housed alone and treated with LPS (to induce sickness) exhibited greater rates of resting behavior compared to male zebra finches who were housed alone and treated with placebo (Lopes, Adelman, Wingfield, & Bentley, 2012). This experiment was repeated with males who were housed in a breeding colony. When housed in the breeding colony, LPS treatment did not lead to increased resting behavior. Apparently, the proximity of potential mates and social competitors provided sufficient alternative motivations to outweigh the sickness-induced motivation to rest. A follow-up study found that LPS-treated birds who spent more time resting exhibited better immune function, as indexed by bacterial killing capacity, haptoglobin-like activity, and ability to modulate body temperature (Lopes, Springthorpe, & Bentley, 2014). This study provides an example of how resting can play a role in promoting effective somatic maintenance.

Sickness does not force an individual to rest. Rather, sickness increases the subjective value of rest. When alternative motivations that require movement are sufficiently compelling, sick individuals will still move to satisfy those motivations (Lopes, 2014).

For example, one study induced sickness by administering LPS to mouse dams with litters of dependent pups (Aubert, Goodall, Dantzer, & Gheusi, 1997). When ambient temperatures were neutral, sick mouse dams reduced their rate of nest building behaviors compared to dams treated with placebo. When experimenters reduced ambient temperatures to colder levels that represented a danger to the pups, sick dams engaged in nearly as much nest building behavior as healthy dams. This study suggests that the increased danger to pups in cold environments generated an alternative motivation sufficiently compelling to at least partially overcome the increased motivation to rest during sickness.

The growing literature on the behavior of sick humans and other animals suggests that the increased subjective value of resting during acute illness is an adaptive response aimed at prioritizing somatic maintenance (Schrock et al., 2019; Shattuck & Muehlenbein, 2015). An alternative hypothesis is that the increased motivation to rest in acutely sick individuals is a pathological byproduct of illness. However, the motivational changes that occur during sickness are mediated by highly organized bidirectional communication circuits between the peripheral immune system and the brain (Maier & Watkins, 1999; McCusker & Kelley, 2013). Such highly organized regulatory systems are unlikely evolve for no reason, much less so if they are a net detriment to survival and reproduction. Furthermore, the broad phylogenetic scope of resting as a response to illness suggests that it has been evolutionarily conserved or that it has evolved independently in different lineages (Lasselin et al.,

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

2020b; Schrock et al., 2019; Shattuck & Muehlenbein, 2015). It should be noted, however, that lethargic states driven by chronic degenerative disease may often be maladaptive (Myers, 2008).

Experiments have demonstrated that sick individuals tend exhibit increased aversion to effort relative to healthy individuals (Vichaya & Dantzer, 2018). In other words, sick individuals perceive a given level effort to be more costly than do healthy individuals. From the viewpoint of resting, this suggests that sickness increases the utility of resting, which, in turn, increases the value a reward must provide in order to make a given level of effort worthwhile.

There has been relatively little direct research on the relationship between sickness and the degree of vigor in patterns of movement. One exception is a study that experimentally induced sickness via LPS administration in human participants and compared walking speed between sick and healthy individuals (Sundelin et al., 2015). The study reported that LPS-treated individuals walked slower than placebo-treated individuals and that individuals who watched films of participants walking rated the LPS-treated individuals as less healthy than placebo individuals. Slower walkers were rated as looking less healthy, sadder, and more tired compared to faster walkers.

Safe doses of LPS can be used to experimentally manipulate sickness in humans and other animals (Lasselin et al., 2020b). The availability of this experimental paradigm opens a wide range of opportunities for novel studies on sickness and movement, including studies of saccade vigor.

Shadmehr and Ahmed briefly touch on resting in one passage of the book, when they discuss a study of locomotion decisions in starlings (Bautista, Tinbergen, & Kacelnik, 2001). The birds were trained to pursue rewards via walking or flying and were allowed to make decisions between walking and flying under varying conditions. The starlings made walk versus fly decisions in a manner that was consistent with maximizing the net rate of energy capture. However, the birds frequently opted not to walk or fly but rested instead. This was viewed as a somewhat puzzling behavior because the net rate of energy capture when resting was always negative. The authors of the starling study surmised that, in some cases, the risk of predation might outweigh the benefits of movement (Bautista et al., 2001). I propose that that somatic maintenance and the utility of rest are missing pieces of the puzzle that would help make sense of scenarios where individuals abstain from effortful movement, including the starling example.

The literature discussed in this commentary suggests that somatic maintenance is a key variable that influences an individual's decisions about whether to rest or move. Given the amount of time that humans and other animals spend resting (Munroe et al., 1983; Pollard & Blumstein, 2008), the utility of resting is not a trivial detail. It should be included in ecological models of vigor and movement.

I have endeavored to show that resting holds utility that the utility of resting varies depending on an individual's circumstances, and that changes in the utility of resting can lead to changes in patterns of movement. I use sickness as an example, but sickness is not the only circumstance that changes the utility of resting. Other factors that may influence the relative utility of resting include nutritional status (Spurr, 1983), physical exertion (Pageaux & Lepers, 2016), ambient light (Hubbard et al., 2013), and gestation (Butte & King, 2005), to name a few. If resting held no utility, we would constantly move through our environments, scooping up any reward we could get our hands on. If we hope to explain variation in movement and vigor, we must account for the utility of resting.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

References

Aubert, A., Goodall, G., Dantzer, R., & Gheusi, G. (1997). Differential effects of lipopolysaccharide on pup retrieving and nest building in lactating mice. *Brain, Behavior, and Immunity*, *11*(2), 107–118.

Bautista, L. M., Tinbergen, J., & Kacelnik, A. (2001). To walk or to fly? How birds choose among foraging modes. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(3), 1089–1094.

Butte, N. F., & King, J. C. (2005). Energy requirements during pregnancy and lactation. *Public Health Nutrition*, *8*(7A), 1010–1027.

Eaton, S. B., & Eaton III, S. B. (2003). An evolutionary perspective on human physical activity: Implications for health. *Comparative Biochemistry & Physiology. Part A, Molecular & Integrative Physiology*, *136*(1), 153–159.

Eaton, S. B., Konner, M., & Shostak, M. (1988). Stone agers in the fast lane: Chronic degenerative diseases in evolutionary perspective. *American Journal of Medicine*, *84* (4), 739–749.

Engeland, C. G., Nielsen, D. V., Kavaliers, M., & Ossenkopp, K.-P. (2001). Locomotor activity changes following lipopolysaccharide treatment in mice: A multivariate assessment of behavioral tolerance. *Physiology and Behavior*, *72*(4), 481–491. https://doi.org/10.1016/s0031-9384(00)00436-4.

Friedman, E. M., Reyes, T. M., & Coe, C. L. (1996). Context-dependent behavioral effects of interleukin-1 in the rhesus monkey (*Macaca mulatta*). *Psychoneuroendocrinology*, *21*(5), 455–468. https://doi.org/10.1016/0306-4530(96)00010-8.

Guthold, R., Stevens, G. A., Riley, L. M., & Bull, F. C. (2018). Worldwide trends in insufficient physical activity from 2001 to 2016: A pooled analysis of 358 population-based surveys with 1.9 million participants. *The Lancet Global Health*, *6*(10), e1077–e1086.

Hart, B. L. (1990). Behavioral adaptations to pathogens and parasites: Five strategies. *Neuroscience & Biobehavioral Reviews*, *14*(3), 273–294.

Hockey, R. (2013). *The psychology of fatigue: Work, effort and control*. Cambridge University Press.

Horan, M. A., Little, R. A., Rothwell, N. J., & Strijbos, P. J. (1989). Comparison of the effects of several endotoxin preparations on body temperature and metabolic rate in the rat. *Canadian Journal of Physiology and Pharmacology*, *67*(9), 1011–1014.

Hubbard, J., Ruppert, E., Gropp, C.-M., & Bourgin, P. (2013). Non-circadian direct effects of light on sleep and alertness: Lessons from transgenic mouse models. *Sleep Medicine Reviews*, *17*(6), 445–452. https://doi.org/10.1016/j.smrv.2012.12.004.

Lasselin, J., Karshikoff, B., Axelsson, J., Akerstedt, T., Benson, S., Engler, H., … Andreasson, A. (2020a). Fatigue and sleepiness responses to experimental inflammation and exploratory analysis of the effect of baseline inflammation in healthy humans. *Brain, Behavior, and Immunity*, *83*, 309–314. https://doi.org/10.1016/j.bbi.2019.10.020.

Lasselin, J., Schedlowski, M., Karshikoff, B., Engler, H., Lekander, M., & Konsman, J. P. (2020b). Comparison of bacterial lipopolysaccharide-induced sickness behavior in rodents and humans: Relevance for symptoms of anxiety and depression. *Neuroscience and Biobehavioral Reviews*, *115*, 15–24. https://doi.org/10.1016/j.neubiorev.2020.05.001.

Lieberman, D. E. (2015). Is exercise really medicine? An evolutionary perspective. *Current Sports Medicine Reports*, *14*(4), 313–319.

Lima, S. L. (2005). Sleeping under the risk of predation. *Animal Behaviour*, *70*(4), 723–736. https://doi.org/10.1016/j.anbehav.2005.01.008.

Llewellyn, D., Brown, G. P., Thompson, M. B., & Shine, R. (2011). Behavioral responses to immune-system activation in an anuran (the cane toad, *Bufo marinus*): Field and laboratory studies. *Physiological and Biochemical Zoology*, *84*(1), 77–86. https://doi.org/10.1086/657609.

Lopes, P. C. (2014). When is it socially acceptable to feel sick? *Proceedings of the Royal Society of London – Series B: Biological Sciences*, *281*(1788), 20140218.

Lopes, P. C., Adelman, J., Wingfield, J. C., & Bentley, G. E. (2012). Social context modulates sickness behavior. *Behavioral Ecology and Sociobiology*, *66*(10), 1421–1428. https://doi.org/10.1007/s00265-012-1397-1.

Lopes, P. C., Springthorpe, D., & Bentley, G. E. (2014). Increased activity correlates with reduced ability to mount immune defenses to endotoxin in zebra finches. *Journal of Experimental Zoology Part A-Ecological Genetics & Physiology*, *321*(8), 422–431.

Maier, S. F., & Watkins, L. R. (1999). Bidirectional communication between the brain and the immune system: Implications for behaviour. *Animal Behaviour*, *57*(4), 741–751. https://doi.org/10.1006/anbe.1998.1068.

McCusker, R. H., & Kelley, K. W. (2013). Immune-neural connections: How the immune system's response to infectious agents influences behavior. *Journal of Experimental Biology*, *216*(Pt 1), 84–98.

Muehlenbein, M. P., Hirschtick, J. L., Bonner, J. Z., & Swartz, A. M. (2010). Toward quantifying the usage costs of human immunity: Altered metabolic rates and hormone levels during acute immune activation in men. *American Journal of Human Biology*, *22*(4), 546–556.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

Munroe, R. H., Munroe, R. L., Michelson, C., Koel, A., Bolton, R., & Bolton, C. (1983). Time allocation in four societies. *Ethnology*, *22*(4), 355–370.

Myers, J. S. (2008). Proinflammatory cytokines and sickness behavior: Implications for depression and cancer-related symptoms. *Oncology Nursing Forum*, *35*(5), 802–807.

Nunn, C. L., & Samson, D. R. (2018). Sleep in a comparative context: Investigating how human sleep differs from sleep in other primates. *American Journal of Physical Anthropology*, *166*(3), 601–612.

Owen-Ashley, N. T., & Wingfield, J. C. (2007). Acute phase responses of passerine birds: Characterization and seasonal variation. *Journal of Ornithology*, *148*(2), 583–591. https://doi.org/10.1007/s10336-007-0197-2.

Pageaux, B., & Lepers, R. (2016). Fatigue induced by physical and mental exertion increases perception of effort and impairs subsequent endurance performance. *Frontiers in Physiology*, *7*, 587. https://doi.org/10.3389/fphys.2016.00587.

Pollard, K. A., & Blumstein, D. T. (2008). Time allocation and the evolution of group size. *Animal Behaviour*, *76*(5), 1683–1699. https://doi.org/10.1016/j.anbehav.2008.08.006.

Schrock, J. M. (2020). *Why our immune systems make us feel sick: Pathologies, adaptations, and evolutionarily novel conditions. Doctoral Dissertation*, University of Oregon, Eugene, Oregon.

Schrock, J. M., Snodgrass, J. J., & Sugiyama, L. S. (2019). Lassitude: The emotion of being sick. *Evolution and Human Behavior*, *41*, 44–57. https://doi.org/10.1016/j.evolhumbehav.2019.09.002.

Shattuck, E. C., & Muehlenbein, M. P. (2015). Human sickness behavior: Ultimate and proximate explanations. *American Journal of Physical Anthropology*, *157*(1), 1–18.

Snodgrass, J. J. (2012). Human energetics. In S. Stinson, B. Bogin & D. O'Rourke (Eds.), *Human biology* (pp. 325–384), Wiley.

Spurr, G. B. (1983). Nutritional status and physical work capacity. *American Journal of Physical Anthropology*, *26*(S1), 1–35. doi: https://doi.org/10.1002/ajpa.1330260503.

Sundelin, T., Karshikoff, B., Axelsson, E., Hoglund, C. O., Lekander, M., & Axelsson, J. (2015). Sick man walking: Perception of health status from body motion. *Brain, Behavior, and Immunity*, *48*, 53–56. https://doi.org/10.1016/j.bbi.2015.03.007.

Vichaya, E. G., & Dantzer, R. (2018). Inflammation-induced motivational changes: Perspective gained by evaluating positive and negative valence systems. *Current Opinion in Behavioral Sciences*, *22*, 90–95. https://doi.org/10.1016/j.cobeha.2018.01.008.

Westerterp, K. R. (2017). Control of energy expenditure in humans. *European Journal of Clinical Nutrition*, *71*(3), 340–344.

Time and the decider

David Spurrett

Department of Philosophy, University of KwaZulu-Natal, Durban, 4041, South Africa.
spurrett@ukzn.ac.za; https://www.researchgate.net/profile/David_Spurrett

doi:10.1017/S0140525X21000194, e133

Abstract

Shadmehr and Ahmed's book is a welcome extension of optimal foraging theory and neuroeconomics, achieved by integrating both with parameters relating to effort and rate of movement. Their most persuasive and prolific data come from saccades, where times before and after decision are reasonably determinate. Skeletal movements are less likely to exhibit such tidy temporal organization.

Shadmehr and Ahmed (2020) give a compelling statement of optimal foraging theory incorporating effort and speed of movement, providing rich targets both for behavioural analysis and for neuroeconomic enquiry into the substrates of selection and control. Their most common and convincing illustrations concern saccades, which are a convenient target for neuroeconomics. Eye movements relative to the skull have a simple geometric organization, with a correspondingly simple topographic representation. Each eye's movements depend on only six specialized muscles, and different movements are strictly mutually exclusive. Eyes rotate around their own centres of mass, making gravitational loads irrelevant. Relative to a stationary head, the relationships between efferent nervous activity and muscle activation, and between muscle activity and movement, are close to direct correspondence. Finally, the "collicular burst" constitutes an uncontroversial culmination of the decision process, clearly demarcating processes before and after it. Varying the reward contingencies associated with cued saccade targets, thus manipulating the *consequences* of movements, while measuring neural activity upstream of oculomotor control is one of the founding experimental paradigms in neuroeconomics (Glimcher & Sparks, 1992; Platt & Glimcher, 1999). Early study measured activity at specific locations in topographic maps of possible movements in advance of cued and rewarded saccades, finding that activity related meaningfully to expected subjective value from those movements, and predicted saccade selection.

Sherrington (1906) introduced the notion of a final common path, referring to the last neural stage at which competition between incompatible deployments of combinations of muscles can be resolved. He recognized that some different movements made conflicting demands on the same muscles. McFarland and Sibly (1975) in turn introduced the notion of a *behavioural* final common path to represent the control processes of a behaving organism, including both perceptual and motor competition. (The qualifier "behavioural" distinguishes their proposal from Sherrington's neural conception.) In highly compressed summary, McFarland and Sibly propose that the revealed preferences of an animal can be represented in a "candidate space" where mutually exclusive actions and activities are ordered along dimensions according to relationships of "displacement" over one another, determining a set of indifference curves. The determinants of the actions and activities of an animal can, in turn, be represented in a "causal factor space" consisting of all variables causally relevant to the animal's behaviour. This space is divided into a "cue space" of external factors to which the animal is sensitive, and a "command space" of internal factors. Considered abstractly, the task of behavioural ecology is to characterize the candidate space, and to determine the structure of the causal factor space, in principle being able to predict how changes in the causal factors will be expressed in behaviour. From this perspective, neuroeconomics can be understood as applying tools of cognitive neuroscience to find the neural basis for value computations in the command space which explain the course of behaviour (Glimcher, 2002). Much neuroeconomic research seeks to identify value representations and computations at or upstream of final common paths, something about which Glimcher (2011) is helpfully explicit. In the case of saccades from a stationary skull, for the reasons glossed above, this task is relatively tractable. Shadmehr and Ahmed's treatment of vigour both articulates the relationships between speed of movement and returns from action, and confirms that neural processes of selection and control are sensitive to these relationships.

Skeletal movements and their corresponding control systems, although, exhibit interacting complications absent in saccades. They are rarely ballistic, involve many more muscles, and often deploy linked series of joints. Most of the enormous variety of possible movements is sensitive to bodily orientation, gravitational loading, inertia, and the disposition and properties of nearby surfaces, which can all change independently of, and because of, the movement itself. As a result, activity in somatotopic maps in the motor cortex doesn't correspond nearly as neatly to bodily movement as it does with fixed-head saccades.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

The *functional* effects of different bodily movements can be substitutable to varying degrees, because different movements can achieve equivalent effects. Movements also stand in highly variable relations of mutual exclusivity, including cases where different goals can be pursued simultaneously. In consequence, the relationships between behavioural function and movement are neither simple nor direct, and opportunity costs harder to determine. Shadmehr and Ahmed are well aware of these considerations (see Shadmehr & Mussa-Ivaldi, 2012), but it is worth focusing on their significance.

There are indeed topographic maps of the body, but the complex mappings noted above mean that different parts of them are relevant to different combinations of functions, movements, and conditions. There aren't determinate final common paths corresponding only to those bodily resources relevant to an effect or function, because many can be achieved in multiple ways. (Some, but not all, ways of removing your spectacles involve your left elbow.) As Gallistel (1980) puts it, this implies that control of skeletal muscles must be expressed through a "lattice hierarchy" in which the level at or before which competition over deployment of degrees of freedom must be resolved is highly variable. Any functional – as opposed to merely anatomical – topographic map or internal model for handling these relationships will have to be abstract and distributed. These considerations pose significant challenges to any attempt to study whole body vigour and its neural control with anything like the temporal specificity available in the saccade case.

Shadmehr and Ahmed, similar to McFarland and Sibly (1975), hold that selection is made in terms of a "currency" which ranks states, or actions conditional on states, in ways that have contributed to success under natural selection (Spurrett, 2021). McFarland and Sibly explicitly specify a *common* currency, but Shadmehr and Ahmed share the presumption of commensurability. McFarland and Sibly note that the hypothesized ranking process, because it should take "all relevant motivational variables" into account, must be "located at a point of convergence in the motivational organization" (1975, p. 290). That is, the supposed optimizing over all of the relevant factors – including bodily needs and their relative evolutionary urgency, the expected costs and returns of available actions, the physics and geometries of the actions themselves in context of the physics and geometry of the environment – requires a place, a "point," where everything comes together. This rings a Dennettian bell.

Dennett has argued that the notion of a determinate "finish line" for the transition to consciousness is untenable over relatively short time-scales, in extended systems such as brains in their bodies which transmit information at finite speeds (Dennett, 1991; Dennett & Kinsbourne, 1992). In such cases, the effective time-ordering of distal events about which information travels at finite speeds isn't generally independent of where and how the determination is made. Dennett's criticism of the pseudo-dualist view he calls "Cartesian materialism," that is, is partly driven by reflection on the implications of the fact that "the 'point' of view of the observer must be smeared over a rather large volume in the observer's brain" (Dennett, 1991, p. 107). This reasoning isn't only relevant to consciousness, and applies to decisions, selection, and control. The shared issue isn't consciousness, but the suggested unproblematic determinacy of times "before," "of," and "after," becoming conscious or being decided. Recall that we're supposing that estimates of all relevant costs – in time, calories, and so on – and rewards in their many modalities are to be integrated into the common currency, and applied to select deployments of the whole body. If we suppose that action selection is comprehensively informed by converging communication from across an extended sensorimotor system, and that there is a definite moment of decision, we need selection to happen at a point, or for there to be a determinate boundary across the lattice hierarchy demarcating events before and after selection. And we must not help ourselves to a supernatural external viewpoint here: Relationships of before and after must be settled by processes operating at the speed of neural activity.

Similar to Cartesian materialism, the view that selection takes place at a determinate moment, let alone at a point, is not openly *defended*. But other things people say and write suggest its influence. McFarland and Sibley's passing reference to a "point of convergence" may be one example. Shadmehr and Ahmed's occasional remarks about the value estimating state of a whole agent at a "moment," or to the rate of reward harvesting at an "instant," and to a determinate "time of decision" suggest it as well. These terms are, of course, meaningful in the mathematical models they are deploying. Those models can be expected to idealize and simplify neural reality, as Shadmehr and Ahmed are fully aware.

Nonetheless, if there can't be a central executive able to integrate everything quickly enough to make selection and control of all skeletal movement consistently sensitive to a single value function responsive to all available information, something else must be going on. If there was a central executive that delayed until all the information was in, the resulting hesitations would be obvious. (Imagine waiting for a whole body "collicular burst" to determine whether to wave hello while walking.) A key feature of Dennett's positive view of consciousness is the simultaneous construction, revision, and propagation of incompletely specified interpretations ("multiple drafts") of the sensorimotor situation, where contingencies in the flow of interaction can contribute to which achieve the celebrity of consciousness, and where represented time can come apart from the temporal course of the vehicles of content. We can imagine an analogous process for selection and control where parallel sensorimotor processes corresponding to opportunities in the environment and occasioned by internal needs estimate the expected costs and returns of taking those opportunities, and compete for execution as long as there's time. Cisek, independently of Dennett and focusing on action selection rather than consciousness, has imagined this, and called it the "affordance competition hypothesis" (Cisek, 2007). This does without the presumption of a determinate finish line by proposing that "the processes of action selection and specification occur simultaneously" (2007, p. 1586). On his view, incoming sensory and bodily information selectively inform the generation of a number of incompletely specified candidate behaviours, which may be released into execution in advance of full specification. (The term "affordances" is from Gibson's [1979] ecological psychology.) Cisek's affordance competition, that is, is a multiple drafts model of action selection and control, in which there's no mandatory bottleneck for all deployments, and specification can sometimes lag behind selection. Shadmehr and Ahmed show that if such a theory is to be taken seriously, candidate actions must vary in vigour, and processes of competition and selection be sensitive to relationships between vigour and reward rate.

It is a likely consequence of this type of view that value-sensitive computation – tracking needs, opportunities, expected costs, and returns of candidate actions – is neurally widespread. Were it not so, the processes corresponding to different actions

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

would be unsuited to flexible and swiftly expressed competition wherever needed in the lattice hierarchy. This picture, offered as a suggested way of talking and thinking that does without the implications of terms like "moment of decision" including the implication of a determinate agent-wide time "before" decision, is potentially consistent with what is revealed in many neuroeconomic experiments. When the expression of choice is severely constrained, when both the options themselves and the means of expressing them kept strictly mutually exclusive, and when time itself is regimented with cues and delays, we might reasonably expect to find that both behaviour and neural processing fit our best theories most neatly. Our best theories should, for reasons Shadmehr and Ahmed convincingly articulate, be sensitive to the importance of vigour. That so many of our most compelling experiments don't discourage interpretation in terms of determinate moments of, and before, choice for the whole agent, however, may tell us less about control on the hoof and in the wild than it does about what it takes to bring value tracking neural processes into empirical focus.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

References

Cisek, P. (2007). Cortical mechanisms of action selection: The affordance competition hypothesis. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *362*, 1585–1599.
Dennett, D. (1991). *Consciousness explained*. Little, Brown.
Dennett, D. C., & Kinsbourne, M. (1992). Time and the observer: The where and when of consciousness in the brain. *Behavioral and Brain Sciences*, *15*, 183–247.
Gallistel, C. R. (1980). *The organisation of action: A New synthesis*. Lawrence Erlbaum.
Gibson, J. J. (1979). *The ecological approach to visual perception*. Houghton Mifflin.
Glimcher, P. (2002). Decisions, decisions, decisions: Choosing a biological science of choice. *Neuron*, *36*, 323–332.
Glimcher, P. (2011). *Foundations of neuroeconomic analysis*. Oxford University Press.
Glimcher, P. W., & Sparks, D. L. (1992). Movement selection in advance of action in the superior colliculus. *Nature*, *355*, 542–545.
McFarland, D. J., & Sibley, R. M. (1975). The behavioural final common path. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *270*, 265–293.
Platt, M. L., & Glimcher, P. W. (1999). Neural correlates of decision variables in parietal cortex. *Nature*, *400*, 233–238.
Shadmehr, R., & Ahmed, A. A. (2020). *Vigor: Neuroeconomics of movement control*. MIT Press.
Shadmehr, R., & Mussa-Ivaldi, S. (2012). *Biological learning and control*. MIT Press.
Sherrington, C. S. (1906). *The integrative action of the nervous systems*. Yale University Press.
Spurrett, D. (2021). The descent of preferences. *British Journal for the Philosophy of Science*, *72*, 485–510.

Vigor of reactive postural responses is set from feedback and feedforward processes

Luis Augusto Teixeira

School of Physical Education and Sport, University of São Paulo, Av. Prof. Mello Moraes, 65. Cidade Universitária, São Paulo, SP 05508-030, Brazil.
lateixei@usp.br

doi:10.1017/S0140525X21000170, e134

Abstract

I explore a distinct perspective from that brought in the book by arguing that in postural control our organism selects the vigor of reactive responses guided by an optimization rule considering first the required postural response for balance recovery as indicated by afferent information from a myriad of sensory receptors, and second the history of previous responses to similar perturbations.

In everyday living, humans are continuously challenged to maintain their body balance against the gravitational force. Particularly, when standing quietly in upright stance, we try to keep our body center of mass at a low energy consumption location over the support base, delimited by the positions of our feet, so that a reduced amount of torque at the ankles is enough to stabilize balance. On the contrary, sudden large-scale balance perturbations, such as tripping or slipping, require energy-consumption vigorous and fast muscular activation throughout the body to prevent a fall. At the first exposure to a perturbation, we are usually able to select a response good and strong enough to allow for balance recovery. Our primary response to an unusual postural perturbation, however, is characterized by poorly coordinated and energetically expensive movements. When suffering repeated balance perturbations, responses become more effective and economic, reducing the magnitude of muscular activation and amplitude of limb movements at the same time that the chance of falling is decreased. In my comments, I will explore a perspective distinct from the core idea brought by Shadmehr and Ahmed in *Vigor: Neuroeconomics of Movement Control* that movement vigor is determined by the amount and rapidity of reward acquisition in relation to the effort expended. Rather, I argue that in postural control our organism selects the vigor of reactive responses to sudden extrinsic perturbations guided by an optimization rule considering two contextual factors. First, the required magnitude of a postural response for balance recovery as indicated by afferent information from a myriad of sensory receptors, and second, the history of previous responses to similar perturbations. In this case, there exists a single relevant and immediately provided reward of achieving successful balance recovery without falling.

As seminal findings supporting my argument, Nashner (1976) compared feet-in-place postural responses to a short set of repetitive displacements of the support base, either through toes-up rotations or backward translations. Results revealed task-specific adaptation over trials, with progressive reduced plantiflexor muscular activation for support base rotations, and progressive increased activation of the same muscles for support base translations. Both muscular response patterns were adaptive, as indicated by increased balance stability in the last as compared to the first perturbation trial. In this classic study, Nashner showed, thus, that response vigor of the plantiflexor muscles was modulated as a function of the particular task requirements for balance recovery and also by the history of consequences from previous responses. Further support for the notion that reactive postural responses are selected on the basis of functional task requirements and history of postural responses to previous perturbations comes from a recent study we conducted by applying stance perturbations leading to forward body sway with magnitudes of 6, 8, and 10% of body mass (Teixeira et al., 2020). Responses were constrained to feet in place reactions to evaluate the effect of load on the

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

magnitude of automatic postural responses at the ankles. One group was exposed to a series of perturbations of progressively increasing load magnitudes, whereas another group faced the opposite decreasing sequence. On the one hand, results showed instantaneous scaling at the very first reactive response to a given perturbation load, with vigor of postural responses corresponding to the magnitude of stance perturbation. On the other hand, the increasing in comparison with the decreasing load sequence led to reduced displacement and velocity of center of pressure under the feet, in parallel with lower activation rate of the agonist plantiflexor muscles. Namely, response magnitude to a given load was decreased or increased depending on whether the previous responses were generated to a lower or to a higher load, respectively. These results indicate that feedback from different sensory receptors signaling fast body sway (e.g., muscle spindles, mechanoreceptors under the feet soles, and vestibular apparatus) guides instantaneously the selection of vigor of postural responses in coherence with the perturbation magnitude, whereas the history of previous responses to a lower or higher load magnitude preset proactively the control system through feedforward processes for down- or up-sizing the postural response vigor.

For repeated similar perturbations vigor of postural responses is diminished, leading to more effective and economic movements. The first perturbation of a sequence has been shown to be featured by excessively strong muscular activation, resulting in exaggerated amplitude of limb and trunk movements (Oude Nijhuis et al., 2009; Tang, Honegger, & Allum, 2012). Interestingly, these strong responses rather than leading to fast recovery of stance stability provokes indeed further balance perturbation. Over repeated perturbations of the same kind, one will see more economic movements associated with increased balance stability. This effect has been explored for improvement of reactive responses in perturbation-based balance training. Results have shown that training reactive balance responses by means of serial perturbations leads to decrement of the following response parameters: (a) hip angular velocity (Krause et al., 2018), (b) number and/or length of compensatory steps (Mansfield, Peters, Liu, & Maki, 2010; McIlroy & Maki, 1995), and (c) amplitude of arms and trunk displacement (Akinlosotu, Alissa, Sorkin, Wittenberg, & Westlake, 2020; Hurt, Rosenblatt, & Grabiner, 2011; Takazono, de Souza, de Oliveira, Coelho, & Teixeira, 2020). Reinforcing the adaptive value of previous exposure to perturbations for selecting response vigor in future events, research has also shown retention of stability gains over time (König et al., 2019; McCrum, Karamanidis, Willems, Zijlstra, & Meijer, 2018), and generalizability of gains to contexts different from that specifically experienced during the perturbation-based balance training (Lee, Bhatt, & Pai, 2016; Takazono et al., 2020). Through different measurements, then, these findings show that the history of previous experiences with perturbatory events to balance stability prospectively attenuates the vigor of ensuing reactive postural responses through feedforward processes, making them at the same time more economic in energy consumption and more effective for balance recovery. Neurophysiologically, response vigor can be thought to be modulated at two control levels. At the lower level, it has been shown that balance training through self-induced perturbations by standing on an unstable support surface leads to attenuation of fast peripheral reactions in the lower limb, as revealed by decreased excitability of the H-reflex following training (Keller, Pfusterschmied, Buchecker, Müller, & Taube, 2012; Taube et al., 2007). At higher control levels, perturbation-based balance training has been shown to lead to increased activation of the prefrontal and parietal cortices (Patel, Bhatt, DelDonno, Langenecker, & Dusane, 2019), which can be thought to underlie adaptive selection and scaling of compensatory responses to unanticipated balance perturbations.

An additional instance supporting the argument that contextual factors guide modulation of vigor of muscular responses can be seen under organismic constraints. In bipedal creatures such as humans, the two legs are coordinated to share the duty of producing muscular forces for maintaining stability of upright balance control. When keeping quiet stance, for example, the two legs share equivalent control responsibilities. In situations that one individual's leg is disabled like in unilateral stroke, the unimpaired leg compensates for the weak responses of the impaired leg in automatic postural reactions to extrinsic stance perturbations (Coelho, Fernandes, Martinelli, & Teixeira, 2019). To study compensatory control between the legs, we recently performed an experiment evaluating reactive lower leg muscular responses to unanticipated forward stance perturbations in the condition that the plantiflexor muscles of one leg only were fatigued (Rinaldin et al., 2021). Results revealed that a low muscular activation of the fatigued leg when responding to stance perturbations was compensated for by stronger muscular activation of the non-fatigued leg in comparison with the pre-fatigue state. As further findings of interest, we observed progressive decrement of muscular activation in the non-fatigued leg over a series of perturbation trials, and an after–effect featured by conservation of greater muscular activation of the non-fatigued leg following fatigue dissipation. In both instances, our findings revealed feedforward processes as previous fatigue-related responses affected ensuing muscular activation for balance recovery. Additionally, the between-leg compensatory control was observed in the medial and lateral gastrocnemii but not in the soleus muscle, suggesting that vigor of muscular activation was set presumably on the basis of the potential contribution of each individual muscle (because of their structural and functional properties) to the aim of reestablishing upright balance following the specific perturbation employed. These results support the perspective that the vigor of reactive postural responses can be predictively up- or down-sized taking into consideration physiological constraints and memory of previous responses.

As concluding remarks, in my comments to *Vigor: Neuroeconomics of Movement Control*, I discussed evidence that vigor of reactive postural responses to sudden extrinsic perturbations to stance stability is modulated on the basis of an optimization rule taking into consideration two contextual factors: The required postural response for balance recovery as signaled by sensory information, and the history of previous responses to similar perturbations. From this perspective, I argue that feedback and feedforward processes interact to determine the vigor with which we respond to extrinsic perturbations to body balance stability.

Financial support. This study was supported by the Brazilian Council of Science and Technology (CNPq), grant number 306323/2019-2.

Conflict of interest. None.

References

Akinlosotu, R. Y., Alissa, N., Sorkin, J. D., Wittenberg, G. F., & Westlake, K. P. (2020). Age-related differences in arm and trunk responses to first and repeated exposure to laterally induced imbalances. *Brain Sciences*, *10*(9), 574. https://doi.org/10.3390/brainsci10090574.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

Coelho, D. B., Fernandes, C. A., Martinelli, A. R., & Teixeira, L. A. (2019). Right in comparison to left cerebral hemisphere damage by stroke induces poorer muscular responses to stance perturbation regardless of visual information. *Journal of Stroke and Cerebrovascular Diseases*, *28*(4), 954–962. https://doi.org/10.1016/j.jstrokecerebrovasdis.2018.12.021.

Hurt, C. P., Rosenblatt, N. J., & Grabiner, M. D. (2011). Form of the compensatory stepping response to repeated laterally directed postural disturbances. *Experimental Brain Research*, *214*, 557–566. https://doi.org/10.1007/s00221-011-2854-1.

Keller, M., Pfusterschmied, J., Buchecker, M., Müller, E., & Taube, W. (2012). Improved postural control after slackline training is accompanied by reduced H-reflexes. *Scandinavian Journal of Medicine & Science in Sports*, *22*(4), 471–477.

König, M., Epro, G., Seeley, J., Catalá-Lehnen, P., Potthast, W., & Karamanidis, K. (2019). Retention of improvement in gait stability over 14 weeks due to trip-perturbation training is dependent on perturbation dose. *Journal of Biomechanics*, *84*, 243–246.

Krause, A., Freyler, K., Gollhofer, A., Stocker, T., Brüderlin, U., Colin, R., … Ritzmann, R. (2018). Neuromuscular and kinematic adaptation in response to reactive balance training – a randomized controlled study regarding fall prevention. *Frontiers in Physiology*, *9*, 1075.

Lee, A., Bhatt, T., & Pai, Y. C. (2016). Generalization of treadmill perturbation to overground slip during gait: Effect of different perturbation distances on slip recovery. *Journal of Biomechanics*, *49*(2), 149–154.

Mansfield, A., Peters, A. L., Liu, B. A., & Maki, B. E. (2010). Effect of a perturbation-based balance training program on compensatory stepping and grasping reactions in older adults: A randomized controlled trial. *Physical Therapy*, *90*(4), 476–491.

McCrum, C., Karamanidis, K., Willems, P., Zijlstra, W., & Meijer, K. (2018). Retention, savings and interlimb transfer of reactive gait adaptations in humans following unexpected perturbations. *Communications Biology*, *1*(1), 1–10.

McIlroy, W. E., & Maki, B. E. (1995). Early activation of arm muscles follows external perturbation of upright stance. *Neuroscience Letters*, *184*(3), 177–180.

Nashner, L. M. (1976). Adapting reflexes controlling the human posture. *Experimental Brain Research*, *26*(1), 59–72.

Oude Nijhuis, L. B., Allum, J. H., Borm, G. F., Honegger, F., Overeem, S., & Bloem, B. R. (2009). Directional sensitivity of "first trial" reactions in human balance control. *Journal of Neurophysiology*, *101*(6), 2802–2814.

Patel, P. J., Bhatt, T., DelDonno, S. R., Langenecker, S. A., & Dusane, S. (2019). Examining neural plasticity for slip-perturbation training: An fMRI study. *Frontiers in Neurology*, *9*, 1181.

Rinaldin, C. D. P., de Oliveira, J. A., de Souza, C. R., Scheeren, E. M., Coelho, D. B., & Teixeira, L. A. (2021). Compensatory control between the legs in automatic postural responses to stance perturbations under single-leg fatigue. *Experimental Brain Research*, *239*(20), 639–653.

Takazono, P. S., de Souza, C. R., de Oliveira, J. Á., Coelho, D. B., & Teixeira, L. A. (2020). High contextual interference in perturbation-based balance training leads to persistent and generalizable stability gains of compensatory limb movements. *Experimental Brain Research*, *238*(5), 1249–1263.

Tang, K. S., Honegger, F., & Allum, J. H. (2012). Movement patterns underlying first trial responses in human balance corrections. *Neuroscience*, *225*, 140–151. doi: 10.1016/j.neuroscience.2012.09.004.

Taube, W., Kullmann, N., Leukel, C., Kurz, O., Amtage, F., & Gollhofer, A. (2007). Differential reflex adaptations following sensorimotor and strength training in young elite athletes. *International Journal of Sports Medicine*, *28*(12), 999–1005.

Teixeira, L. A., Maia Azzi, N., de Oliveira, J. Á., Ribeiro de Souza, C., da Silva Rezende, L., & Coelho, D. B. (2020). Automatic postural responses are scaled from the association between online feedback and feedforward control. *European Journal of Neuroscience*, *51*(10), 2023–2032.

Reducing behavioral dimensions to study brain–environment interactions

David Thura

Lyon Neuroscience Research Center – ImpAct team, Inserm U1028 – CNRS UMR5292 – Lyon 1 University, 69676 Bron, France.
david.thura@inserm.fr; davidthura.com

doi:10.1017/S0140525X21000169, e135

Abstract

Movement vigor provides a window on action valuation. But what is vigor, and how to measure it in the first place? Strikingly, many different co-varying vigor-related metrics can be found in the literature. I believe this is because vigor, just like the neural circuits that determine it, is an integrated, low-dimensional parameter. As such, it can only be roughly estimated.

In *Vigor: Neuroeconomics of Movement Control*, Shadmehr and Ahmed convincingly argue that movement vigor can be used as a proxy to measure how the brain assigns value to action goals (Shadmehr & Ahmed, 2020). The authors demonstrate that because goal-oriented decisions and actions involve some kind of "economic" computations in which effort, time, and reward are evaluated, subjects react and move more vigorously when the option is more desirable (i.e., they value it more), and conversely slow their behavior in the prospect of unpleasant events.

Although appealing, this proposal lacks an important precision in my opinion: What is vigor, and how to measure it in the first place? The notion of vigor is rather intuitive, but it's commonly associated with very different behavioral variables in the system neuroscience literature. Vigor sometimes refers to movement speed and/or duration (Muhammed, Dalmaijer, Manohar, & Husain, 2020; Thura, Cos, Trung, & Cisek, 2014), to speed or duration scaled by amplitude (Baraduc, Thobois, Gan, Broussolle, & Desmurget, 2013; Berret, Castanier, Bastide, & Deroche, 2018; Choi, Vaswani, & Shadmehr, 2014; Reppert, Lempert, Glimcher, & Shadmehr, 2015; Reppert et al., 2018; Thura, 2020), to movement kinematics and reaction times (Milstein & Dorris, 2007; Sedaghat-Nejad, Herzfeld, & Shadmehr, 2019; Summerside, Shadmehr, & Ahmed, 2018), or to reaction times only (Griffiths & Beierholm, 2017; Guitart-Masip, Beierholm, Dolan, Duzel, & Dayan, 2011). Vigor is also sometimes qualified via the rate of responses (Dezfouli, Balleine, & Nock, 2019; Niv, Daw, Joel, & Dayan, 2007), the level of engagement, arousal, or motivation in a task (Mazzoni, Hristova, & Krakauer, 2007; Turner & Desmurget, 2010).

Despite a lack of consistent definition, it is safe, however, to say that most of the vigor-related metrics listed above strongly co-vary with each other: Increasing movement speed for a given amplitude typically reduces its duration and increases its energetic cost; or increasing movement amplitude increases its duration and speed. The same problem arises for the notion of "value," which is naturally confounded by many factors, including pleasure, curiosity, pain, and so on, and for which the existence of a proper neural substrate is still debated despite decades of investigations (Ballesta, Shi, Conen, & Padoa-Schioppa, 2020; Hayden & Niv, 2020). In their book, Shadmehr and Ahmed demonstrate that movement vigor is actually another confounding factor that one should take into account in order to identify the neural circuits of valuation. Recent publications even suggest that valuation and motor invigoration are two undistinguishable functions, mediated by shared/common neural networks (Collins & Frank, 2016; Hayden & Niv, 2020).

Beyond semantic debates (Baker, Lansdell, & Kording, 2021; Brette, 2019; Cisek, 1999), one might wonder why the brain would bother having to compute multiple discrete quantities that are all so tightly linked? Wouldn't it benefit, in terms of accuracy-energy expenditure trade-off, from computing fewer

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

but integrated quantities that capture, if not all, most of parameters variability? In this view, movement vigor would approximate the reciprocal of the chosen behavior duration (or its speed) that integrates the context-dependent reward rate computation based on costs (opportunity and energy) and rewards. Because each individual perceives reward and costs differently, vigor is idiosyncratic in nature (Berret et al., 2018; Reppert et al., 2018). And because in a given task, different motor repertoires serve different goals (e.g., exploration vs. interaction), oculomotor vigor should not necessarily co-vary with arm movement vigor, or locomotion vigor. Thura et al. (2014), for instance, report in monkey that saccade velocity is less influenced by reward rate than reach velocity in a reaching decision-task. Reppert et al.'s (2018) also show in human that vigor, defined here as a "latent" variable, is shared among skeletomuscular motor modalities, but has no relationship with oculomotor behavior. Thus, by establishing a desired level of vigor for a given goal, the brain does not necessarily need to separately compute movement planning and execution durations, speed, and acceleration, and can even maybe flexibly exchange deliberation time for movement planning/execution time depending on the subject's needs and preferences (Reynaud, Saleri Lunazzi, & Thura, 2020).

Most of the recent neurophysiological results fit an integrated view of neural organization (Cisek & Kalaska, 2010). For example, studies on monkey have long reported that dorsal premotor (PMd) and primary motor (M1) neurons vary their activity as a function of movement duration, velocity, acceleration and distance (see Kalaska, 2009 for a review). More surprisingly, these motor neurons also "encode" estimation of elapsing time (Renoult, Roux, & Riehle, 2006) and reward (Ramkumar, Dekleva, Cooler, Miller, & Kording, 2016). Perhaps even more dramatically, dopamine neurons have been shown to be crucial for action valuation during reinforcement learning (e.g., Glimcher, Dorris, & Bayer, 2005; Lee, Seo, & Jung, 2012), to be a key component of the neural circuits that regulate the effort and motivation required to obtain a reward (e.g., Jurado-Parras et al., 2020; Salamone et al., 2016), and to determine the level of vigor with which the selected movement is executed (Collins & Frank, 2016; da Silva, Tecuapetla, Paixão, & Costa, 2018; Panigrahi et al., 2015; Rueda-Orozco & Robbe, 2015; Yttri & Dudman, 2016; Zenon, Devesse, & Olivier, 2016).

How such a degree of neural integration, at least for some brain areas, is related to "good-enough" policies at the behavior level is an open question. Yet, monkey and human studies indicate that subjects rarely aim for "perfection" or optimality during tasks execution in the lab. In the motor domain for instance, participants typically perform highly variable movements (in terms of speed and accuracy) as long as those actions still lead to rewards. Similarly, human decision-makers easily adopt heuristics approaches in a large number of decision conditions, sometimes more successfully than if they opted for a rational strategy (Gigerenzer & Gaissmaier, 2011). In the optimal foraging context, Shadmehr and Ahmed (2020) note that "the actual behavior of animal disagrees with the exact formulation of the theory in a number of experiments" (p. 73). Therefore, many situations seem to favor goal-driven good-enough policies dictated by an accuracy-energy expenditure trade-off much more than rational and normative operations requiring a vast *a priori* knowledge of the world as well as costly computations of multiple low-level behavioral parameters. Interestingly, some sub-optimal behavioral patterns have been proposed to emerge from pre-wired neural organizations and pre-defined computations (Buzsáki, 2019).

A given behavior emerges because integrated, distributed, and recurrent neural activities take place in a body surrounded by an environment, in service of a goal (Gomez-Marin & Ghazanfar, 2019). We thus need to address behavior from the viewpoint of the brain, considering why and how its species-specific circuits successfully evolved over time to control interactions with the world (Cisek, 2019; Jourjine & Hoekstra, 2021). To this end, neglecting behavior would obviously be an error (Cisek & Kalaska, 2010; Krakauer, Ghazanfar, Gomez-Marin, MacIver, & Poeppel, 2017; Niv, 2020). But could it be that "over-analyzing" behavior turns out to be ultimately more misleading than insightful? We all know that studying behavior in a lab means immediately giving up many aspects of real-life behavior. In addition, because behaviors are complex and variable, tasks often decouple parameters in a given number of dimensions of the full outputs space, allowing one to observe whether neural activity follows more closely one or the other of the decoupled parameters (Reimer & Hatsopoulos, 2009). In such tasks though, animal's behavior deviates even further from its ethological repertoire, calling into question our ability to ultimately map this behavior with the neural circuits shaped by millions years of interactions with the external world in natural conditions. Even when a task is ethologically compatible, one should avoid, at least initially, to over-decompose behavior during data analysis, considering that the same neural circuit can generate different behavior patterns as long as the animal's goal is reached (Katz, 2016). In other words, just as dimension reduction of neural activities may reveal how neural circuits operate and compute (Humphries, 2020; Kalaska, 2019; Saxena & Cunningham, 2019; Vyas, Golub, Sussillo, & Shenoy, 2020), a heuristics-oriented "dimensions reduction" of the behavioral variables under investigation might be fruitful too if one hopes to eventually shed light on the brain–behavior mapping mystery.

One way to implement this strategy in neuroscience studies is to complement and compare "controlled" experiments with tests made in "naturalistic" settings, using hypothesis-based and ethologically-relevant tasks, and to initially analyze integrated behavioral parameters only. Although more challenging technically, especially for studies on large animals, recent developments in unconstrained *in-vivo* electrophysiology methods (Berger, Agha, & Gail, 2020) combined with virtual reality systems (Dombeck & Reiser, 2012; Noel et al., 2021) or powerful AI-based pose estimation algorithms (Mathis et al., 2018) should make this naturalistic approach more accessible in the near future.

For example, a naturalistic setting would allow one to test a recent hypothesis about the role of the monkey basal ganglia (BG) in the selective invigoration of behavioral repertoires (Cisek & Thura, 2018). In this proposal, the monkey premotor/motor and posterior parietal cortices are organized in "zones" of ethologically relevant types of motor repertoires, such as reaching or climbing movements (Graziano, 2006). The dopamine-dependent putamen neurons receive massive inputs from all cortical areas and project to downstream structures of the BG organized as segregated functional modules (Grillner & Robertson, 2016) connected to a given cortical zone, via connections in the

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

thalamus. Now imagine a cage designed so that a monkey can adopt a "foraging" behavior and interact at its convenience with two touch screens, one accessible from the lower part of the cage, the other placed higher up. Each screen displays visual stimuli associated with evolving cost/reward contingencies. The monkey would have the choice to directly reach the screen in front of him ("exploitation" decisions, within a given behavioral repertoire) or, as the animal would do in a tree, move in the cage ("exploration" decisions, between behavioral repertoires) to place himself in front of the other screen and start a new sequence of exploitation decisions. With wireless neural recordings and a set of video cameras installed in the cage, we could assess whether during exploitation, the reaching repertoire is selected and invigorated whereas the other repertoires (climbing, walking, eating, etc.) are suppressed through the cortico-BG-thalamo-cortical loops, and whether deliberations within the selected repertoire are resolved through competitions in cortical areas (Cisek, 2007; Thura & Cisek, 2017).

To summarize, I argue in this commentary that behavioral neuroscience, including my own work, suffers from a temptation to "disintegrate" behavior so that artificially defined subsystems appear more easy to investigate. I believe that such an approach confuses terminology, encourages unnatural behavior, and eventually limits the production of insightful evidence about what neural systems have been designed for. I agree with Shadmehr and Ahmed that movement vigor informs us about how we value our actions. However, as an evaluation tool, a clear definition of vigor and quantification methods is lacking. I believe this is because vigor is one of the low-dimensional parameters that approximate how long and/or how fast the brain interacts with its environment given particular circumstances. Consequently, vigor cannot be precisely quantified, but only roughly characterized based on arbitrary-selected decision and/or movement variables.

Acknowledgments. I thank Fadila Hadj-Bouziane, Amélie J. Reynaud, and Clara Saleri for their comments on the manuscript.

Financial support. D.T. is funded by an ATIP/Avenir (Inserm/CNRS) grant.

Conflict of interest. None.

References

Baker, B., Lansdell, B., & Kording, K. (2021). A philosophical understanding of representation for neuroscience. *ArXiv*:2102.06592, 15.

Ballesta, S., Shi, W., Conen, K. E., & Padoa-Schioppa, C. (2020). Values encoded in orbitofrontal cortex are causally related to economic choices. *Nature*, *588*(7838), 450–453. https://doi.org/10.1038/s41586-020-2880-x.

Baraduc, P., Thobois, S., Gan, J., Broussolle, E., & Desmurget, M. (2013). A common optimization principle for motor execution in healthy subjects and Parkinsonian patients. *Journal of Neuroscience*, *33*(2), 665–677. https://doi.org/10.1523/JNEUROSCI.1482-12.2013.

Berger, M., Agha, N. S., & Gail, A. (2020). Wireless recording from unrestrained monkeys reveals motor goal encoding beyond immediate reach in frontoparietal cortex. *eLife*, *9*, e51322. https://doi.org/10.7554/eLife.51322.

Berret, B., Castanier, C., Bastide, S., & Deroche, T. (2018). Vigour of self-paced reaching movement: Cost of time and individual traits. *Scientific Reports*, *8*(1), 10655. https://doi.org/10.1038/s41598-018-28979-6.

Brette, R. (2019). Is coding a relevant metaphor for the brain? *Behavioral and Brain Sciences*, *42*, e215. https://doi.org/10.1017/S0140525X19000049.

Buzsáki, G. (2019). *The brain from inside out*. Oxford University Press.

Choi, J. E. S., Vaswani, P. A., & Shadmehr, R. (2014). Vigor of movements and the cost of time in decision making. *Journal of Neuroscience*, *34*(4), 1212–1223. https://doi.org/10.1523/JNEUROSCI.2798-13.2014.

Cisek, P. (1999). Beyond the computer metaphor: Behaviour as interaction. *Journal of Consciousness Studies*, *6*(11–12), 125–142.

Cisek, P. (2007). Cortical mechanisms of action selection: The affordance competition hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1485), 1585–1599. https://doi.org/10.1098/rstb.2007.2054.

Cisek, P. (2019). Resynthesizing behavior through phylogenetic refinement. Attention, Perception, *& Psychophysics*, *81*(7), 2265–2287. https://doi.org/10.3758/s13414-019-01760-1.

Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience*, *33*(1), 269–298. https://doi.org/10.1146/annurev.neuro.051508.135409.

Cisek, P., & Thura, D. (2018). Neural circuits for action selection. In D. Corbetta & M. Santello (Eds.), *Reach-to-grasp behavior: Brain, behavior, and modelling across the life span* (pp. 91–118). Taylor & Francis Group.

Collins, A. G. E., & Frank, M. J. (2016). Surprise! Dopamine signals mix action, value and error. *Nature Neuroscience*, *19*(1), 3–5. https://doi.org/10.1038/nn.4207.

da Silva, J. A., Tecuapetla, F., Paixão, V., & Costa, R. M. (2018). Dopamine neuron activity before action initiation gates and invigorates future movements. *Nature*, *554*(7691), 244–248. https://doi.org/10.1038/nature25457.

Dezfouli, A., Balleine, B. W., & Nock, R. (2019). Optimal response vigor and choice under non-stationary outcome values. *Psychonomic Bulletin & Review*, *26*(1), 182–204. https://doi.org/10.3758/s13423-018-1500-3.

Dombeck, D. A., & Reiser, M. B. (2012). Real neuroscience in virtual worlds. *Current Opinion in Neurobiology*, *22*(1), 3–10. https://doi.org/10.1016/j.conb.2011.10.015.

Gigerenzer, G., & Gaissmaier, W. (2011). Heuristic decision making. *Annual Review of Psychology*, *62*(1), 451–482. https://doi.org/10.1146/annurev-psych-120709-145346.

Glimcher, P. W., Dorris, M. C., & Bayer, H. M. (2005). Physiological utility theory and the neuroeconomics of choice. *Games and Economic Behavior*, *52*(2), 213–256. https://doi.org/10.1016/j.geb.2004.06.011.

Gomez-Marin, A., & Ghazanfar, A. A. (2019). The life of behavior. *Neuron*, *104*(1), 25–36. https://doi.org/10.1016/j.neuron.2019.09.017.

Graziano, M. (2006). The organization of behavioral repertoire in motor cortex. *Annual Review of Neuroscience*, *29*(1), 105–134. https://doi.org/10.1146/annurev.neuro.29.051605.112924.

Griffiths, B., & Beierholm, U. R. (2017). Opposing effects of reward and punishment on human vigor. *Scientific Reports*, *7*(1), 42287. https://doi.org/10.1038/srep42287.

Grillner, S., & Robertson, B. (2016). The basal ganglia over 500 million years. *Current Biology*, *26*(20), R1088–R1100. https://doi.org/10.1016/j.cub.2016.06.041.

Guitart-Masip, M., Beierholm, U. R., Dolan, R., Duzel, E., & Dayan, P. (2011). Vigor in the face of fluctuating rates of reward: An experimental examination. *Journal of Cognitive Neuroscience*, *23*(12), 3933–3938. https://doi.org/10.1162/jocn_a_00090.

Hayden, B. Y., & Niv, Y. (2020). The case against economic values in the brain. PsyArXiv Preprints. https://doi.org/10.31234/osf.io/7hgup.

Humphries, M. D. (2020). Strong and weak principles of neural dimension reduction. *ArXiv:2011.08088 [q-Bio]*. http://arxiv.org/abs/2011.08088.

Jourjine, N., & Hoekstra, H. E. (2021). Expanding evolutionary neuroscience: Insights from comparing variation in behavior. *Neuron*, *109*(7), 1084–1099. https://doi.org/10.1016/j.neuron.2021.02.002.

Jurado-Parras, M.-T., Safaie, M., Sarno, S., Louis, J., Karoutchi, C., Berret, B., & Robbe, D. (2020). The dorsal striatum energizes motor routines. *Current Biology, 16*; *30*(22), 4362–4372, e6. https://doi.org/10.1016/j.cub.2020.08.049.

Kalaska, J. F. (2009). From intention to action: Motor Cortex and the control of reaching movements. In D. Sternad (Ed.), *Progress in motor control* (Vol. *629*, pp. 139–178). Springer US. https://doi.org/10.1007/978-0-387-77064-2_8.

Kalaska, JF (2019). Emerging ideas and tools to study the emergent properties of the cortical neural circuits for voluntary motor control in non-human primates. *F1000Research*, *8*(F1000 Faculty Rev):749. https://doi.org/10.12688/f1000research.17161.1.

Katz, P. S. (2016). Evolution of central pattern generators and rhythmic behaviours. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1685), 20150057. https://doi.org/10.1098/rstb.2015.0057.

Krakauer, J. W., Ghazanfar, A. A., Gomez-Marin, A., MacIver, M. A., & Poeppel, D. (2017). Neuroscience needs behavior: Correcting a reductionist bias. *Neuron*, *93*(3), 480–490. https://doi.org/10.1016/j.neuron.2016.12.041.

Lee, D., Seo, H., & Jung, M. W. (2012). Neural basis of reinforcement learning and decision making. *Annual Review of Neuroscience*, *35*(1), 287–308. https://doi.org/10.1146/annurev-neuro-062111-150512.

Mathis, A., Mamidanna, P., Cury, K. M., Abe, T., Murthy, V. N., Mathis, M. W., & Bethge, M. (2018). DeepLabCut: Markerless pose estimation of user-defined body parts with deep learning. *Nature Neuroscience*, *21*(9), 1281–1289. https://doi.org/10.1038/s41593-018-0209-y.

Mazzoni, P., Hristova, A., & Krakauer, J. W. (2007). Why don't we move faster? Parkinson's disease, movement vigor, and implicit motivation. *Journal of Neuroscience*, *27*(27), 7105–7116. https://doi.org/10.1523/JNEUROSCI.0264-07.2007.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

Milstein, D. M., & Dorris, M. C. (2007). The influence of expected value on saccadic preparation. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *27*(18), 4810–4818. https://doi.org/10.1523/JNEUROSCI.0577-07.2007.

Muhammed, K., Dalmaijer, E., Manohar, S., & Husain, M. (2020). Voluntary modulation of saccadic peak velocity associated with individual differences in motivation. *Cortex*, *122*, 198–212. https://doi.org/10.1016/j.cortex.2018.12.001.

Niv, Y. (2020). *The primacy of behavioral research for understanding the brain* [Preprint]. PsyArXiv. https://doi.org/10.31234/osf.io/y8mxe.

Niv, Y., Daw, N. D., Joel, D., & Dayan, P. (2007). Tonic dopamine: Opportunity costs and the control of response vigor. *Psychopharmacology*, *191*(3), 507–520. https://doi.org/10.1007/s00213-006-0502-41

Noel, J.-P., Caziot, B., Bruni, S., Fitzgerald, N. E., Avila, E., & Angelaki, D. E. (2021). Supporting generalization in non-human primate behavior by tapping into structural knowledge: Examples from sensorimotor mappings, inference, and decision-making. *Progress in Neurobiology*, *201*:101996. doi: 10.1016/j.pneurobio.2021.101996. Epub 2021 Jan 14. PMID: 33454361; PMCID: PMC8096669. https://doi.org/10.1016/j.pneurobio.2021.101996.

Panigrahi, B., Martin, K. A., Li, Y., Graves, A. R., Vollmer, A., Olson, L., … Dudman, J. T. (2015). Dopamine is required for the neural representation and control of movement vigor. *Cell*, *162*(6), 1418–1430. https://doi.org/10.1016/j.cell.2015.08.014.

Ramkumar, P., Dekleva, B., Cooler, S., Miller, L., & Kording, K. (2016). Premotor and motor cortices encode reward. *PLoS ONE*, *11*(8), e0160851. https://doi.org/10.1371/journal.pone.0160851.

Reimer, J., & Hatsopoulos, N. G. (2009). The problem of parametric neural coding in the motor system. *Advances in Experimental Medicine and Biology*, *629*, 243–259. https://doi.org/10.1007/978-0-387-77064-2_12.

Renoult, L., Roux, S., & Riehle, A. (2006). Time is a rubberband: Neuronal activity in monkey motor cortex in relation to time estimation. *The European Journal of Neuroscience*, *23*(11), 3098–3108. https://doi.org/10.1111/j.1460-9568.2006.04824.x.

Reppert, T. R., Lempert, K. M., Glimcher, P. W., & Shadmehr, R. (2015). Modulation of saccade vigor during value-based decision making. *Journal of Neuroscience*, *35*(46), 15369–15378. https://doi.org/10.1523/JNEUROSCI.2621-15.2015.

Reppert, T. R., Rigas, I., Herzfeld, D. J., Sedaghat-Nejad, E., Komogortsev, O., & Shadmehr, R. (2018). Movement vigor as a traitlike attribute of individuality. *Journal of Neurophysiology*, *120*(2), 741–757. https://doi.org/10.1152/jn.00033.2018.

Reynaud, A. J., Saleri Lunazzi, C., & Thura, D. (2020). Humans sacrifice decision-making for action execution when a demanding control of movement is required. *Journal of Neurophysiology*, *124*(2), 497–509. https://doi.org/10.1152/jn.00220.2020.

Rueda-Orozco, P. E., & Robbe, D. (2015). The striatum multiplexes contextual and kinematic information to constrain motor habits execution. *Nature Neuroscience*, *18*(3), 453–460. https://doi.org/10.1038/nn.3924.

Salamone, J. D., Pardo, M., Yohn, S. E., López-Cruz, L., SanMiguel, N., & Correa, M. (2016). Mesolimbic dopamine and the regulation of motivated behavior. In E. H. Simpson & P. D. Balsam (Eds.), *Behavioral neuroscience of motivation* (pp. 231–257). Springer International Publishing. https://doi.org/10.1007/7854_2015_383.

Saxena, S., & Cunningham, J. P. (2019). Towards the neural population doctrine. *Current Opinion in Neurobiology*, *55*, 103–111. https://doi.org/10.1016/j.conb.2019.02.002.

Sedaghat-Nejad, E., Herzfeld, D. J., & Shadmehr, R. (2019). Reward prediction error modulates saccade vigor. *The Journal of Neuroscience*, *39*(25), 5010–5017. https://doi.org/10.1523/JNEUROSCI.0432-19.2019.

Shadmehr, R., & Ahmed, A. A. (2020). *Vigor: Neuroeconomics of movement control*. The MIT Press. https://doi.org/10.7551/mitpress/12940.001.0001.

Summerside, E. M., Shadmehr, R., & Ahmed, A. A. (2018). Vigor of reaching movements: Reward discounts the cost of effort. *Journal of Neurophysiology*, *119*(6), 2347–2357. https://doi.org/10.1152/jn.00872.2017.

Thura, D. (2020). Decision urgency invigorates movement in humans. *Behavioural Brain Research*, *382*, 112477. https://doi.org/10.1016/j.bbr.2020.112477.

Thura, D., & Cisek, P. (2017). The basal ganglia do not select reach targets but control the urgency of commitment. *Neuron*, *95*(5), 1160–1170.e5. https://doi.org/10.1016/j.neuron.2017.07.039.

Thura, D., Cos, I., Trung, J., & Cisek, P. (2014). Context-dependent urgency influences speed-accuracy trade-offs in decision-making and movement execution. *The Journal of Neuroscience*, *34*(49), 16442–16454. https://doi.org/10.1523/JNEUROSCI.0162-14.2014.

Turner, R. S., & Desmurget, M. (2010). Basal ganglia contributions to motor control: A vigorous tutor. *Current Opinion in Neurobiology*, *20*(6), 704–716. https://doi.org/10.1016/j.conb.2010.08.022.

Vyas, S., Golub, M. D., Sussillo, D., & Shenoy, K. V. (2020). Computation through neural population dynamics. *Annual Review of Neuroscience*, *43*(1), 249–275. https://doi.org/10.1146/annurev-neuro-092619-094115.

Yttri, E. A., & Dudman, J. T. (2016). Opponent and bidirectional control of movement velocity in the basal ganglia. *Nature*, *533*(7603), 402–406. https://doi.org/10.1038/nature17639.

Zenon, A., Devesse, S., & Olivier, E. (2016). Dopamine manipulation affects response vigor independently of opportunity cost. *Journal of Neuroscience*, *36*(37), 9516–9525. https://doi.org/10.1523/JNEUROSCI.4467-15.2016.

A role of serotonin and the insula in vigor: Tracking environmental and physiological resources

Mattie Tops[a], Maarten A. S. Boksem[b],
Jesus Montero-Marin[c] and Dimitri van der Linden[d]

[a]Developmental and Educational Psychology Unit, Institute of Psychology, Wassenaarseweg 52, NL-2333 AK Leiden, The Netherlands; [b]Department of Marketing Management, Rotterdam School of Management, Erasmus University, 3000 DR Rotterdam, The Netherlands; [c]Department of Psychiatry, Warneford Hospital, Warneford Ln, Headington, Oxford OX3 7JX, UK and [d]Department of Psychology, Education, and Child Studies, Erasmus University Rotterdam, 3000 DR Rotterdam, The Netherlands
m.tops@fsw.leidenuniv.nl
http://loop.frontiersin.org/people/8492/overview
mboksem@rsm.nl
www.rsm.nl/people/maarten-boksem/
jesus.monteromarin@psych.ox.ac.uk
https://www.psych.ox.ac.uk/team/jesus-montero-marin
vanderlinden@essb.eur.nl
https://www.eur.nl/en/people/dimitri-van-der-linden

doi:10.1017/S0140525X21000261, e136

Abstract

We describe a neural monitor of environmental and physiological resources that informs effort expenditure. Depending on resources and environmental stability, serotonergic and dopaminergic neuromodulations favor different behavioral controls that are organized in corticostriatal loops. This broader perspective produces some suggestions and questions that may not be covered by the foraging approach to vigor of Shadmehr and Ahmed (2020).

In both animals and humans, there is support for a basic distinction between survival needs and needs to invest in future benefits (Schneider, Wise, Benton, Brozek, & Keen-Rhinehart, 2013; Tang & West, 1997). Animal research suggests that neural systems are fundamentally organized to distinguish conditions of low resources and unmet energy need from conditions of high levels of resources and met energy needs, and to regulate behavior, effort, and homeostasis accordingly. Energy acquisition and storage is an important prerequisite for reproductive success. Thus, in most species, behavioral sequences are organized so that a period of eating and fattening typically precedes a period of mating and caring for offspring. This is particularly important in habitats where food availability fluctuates in an unpredictable manner (Schneider et al., 2013). Perceptions of predictability and having a surplus of resources and energy shift the regulatory focus from immediate, momentary concerns and harm prevention toward future-directed behavior and long-term investments. Human evolution has taken this shift from immediate survival toward mating and caring for offspring further, exploiting environmental predictability through the development of a large neocortex and extended parental investment, facilitating the development and learning of prospective abilities (Carter, 2014).

The different systems for behavioral control, as referred to above, are the main focus of the predictive and reactive control

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

systems (PARCS) theory (Tops et al. 2017, 2021). PARCS theory proposes that people are equipped with separate neural systems for dealing with different types of environments, organized in a ventral-to-dorsal direction in corticostriatal loops and associated large-scale networks.

The relatively right-lateralized reactive control system includes the salience network (Downar, Crawley, Mikulis, & Davis, 2002), and the ventral attentional system (Shulman et al., 2009), for example, the anterior insula (AI) and inferior frontal gyrus (IFG). Reactive control systems are for dealing with unfavorable environments that are unpredictable, unstable and novel, and for times when resources are low. When behavior is under reactive control, autonomic, homeostatic, and motor control is guided by feedback from environmental stimuli.

By contrast, predictive control systems are for dealing with predictable, familiar, and stable environments. Predictive control is guided by internally organized, model-based predictions and expectancies that are based on people's prior experiences. This control includes, among other areas, the dorsal attentional network (Shulman et al., 2009; e.g., FEF). Predictive control can be "proactive": impulsive but rigid, still very much driven by predicted rewards. However, especially in humans there is further development of flexible predictive control. Flexible predictive control involves the default mode network (DMN). This control is detached from the immediate environment and takes place at rest, as well as simultaneously with habitual motor control (Vatansever, Menon, & Stamatakis, 2017). The DMN is thought to be implicated in prospection by simulating and comparing alternative actions and outcomes (Buckner & Carroll, 2007) and in rapidly selecting appropriate responses and applying learned rules under predictable behavioral contexts (Vatansever et al., 2017).

Our theory suggests that different brain areas should control behavior in future- versus present moment-focused ways depending on the stability and predictability of the environment. There is support from human functional magnetic resonance imaging (fMRI) studies. One study showed graded maps of time scales within the right IFG–insula and the striatum: ventroanterior regions predicted immediate rewards and dorsoposterior striatal regions (and dorsolateral prefrontal cortex, posterior cingulate cortex) predicted future rewards (Tanaka et al., 2004). A follow-up study showed that the different learning systems in corticostriatal loops are sensitive to the predictability of the environment: the IFG–ventral striatum loop is involved in action learning based on the present state, whereas the dorsolateral prefrontal cortex–dorsal striatum loop is involved in action learning based on predictable future states (Tanaka et al., 2006). When subjects chose small-immediate or large-delayed liquid rewards under dietary regulation of tryptophan, a precursor of serotonin, activity of the ventral part of the striatum correlated with reward prediction at shorter time scales, and this correlated activity was stronger at low serotonin levels (Tanaka et al., 2007). By contrast, the activity of the dorsal part of the striatum was correlated with reward prediction at longer time scales, and was stronger at high serotonin levels.

The function of serotonin may lay in its relative promotion of dorsal systems and flexible predictive control (Carver, Johnson, & Joormann, 2009; Tops, Russo, Boksem, & Tucker, 2009). We proposed that serotonin facilitates predictive control that guides behavior that is best performed without interference from high levels of unpredictable environmental stimulation (Tops et al., 2009, 2010). Serotonin may function as a neuromodulator of a drive to withdraw: a phylogenetically conserved motive to reduce the present or anticipated environmental stimulation mentally or behaviorally, such as by moving into an environment of lower stimulation levels (Tops et al., 2009; cf. Lowry, Lightman, & Nutt, 2009). Serotonin increases satiety and decreases responsiveness to motivational stimuli. By increasing restraint, it allows for responding to cues of longer-term outcomes and delay of gratification (Depue, 1995). The associations described by Shadmehr and Ahmed (2020) of 5-HT with sensitivity to the history of reward, longer harvest time, decreased foraging drive, reductions in locomotor activity, but sparing of habitual movements, are consistent with facilitation of flexible predictive control: as we have seen, flexible predictive control takes place at rest or during habitual control. The latter two effects were not observed in tasks with highly motivational or highly threatening components which would trigger reactive control.

Serotonin may facilitate flexible predictive control not only in stable, predictable environments according to history of reward and reward prediction at longer time scales. Serotonin may also be sensitive to the levels of environmental and physiological resources. Tryptophan, the precursor of serotonin, is the amino acid most sensitive to depletion. Russo et al. (2003) proposed that tryptophan has a signaling role in physiology. The state in which tryptophan becomes depleted is associated with both external and internal unfavorable circumstances such as inflammation, stress, and food shortage. Under such conditions, chances of survival may increase by more aggressiveness and vigor in an attempt to obtain food (Russo et al., 2003). Decreases in serotonin may facilitate such behavior by disinhibition of catecholaminergic (e.g., dopamine) systems. Conversely, high serotonin indicates sufficiency of resources.

Interestingly, environmental energy conditions have also been proposed to be central in dopamine function. According to Beeler, Frazier, and Zhuang (2012), the primary role of dopamine in behavior is to modulate activity such that it matches energy expenditure to the prevailing environmental energy conditions. In other words, it couples energy sensing to regulated voluntary energy expenditure. Similarly, Berke (2018) proposed that dopamine provides a dynamic estimate of whether it is worth expending a limited internal resource, such as energy, attention, or time.

In terms of neural structures, the AI is involved in monitoring the conditions of peripheral resources and may influence actions by signaling the adequacy of these resources (Tops, Boksem, & Koole, 2013, 2015; Tops & de Jong, 2006). Already in 1964, Gellhorn argued that neural networks of interoception are involved in a peripheral feedback mechanism on implicit motivation. Evidence suggests that the right AI integrates interoceptive information (e.g., energy levels and muscle condition) to connect motor control with feelings and motivation (Craig, 2002; Damasio, 1999). The AI has been described as a critical relay between interoceptive and motor cortices, limbic motivational areas, and the orbital frontal cortex, which is thought to be involved in valuation (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003). Similarly, Tinaz et al. (2018) highlighted the interaction between the AI and dACC in generating intentional movements. Integration by the insula of sensory signals from the body and the emotional and motivational context provides the impetus to the dACC to initiate and sustain movement (cf. Tops & Boksem 2011; Tops et al., 2015). Neuroimaging studies

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

using such paradigms as the sustained static handgrip exercise and extension/flexion wrist movements have shown that muscle force sense and effort sense relate to insula activity (e.g., de Graaf et al., 2004). Connecting such monitoring functions to the regulation of effort mobilization, good heartbeat perceivers showed a more finely tuned behavioral feedback-regulation of physical load than poor heartbeat perceivers (Herbert, Ulbrich, & Schandry, 2007).

A phenomenon often observed in sports could reflect the insula in action: clenching a fist for self-encouragement or the encouragement of others and to invigorate performance. This "encouragement gesture" may be part of a physiological feedback mechanism that functions to increase or sustain levels of vigor in challenging situations by signaling the sufficiency of resources such as muscle strength (Tops & de Jong, 2006). It involves the contraction of forearm flexors, similar to the grasping action that is part of acquisitive actions. Notice the paradox in this effect: in a challenging and taxing situation, effort is spent on an instrumentally useless action. The use of the action is rewarding the overcoming of challenge and facilitating persistence. This mechanism may be implicated in other examples of paradoxes of effort (Inzlicht, Shenhav, & Olivola, 2018). For instance, Shadmehr and Ahmed (2020) described their finding (Yoon, Geary, Ahmed, & Shadmehr, 2018) that exertion of effort, apparently associated with increased dopamine, increased harvest time, and subsequent vigor.

Persistence is adaptive in stable environments with sufficient resources. In reactive control, on the contrary, exertion of effort should be subjectively effortful (i.e., aversive) to prevent loss of resources and because persistence is not adaptive in unpredictable situations. However, when the environment is stable and resources are sufficient, exertion of effort and persistence can be investments in long-term rewards and long-term resources such as skills and self-efficacy (Ainslie, 2020). For instance, overcoming the challenge of putting together a piece of furniture creates an internal model of how to do this, and increases self-efficacy in this domain. The piece of furniture itself has become proof of the skill. As we have seen in the example of the encouragement gesture, exertion of effort is not always subjectively effortful, but can be rewarding. Possibly, dopamine functioning to overcome response costs (Salamone et al., 1991) could be a mechanism behind why exertion of effort is less subjectively effortful and more rewarding in predictive control than reactive control, if the former involves higher dopamine function.

Alternatively, there may be a difference between hemispheres. Support for laterality in motivation to expend effort to obtain reward was found in Parkinson's patients with asymmetric dopamine loss (Porat, Hassin-Baer, Cohen, Markus, & Tomer, 2014). Predominant left-sided loss impaired the expending of effort to increase gains whereas right-sided loss impaired the expending of effort to minimize losses. This is consistent with laterality in PARCS, given that reactive control is more concerned with preventing losses in low resource conditions whereas predictability and resources allow predictive control to invest in gains (Tops et al., 2017). The reactive system is relatively right-lateralized. By contrast, the corresponding ventral system in the left hemisphere is implicated in language functions that are important in the construction of internal models in dorsal networks. This organizational pattern is also reflected in human handedness (Sainburg, 2014). That is, the left hemisphere (in right handers) relies on feedforward use of vision and proprioception in control that is most effective under predictable and stable mechanical conditions, whereas the right hemisphere is specialized for impedance (i.e., online feedback-guided) control, which imparts stability when mechanical conditions are unpredictable. The left hemisphere exploits predictive processes that assure mechanical efficiency and minimize costs, such as energy and smoothness, when environmental conditions are predictable (Sainburg, 2014).

We think the stable reward-acquisition (foraging) paradigms described in Shadmehr and Ahmed (2020) trigger and measure mostly rigid predictive (i.e., proactive) control. They also describe shifts toward flexible predictive control in terms of increased serotonergic function. Reactive control seems to be missing. In unpredictable and urgent situations there is often over-mobilization of effort because efficient responses cannot be predicted. Moreover, specifically in reactive control, sufficiency and loss of resources are important. We probably all know from experience that external and internal conditions and resources (i.e., temperature, dimness, hunger, and sickness) impact on our subjective and motor vigor alike. Therefore, we would like to challenge Shadmehr and Ahmed to consider the role of resources in their model of vigor (cf. Boksem and Tops, 2008). Could resource be the common currency between reward (resource obtainment) and effort (resource mobilization/expenditure/cost)? (Tops et al., 2015).

Financial support. JMM is supported by the Wellcome Trust Grant (104908/Z/14/Z/). This research received no further specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

References

Ainslie, G. (2020). Willpower with and without effort. *Behavioral and Brain Sciences*, *44*, e30. https://doi.org/10.1017/S0140525X20000357

Beeler, J. A., Frazier, C. R., & Zhuang, X. (2012). Putting desire on a budget: Dopamine and energy expenditure, reconciling reward and resources. *Frontiers in integrative neuroscience*, *6*, 49. https://doi.org/10.3389/fnint.2012.00049

Berke, J. D. (2018). What does dopamine mean?. *Nature neuroscience*, *21*(6), 787–793. https://doi.org/10.1038/s41593-018-0152-y

Boksem, M. A. S., & Tops, M. (2008). Mental fatigue: Costs and benefits. *Brain Research Reviews*, *59*, 125–139.

Buckner, R. L., & Carroll, D. C. (2007) Self-projection and the brain. *Trends in Cognitive Sciences*, *11*, 49–57.

Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(9), 5497–5502. https://doi.org/10.1073/pnas.0935845100AI

Carter C. S. (2014). Oxytocin pathways and the evolution of human behavior. *Annual review of psychology*, *65*, 17–39. https://doi.org/10.1146/annurev-psych-010213-115110

Carver, C. S., Johnson, S. L., & Joormann, J. (2009). Two-mode models of self-regulation as a tool for conceptualizing effects of the serotonin system in normal behavior and diverse disorders. *Current Directions of Psychological Science*, *18*, 195–199.

Craig, A. D. (2002). How do you feel? Interoception: The sense of the physiological condition of the body. *Nature Reviews Neuroscience*, *3*(8), 655–666.

Damasio, A. R. (1999). *The feelings of what happens: Body and emotion in the making of consciousness*. Houghton Mifflin Harcourt.

de Graaf, J. B., Gallea, C., Pailhous, J., Anton, J. L., Roth, M., & Bonnard, M. (2004). Awareness of muscular force during movement production: An fMRI study. *NeuroImage*, *21*,1357–1367.

Depue, R. A. (1995). Neurobiological factors in personality and depression. *European Journal of Personality*, *9*, 413–439.

Downar, J., Crawley, A. P., Mikulis, D. J., & Davis, K. D. (2002) A cortical network sensitive to stimulus salience in a neutral behavioral context across multiple sensory modalities. *Journal of Neurophysiology*, *87*(1), 615–620.

Herbert, B. M., Ulbrich, P., & Schandry, R. (2007) Interoceptive sensitivity and physical effort: Implications for the self-control of physical load in everyday life. *Psychophysiology*, *44*(2), 194–202.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

Inzlicht, M., Shenhav, A., & Olivola, C. Y. (2018). The effort paradox: Effort is both costly and valued. *Trends in Cognitive Sciences*, *22*(4), 337–349. doi.org/10.1016/j.tics.2018.01.007.

Lowry, C. A., Lightman, S. L., & Nutt, D. J. (2009). That warm fuzzy feeling: Brain serotonergic neurons and the regulation of emotion. *Journal of Psychopharmacology*, *23*, 392–400.

Porat, O., Hassin-Baer, S., Cohen, O. S., Markus, A., & Tomer, R. (2014). Asymmetric dopamine loss differentially affects effort to maximize gain or minimize loss. *Cortex*, *51*, 82–91. http://dx.doi.org/10.1016/j.cortex.2013.10.004

Russo, S., Kema, I. P., Fokkema, M. R., Boon, J. C., Willemse, P. H. B., de Vries, E. G. E., Korf, J. (2003). Tryptophan as a link between psychopathology and somatic states. *Psychosomatic Medicine*, *65*(4), 665–671.

Sainburg, R. L. (2014). Convergent models of handedness and brain lateralization. *Frontiers in Psychology*, *5*, 1092.

Salamone, J. D., Steinpreis, R. E., McCullough, L. D., Smith, P., Grebel, D., & Mahan, K. (1991). Haloperidol and nucleus accumbens dopamine depletion suppress lever pressing for food but increase free food consumption in a novel food choice procedure. *Psychopharmacology* (*Berl*), *104*, 515–521.

Schneider, J. E., Wise, J. D., Benton, N. A., Brozek, J. M., & Keen-Rhinehart, E. (2013). When do we eat? Ingestive behavior, survival, and reproductive success. *Hormones and Behavior*, *64* (4), 702–728. http://dx.doi.org/10.1016/j.yhbeh.2013.07.005

Shadmehr, R., & Ahmed, A. A. (2020). *Vigor. Neuroeconomics of movement control*. Massachusetts London, England: MIT Press Cambridge.

Shulman, G. L., Astafiev, S. V., Franke, D., Pope, D. L., Snyder, A. Z., McAvoy, M. P., & Corbetta, M. (2009). Interaction of stimulus-driven reorienting and expectation in ventral and dorsal frontoparietal and basal ganglia-cortical networks. *Journal of Neuroscience*, *29*, 4392–4407.

Tanaka, S. C., Schweighofer, N., Asahi, S., Shishida, K., Okamoto, Y., Yamawaki, S. (2007). Serotonin differently regulates short- and long-term prediction of rewards in the ventral and dorsal striatum. *PLoS ONE*, *2*, e1333.

Tanaka, S. C., Doya, K., Okada, G., Ueda, K., Okamoto, Y., & Yamawaki, S. (2004). Prediction of immediate and future rewards differentially recruits cortico-basal ganglia loops. *Nature Neuroscience*, *7*, 887–893.

Tanaka, S. C., Samejima, K., Okada, G., Ueda, K., Okamoto, Y., Yamawaki, S., & Doya, K. (2006). Brain mechanism of reward prediction under predictable and unpredictable environmental dynamics. *Neural Networks*, *19*, 1233–1241.

Tang, T. L., & West, W. B. (1997). The importance of human needs during peacetime, retrospective peacetime, and the Persian Gulf War. *International Journal of Stress Management*, *4*, 47–62. http://dx.doi.org/10.1007/BF02766072

Tinaz, S., Para, K., Vives-Rodriguez, A., Martinez-Kaigi, V., Nalamada, K., Sezgin, M., & Constable, R. T. (2018). Insula as the interface between body awareness and movement: A neurofeedback-guided kinesthetic motor imagery study in Parkinson's disease. *Frontiers in Human Neuroscience*, *12*, 496. https://doi.org/10.3389/fnhum.2018.00496

Tops, M., & Boksem, M. A. S. (2011). A potential role of the inferior frontal gyrus and anterior insula in cognitive control, brain rhythms and event-related potentials. *Frontiers in Psychology*, *2*(330), 1–14.

Tops, M., Boksem, M. A. S., & Koole, S. (2013). Subjective effort derives from a neurological monitor of performance costs and physiological resources. *Behavioral and Brain Sciences*, *36*(6), 703–704.

Tops, M., & de Jong, R. (2006). Posing for success: Clenching a fist facilitates approach. *Psychonomic Bulletin and Review*, *13*(2), 229–234.

Tops, M., IJzerman, H., & Quirin, M. (2021). Personality dynamics in the brain: Individual differences in updating of representations and their phylogenetic roots. In J. F. Rauthmann (Ed.), *The handbook of personality dynamics and processes*. (pp. 125–254) Elsevier. https://psyarxiv.com/4yj6r

Tops, M., Luu, P., Boksem, M. A. S., & Tucker, D. M. (2010). Brain substrates of behavioral programs associated with self-regulation. *Frontiers in Cognition*, *1*, 152.

Tops, M., Quirin, M., Boksem, M. A. S., & Koole, S. L. (2017). Large-scale neural networks and the lateralization of motivation and emotion. *International Journal of Psychophysiology*, *119*, 41–49. doi: 10.1016/j.ijpsycho.2017.02.004

Tops, M., Russo, S., Boksem, M. A., & Tucker, D. M. (2009). Serotonin: Modulator of a drive to withdraw. *Brain and Cognition*, *71*, 427–436.

Tops, M., Schlinkert, C., Tjew, A., Sin, M., Samur, D., & Koole, S. L. (2015). Protective inhibition of self-regulation and motivation: Extending a classic Pavlovian principle to social and personality functioning. In Gendolla, G. H. E., Tops, M. & Koole, S. L. (Eds.), *Handbook of biobehavioral approaches to self-regulation*. Springer, pp. 68–85. doi: 10.1007/978-1-4939-1236-0

Vatansever, D., Menon, D. K., & Stamatakis, E. A. (2017). Default mode contributions to automated information processing. *Proceedings of the National Academy of Sciences USA*, *114*(48), 12821–12826.

Yoon, T., Geary, R. B., Ahmed, A. A., & Shadmehr, R. (2018). Control of movement vigor and decision making during foraging. *Proceedings of the National Academy of Sciences USA*, *115*, E10476–E10485.

Foundational assumption reasonable but uncertain

Rex A. Wright[a,b] and Christopher Mlynski[c,d]

[a]University of Texas Dell School of Medicine, Austin, TX 78712, USA; [b]University of North Texas, Denton, TX, 76203, USA; [c]Technical University Dresden, 01069 Dresden, Germany and [d]University of Vienna, 1010 Vienna, Austria

doi:10.1017/S0140525X21000339, e137

Abstract

We offer thoughts on Shadmehr and Ahmed's foundational assumption that behavioral intensity (vigor) is proportional to the perceived value of outcomes driving behavior (incentives). The assumption is reasonable considering classical motivational thought and scholarship in related literatures but called into question by an influential contemporary theory of motivation by Brehm. Brehm's theory suggests that the assumption is warranted in some, but not all, performance circumstances. Furthermore, proportionality between vigor and value might be generated through a deliberative goal-setting process rather than through intrinsic neural linkages.

We appreciate the opportunity to comment on *Vigor: Neuroeconomics of Movement Control*, by Shadmehr and Ahmed. The authors' ideas are profoundly important and relate directly to analyses that guide work in our laboratories. We offer thoughts on the authors' foundational assumption that behavioral intensity (vigor) is proportional to the perceived value of outcomes driving behavior (incentives). The assumption is reasonable considering classical motivational thought and scholarship in related literatures (Heckhausen, 1991; Heckhausen & Heckhausen, 2010). However, it is called into question by an influential contemporary theory by Brehm (e.g., Brehm and Self, 1989), which provides a distinctive and well-investigated perspective regarding relevant motivational processes (Gendolla, Wright, & Richter, 2012; Richter, Gendolla, & Wright, 2016; Wright, 1996).

Brehm's theory concerns motivational intensity – effort deployed at a point in time. The theory assumes that effort deployment is governed by a principle of conservation and distinguishes circumstances in which difficulty is fixed from ones in which difficulty is unfixed or unknown. Difficulty is fixed if performers can secure a desired outcome by attaining an established performance standard. Difficulty is unfixed if performers can secure outcomes of different value by attaining different performance standards. Difficulty is unknown if performers have no understanding of what will be required to secure a desired outcome.

Examples of the different difficulty circumstances might involve workers challenged to produce widgets. Difficulty would be fixed if the workers were told they could earn an amount of money for producing a set number within a particular timespan. Production lower than the set number would yield no money and production above would yield no more money than the designated amount. Difficulty would be unfixed if the workers were told they could earn different amounts of money depending on how many widgets they produced within the timespan.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

Difficulty would be unknown if the workers were told they could earn an amount of money for producing an unspecified number of widgets within the timespan.

How should effort be deployed in these circumstances? Brehm's theory argues that in all cases effort should be determined proximally (immediately) by appraisals of instrumental task difficulty. However, there are steps to consider and devils in detail. Consider workers presented the fixed widget challenge. Their first decision should be whether to meet the established performance standard, that is, generate the set number of widgets. Workers should decide affirmatively if they believe (a) they can succeed, and (b) the financial incentive justifies the effort that must be deployed. They should decide negatively if these conditions are not met. If the workers decide affirmatively, they should do what they believe is required, but – following the conservation principle – no more than what they believe is required. In other words, they should deploy effort that is consistent with their perception of task difficulty. If the workers decide negatively, they should do nothing. For them, effort deployment would violate the conservation principle either because it would be futile (fully wasteful) or because the value of effort deployed would exceed the perceived value of the incentive (relatively wasteful).

The resulting pattern of effort is striking. If incentive value is low, effort should correspond to difficulty at low difficulty levels, but be consistently low at moderate and high difficulty levels. If incentive value is moderate, effort should correspond to difficulty at low and moderate difficulty levels but be low at high difficulty levels. If incentive value is high, effort should correspond to difficulty at low, moderate, and high difficulty levels so long as success at the high levels is understood to be possible.

Notably, effort in this fixed circumstance should not be proportional to incentive value. It should comport with difficulty regardless of value where success is perceived as possible and worthwhile and be low regardless of value where success is perceived as impossible or excessively difficult considering incentive value. The only time incentive value should relate to effort is where it justifies requirements of a possible task when high, but not when low. Thus, for example, if some workers were offered a strong financial incentive for meeting a difficult, but possible, widget performance standard, and others were offered a weak financial incentive for doing so, effort should be high for the former group and low for the latter group.

Consider now workers presented the unfixed widget challenge. Their first decision should not be whether to meet an established performance standard. Rather, it should be what – if any – standard to pursue. Workers should decide considering what standards they can meet and what they can secure by performing at different levels. Possible associations between performance standard met and value of the outcome secured are variable. However, the association should commonly be linear, such that performers can secure steadily more value the better they perform. An example would be where workers were told they could earn 1 USD for each widget produced. Production at the first level would yield 1 USD. Production at the second would yield 2 USD. Production at the third would yield 3 USD. And so forth. In such a case, workers could be expected to select the most difficult performance standard that is (a) possible to meet, and (b) justified by the value of the outcome with which it is associated. Once workers select that standard, they should deploy effort correspondent to difficulty.

An insight associated with the linear widget example above relates to the value of the incentive at the first level of performance. The greater the value, the higher should be the maximum effort justified at each available performance level, with increasingly higher performance standard adoptions tending to follow. More specifically, as value increases, performers should tend to adopt increasingly higher performance standards until they reach the most difficult possible standard that is justified. Beyond this last point, increases in incentive value at the first level of performance should not alter standard adoption – and therefore effort – because performers will have attained their performance peak. Thus, in this special unfixed difficulty circumstance, we can expect behavioral vigor to reflect the value of the outcome driving behavior until performers are fully extended in terms of effort and can deploy no more.

Preceding points can be illustrated by considering scenarios in which workers were told they could earn more than 1 USD for each widget produced. Workers might view a 20-widget performance standard as excessively difficult (unjustified) if success would yield only 20 USD (1 USD × 20) but justified if success would yield 40 USD (2 USD × 20). Similarly, they might view a 25-widget performance standard as excessively difficult (unjustified) if success would yield 25 USD (1 USD × 25) but justified if success would yield 75 USD (3 USD × 25). If workers believe they can produce no more than 30 widgets and view that performance standard as justified by 120 USD (4 USD × 30), but nothing less than that, then increases in payment beyond 4 USD per widget should have no impact on standard choice or effort. To be clear, there are other details to consider, such as the difficulty of individual widget production. But the gist is the same for present purposes.

Consider finally workers presented the unknown widget challenge, the chance to earn an amount of money for producing an unspecified number of widgets. Once again, the first decision should not be whether to meet an established performance standard, because no standard is specified. Rather, the decision should be what – if any – standard to pursue and workers should decide considering what standards they can meet and what they can secure. A crucial point of note is that the likelihood of meeting the unspecified standard should increase directly with the standard met. Workers who aim high should have a better chance of meeting the unspecified standard than workers who aim low. This means that performers can secure a steadily more valuable outcome the better they perform. Outcome value at each performance level should be a function of the likelihood of meeting the standard at that level and the amount of money offered for meeting the unspecified standard. The greater the money offered, the greater should be value at each performance level.

As discussed above, when there is a linear association between performance standard met and value of the outcome secured, performers should (a) select the most difficult performance standard that is possible to meet and justified by the value of the outcome with which it is associated, and then (b) deploy the effort correspondent with difficulty. Consequently, we could expect workers presented the unknown widget challenge to do this. We also could expect their effort to reflect the value of the financial incentive up to the point that they attain their performance peak.

It is beyond the scope of this commentary to review empirical evidence for Brehm's effort arguments. Suffice it to say that it is considerable, with the most compelling coming from over 100 studies that have examined implications using focused cardiovascular responses as indices of effort (e.g., Richter et al., 2016). Studies include experiments that have manipulated the difficulty of behavioral challenges, the value of approach and avoidance incentives,

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

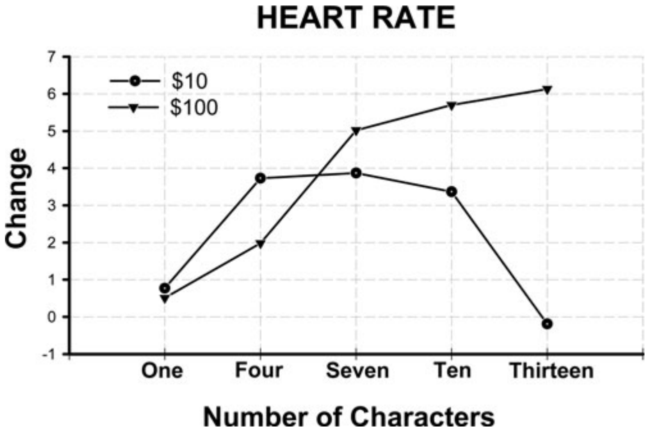

Figure 1 (Wright and Mlynski). Heart rate responses as a function of incentive value across five levels of memory task difficulty (from Eubanks et al., 2002).

and the nature (e.g., fixedness) of behavioral challenges – generating remarkable consistency in support.

A single example study is an experiment that examined the interactional influence of difficulty and incentive value operationalizing value in monetary terms (Eubanks, Wright, & Williams, 2002). It presented participants over a series of work periods less or more difficult versions of a recognition memory task. More specifically, it presented character strings followed by a probe asking if a particular character was in the preceding string. Character string lengths were 1, 4, 7, 10, and 13, creating the different difficulty conditions. Instructions indicated that participants would earn chances to win a $10 prize (incentive value low) or a $100 prize (incentive value high) by maintaining a 90% success rate. Analysis of cardiovascular data collected during the work periods showed a difficulty × value interaction for heart rate. Heart rate increased steadily with difficulty among those who could win $100 but increased with difficulty only to a point for those who could win $10. As seen in Figure 1, heart rate corresponded with incentive value only at the highest difficulty level, presumably where effort was justified only if the high value incentive was available.

Insofar as Brehm's arguments have merit, they suggest that Shadmer and Ahmed's foundational assumption regarding the relationship between behavioral vigor and subjective value is warranted in some, but not all, performance circumstances. They also suggest that proportionality between vigor and value might be generated differently than the authors suppose. Specifically, it might be generated through a deliberative goal-setting process rather than through intrinsic neural linkages (Locke & Latham, 2019). Means of reconciliation between Shadmer and Ahmed's perspective and Brehm's perspective are uncertain but could be available and would be well worth exploring.

Financial support. This study received no specific grant from any funding agency, commercial or not-for-profit sectors.

Conflict of interest. None.

References

Brehm, J. W., & Self, E. (1989). The intensity of motivation. In M. R. Rozenweig & L. W. Porter (Eds.), *Annual review of psychology* (pp. 109–131). Annual Reviews, Inc.

Eubanks, L., Wright, R. A., & Williams, B. J. (2002). Reward and the heart: Incentive value influence on cardiovascular response at five levels of task demand. *Motivation and Emotion*, *26*, 139–152.

Gendolla, G. H. E., Wright, R. A, & Richter, M. (2012). Effort intensity: Some insights from the cardiovascular system. In R. A. Ryan (Ed.), *Oxford Handbook of human motivation* (pp. 420–438). Oxford University Press. doi: 10.1093/oxfordhb/9780195399820.013.0024.

Heckhausen, H. (1991). *Motivation and action* (P. K. Leppman, trans.). Springer-Verlag.

Heckhausen, J., & Heckhausen, H. (2010). *Motivation and action* (2nd ed.). Cambridge University Press.

Locke, E. A., & Latham, G. P. (2019). The development of goal setting theory: A half century retrospective. *Motivation Science*, *5*(2), 93–105. https://doi.org/10.1037/mot0000127

Richter, M., Gendolla, G. H. E., & Wright, R. A. (2016). Three decades of research on motivational intensity theory: What we have learned about effort and what we still don't know. In A. Elliot (Ed.), *Advances in motivation science*. Elsevier Press.

Wright, R. A. (1996). Brehm's theory of motivation as a model of effort and cardiovascular response. In P. M. Gollwitzer & J. A. Bargh (Eds.), *The psychology of action: Linking cognition and motivation to behavior* (pp. 424–453). Guilford.

Authors' Response

Movement control, decision-making, and the building of Roman roads to link them

Reza Shadmehr[a] and Alaa A. Ahmed[b]

[a]Department of Biomedical Engineering, Johns Hopkins University, Baltimore, MD 21205, USA and [b]Department of Mechanical Engineering, University of Colorado Boulder, Boulder, CO 80027, USA

doi:10.1017/S0140525X2100090X, e138

Abstract

In science, as in life, one can only hope to both inform others, and be informed by them. The commentaries associated with our book *Vigor* have highlighted the many ways in which the theory that we proposed can be improved. For example, there are a myriad of factors that need to be considered in a fully encompassing objective function. The neural mechanisms underlying the links between movement and decision-making have yet to be unraveled. The implications of a two-way interaction between movement and decisions at both the individual and social levels remain to be understood. The commentaries outline future questions, and encouragingly highlight the diversity of science communities that may be linked via the concept of vigor.

In neurobiology, reductionism has proven to be an effective approach to uncovering facts. Yet, facts by themselves are like colorful but tiny pieces of fabric that we might store in a drawer. To understand behavior, we also need a theory that acts as the creative seamstress, connecting the pieces, stitching together a tapestry. But what are the critical facts, and which theory might bring the pieces together?

Suppose at a family gathering your mother brings over a small tray with a few desserts. You look over the various options and select a cookie with a sliver of almond on top, reach for it and take a bite. What are the critical facts in this simple act? You might focus on the act of decision-making, consider the chosen cookie as a demonstration of preference, and rationalize it using a theory of economics. On the contrary, you might focus on the reaching movement, the patterns of kinematics and muscle

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

activations, and justify it with a theory born in robotics. But what if both facts are important, and neither theory is sufficient?

In *Vigor*, we argued that the acts of decision-making and movement are linked because our preferences affect how we move, and the effort it takes to move affects what we prefer. A theory that provides a link between decision-making and movement is optimal foraging. And the colorful fabrics that the theory brings together are as diverse as the behavior of crows when they choose between clams on a sandy beach, and the release of dopamine as monkeys view images of fractals on a video screen.

To be sure, there are many aspects of the theory that can be improved. As **Clark** points out, there are known paradoxes in decision-making regarding preference of certainty over risk. Does this certainty preference translate into greater vigor? Experiments that include probabilistic terms in the reward and effort variables, and then simultaneously measure preferences and movements, can answer this question. **Teixeira** points out that an important term missing in the mathematical formulation of utility is stability. That is, the act of moving can affect postural stability, which in turn may act as a cost. **Schrock** notes that although resting is a state that incurs a negative cost because of energetic loss, it also has a positive gain in terms of somatic maintenance (repairing tissue damage, etc.). This view is notable because it helps explain puzzling data in which given two rewarding options that each require some effort, animals sometimes choose to not make a choice, and simply rest (Bautista, Tinbergen & Kacelnik, 2001). **Bookstein** also reminds us that there are many factors that can affect the speed of movement, such as age, general health, and even social context. It is important to understand why vigor would change in these situations, because the analysis may reveal additional factors that need to be considered such as physical and emotional pain. This would help explain the finding by Hunter and colleagues that individuals walk slowly down inclines even though a faster pace would cost less energy: These savings would come at the expense of a sharper impact with each step (Hunter, Hendrix & Dean, 2010). Thus, the nature of the cost function is broader than metabolic costs of action and energetic gains of reward, and likely includes probabilistic terms, as well as terms that convey costs of stability, and benefits of rest.

Mastrogiorgio notes that our proposed isomorphism between vigor and subjective value is a powerful idea because it overcomes a basic limitation of standard economic theory: The standard theory does not admit a cardinal representation, but only an ordinal one (Shadmehr et al., 2019; Yoon et al., 2020). However, instead of maximizing an objective function during the process of decision-making, agents often choose so that they can satisfy a minimum set of requirements. A similar point is raised by **Thura**, who notes that actions often meet a minimum standard, rather than maximize a global function. For instance, "when we look for a restaurant in a new city, we plausibly choose the first one that is acceptable to us – it reaches the threshold of our own aspiration level – instead of comparing (all) the restaurants of the city." Thus, these authors suggest an alternate theory in which the individual preferences are viewed through the lens of bounded rationality.

In this alternate view, the prediction is that we move faster toward things that surpass our aspirational level. This view is important because items that surpass our aspirational level may also produce a reward prediction error. Notably, a component of vigor is related to release of dopamine, which in turn is related to reward prediction error: When an option is better than expected, vigor may be higher than when the same option is worse than expected. Another component of vigor is related to serotonin, which as **Tops, Boksem, Montero-Marin, & van der Linden** (**Tops et al.**) point out, may function as a neuromodulator that increases satiety, signaling sufficiency of resources, thus indicating proximity to an aspiration level. Serotonin would encourage restraint, enhancing response to longer-term outcomes and delay of gratification. Indeed, under conditions of food shortage, there is depletion of tryptophan, a precursor of serotonin. Under such conditions, the chances of survival may increase by being more vigorous.

However, production of greater vigor during periods of low reward rate is inconsistent with our framework of optimal foraging. In *Vigor*, we point out a paradoxical function of serotonin in the study of Seo et al. (2019), who found that whereas under normal conditions, suppression of serotonin enhanced vigor, under threat conditions this effect was reversed. Under low-threat conditions, activation of 5-HT neurons leads to immediate and dramatic reductions in locomotor activity, while sparing more habitual movements such as grooming (Seo et al., 2019). Effects were context-specific and not observed in tasks with high motivational or threatening components.

There is an intriguing implication to the observation that vigor is affected by dopamine and serotonin. These are ancient neuromodulatory systems that project throughout the brain and the spinal cord, reaching far beyond the motor system. For example, **Hanakawa** suggests that the idea of vigor control may be extended to mental operations. "Does mental vigor have similar control mechanisms and neural correlates with motor vigor?" In Parkinson's disease, although loss of dopamine clearly reduces vigor of movements, it also affects speed of mental operations (slowing of thinking, bradyphrenia). "My claim here is that the concept of vigor may be extended into the non-motor cognitive domains, and cognitive vigor is also likely supported by the midbrain dopaminergic system."

But why might vigor be regulated by global neuromodulators such as dopamine and serotonin, rather than via a specific factor that affects the motor system alone? The commentary of **Rolfs and Ohl** highlights an intriguing possibility. There is a link between movements and allocation of attention for the purpose of accelerating or decelerating the rate of information processing. When movement vigor increases, there is also a need for an increase in the efficiency in the sensory system. For example, some 100 ms before the eyes move to a new location, the part of the visual space that the saccade is aiming has a virtual spotlight that stands out from the background (Rolfs & Carrasco, 2012), resulting in a pre-saccadic shift of attention. Thus, during periods of high vigor, the reduced reaction times and increased saccade velocity affect not just the motor system, but also the visual system's ability to receive information (Jonikaitis & Deubel, 2011). This seems to beg for a global brain mechanism, rather than one that is specific to the motor system. Perhaps this is why neuromodulators such as dopamine and serotonin play such an integral role in the control of vigor, and perhaps these same systems are also involved in regulating information processing in the sensory system.

R1. Who computes the costs and rewards?

Spurrett notes that in order to move well, there needs to be an estimate of the relevant costs, in time, calories, and so on, and potential rewards, and then an integration into a common currency, applied to select deployment of the whole body. "Nonetheless, if there can't be a central executive able to integrate everything quickly enough to make selection and control of all skeletal movement consistently sensitive to a single value function responsive to all available information, something else must be

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

going on." In *Vigor*, we show that even in the context of an elementary movement like a saccade, there is no central executive. Rather, numerous structures, including some in the cortex, and others in the basal ganglia, express their opinions about where to move to, and how to make that movement. These opinions arrive via excitation and inhibition upon the superior colliculus, which in turn houses the neural machinery to make movements. The various opinions become potential control policies in the colliculus, with each policy translating the perceived costs and rewards into a potential goal directed movements with a specific vigor. Through a process akin to a race, one policy rises above the rest, achieves a threshold, and becomes action.

As **Matsushima, Kawamori, & Ogura** (**Matsushima et al.**) point out, the question of how the brain computes utility has been largely the focus of cortical neurophysiologists; yet fishes and birds, to name just a few species, make do quite well despite less developed cortical structures. Indeed, there is a fundamental role for the subcortical structures in decision-making. For example, in order to make a saccade, the decision-making process in mammals involves not only the attention allocation and value-based judgment of parietal and frontal lobe structures, but also the motor costs computed by the superior colliculus (Lovejoy & Krauzlis, 2010). For example, a small regional deactivation of the colliculus not only makes movements to that region more difficult, but more importantly, it makes attention allocation for that region more costly. This implies that the process of decision-making is a collaboration between cortical and subcortical structures.

We might naively guess that this cortical and subcortical collaboration is proforma, because the ultimate arbiter is the cortex. Surprisingly, the opposite may be true, as illustrated by the fact that the nucleus that sets the threshold for making a saccade is not in the cortex, but in the brainstem. Omnipause neurons integrate excitatory and inhibitory inputs from the cortex, basal ganglia, and the colliculus, and then pause when the sum exceeds a threshold, thereby allowing the saccade that is encoded by the upstream neurons to take place. Thus, the fabled threshold that determines arrival of a decision to move is not in the cortex, but in the brainstem.

From an evolutionary point of view, all the basic mechanisms for decision-making, including representation of a global capture rate, risks, rewards, and effort, exist in the brainstem, thus allowing numerous species without a highly developed cerebral cortex to make good decisions that lead to fecundity. With the development of a cerebral cortex, computing utility has become more sophisticated, but not divorced from the evaluation performed in the brainstem.

R2. Competition for reward can increase vigor

Although optimal foraging provides a metabolic perspective on why movement vigor may be linked to the subjective valuation of the goal, **Becchio, Pullar, & Panzeri** (**Becchio et al.**) make the novel suggestion that our vigor can act as a signal to others regarding how we value the objects in our environment. For example, the speed of our movement toward an empty seat on the train can serve as a clear indication to others that we subjectively have placed a high value on this seat, underlining our intentions for this limited resource, which in turn may result in a reduction in their vigor. This presents a novel view on why we run toward people we love: to let them know that we love them. Thus, vigor has benefits that go beyond energetics, conveying information regarding how we value the goal at our destination.

On the day after Thanksgiving in America, people line up outside of stores early in the morning and then when the doors open, run to grab the few televisions or gaming consoles that have been advertised at exceptionally low prices. For those standing in line, the probability of acquiring this reward is low, but they are willing to expend the energy required to acquire it. As **Bufacchi and Iannetti** correctly point out, competition and scarcity can produce increased vigor. Indeed, as they show in their simulations, this scenario reverses the usual relationship between expected reward and vigor, but remains entirely consistent with optimal foraging theory. Thus, the theory correctly predicts that facing competition, increased vigor is justified if it increases the probability of acquiring the scare reward.

In a recent experiment (Yoon et al., 2018), we tested the prediction that scarcity of reward would increase vigor. Human subjects looked at a fixation point while an image was presented to a side of the screen. To simulate scarcity, they were limited in the amount of time that they had to view the image. Thus, when they made a saccade to the image, on one block of trials they only had 0.4 s to gaze at it, whereas in other blocks they had 1.0 or 1.5 s. This modulation of harvest duration had a strong effect on both reaction time and saccade velocity: Subjects reacted sooner, and moved with greater saccade velocity toward the image that was available for the shorter period of time (Figure 3.11 of *Vigor*). Importantly, the expected reward in the short gaze period was smaller than in the long gaze period, but as the theory predicted, subjects moved with greater vigor toward the reward that was available for the shorter period of time. However, an important direction to explore these theories is to present a limited quantity of reward and introduce competition between agents. These richer, more ecologically relevant experiments await to be performed.

Indeed, **Wright and Mlynski** point out that when considering effort expenditure, the critical variables are not just the value of the incentive, but also the probability that expenditure of effort will be successful in acquiring that incentive. Is there evidence that movement vigor shows sensitivity to probability of attaining the incentive?

There is little research on this topic but there is one example that touches on this in *Vigor*. Seideman et al. (2018) trained monkeys to watch a monitor in which two yellow targets appeared to the left and right of a fixation point. After a short fixation period, the fixation point disappeared, instructing the animal to go, and a reward cue appeared shortly after identifying which of the two targets was to be rewarded. Once the rewarding target was identified, the monkeys had a maximum of 450 ms following the go cue to start the saccade.

Cue processing time refers to the time from the cue onset to the saccade onset, and reflects the amount of time the monkeys had to acquire information about the identity of the rewarding target. The greater the cue processing time, the more certain the animal would be regarding its decision. Indeed, the probability of choosing the rewarding target increased with greater cue processing time (Figure 3.15 in *Vigor*). Interestingly, saccade vigor also increased with cue processing time suggesting that the animal was more confident that they would be rewarded. However, as cue processing time became very long, vigor decreased to baseline. This surprising result can also be explained by considering the probability of attaining reward. As cue processing time increased, the monkey was more likely to exceed the maximum time limit of 450 ms, which would remove the possibility of reward entirely. That is, as cue processing time became very long, it became less likely that the animal would be rewarded, and vigor was reduced.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press

Thus, in the data of Seideman et al. (2018), we see that as cue processing time increases, the probability of incentive attainment increases, and so does saccade vigor. But, as the processing time becomes too long, the probability of acquiring the incentive drops to zero, and now saccade vigor returns to baseline. Thus, for this elementary movement, vigor investment is responsive to probability of successful attainment of the incentive.

R3. Threats can increase vigor

Bufacchi and Iannetti note that as the level of threat increases, an animal is more likely to spend energy to defend or escape that threat. Thus, avoidance of loss can lead to increased vigor. Indeed, the foraging literature documents a distinct effect of starvation threat on risk-taking behavior, with animals more likely to engage in risky behavior when they are close to starvation than when they are not (Barnard & Brown, 1985). A recent experiment illustrates the dual nature of serotonin in control of vigor in low- and high-threat environments.

Seo et al. (2019) optogenetically stimulated serotonin neurons during open field locomotion and noted that this caused an immediate reduction in vigor: walking speed declined. Similarly, when the mice were placed in a chamber where they had learned to associate a tone with availability of water, stimulation of the serotonin neurons reduced their approach speed toward the water spout. In contrast to these low-threat scenarios in which increase in serotonin reduced vigor, the effect of serotonin release reversed during high-threat scenarios. To produce a high-threat condition that encouraged an attempt to escape, the authors hung the animals by their tail to a horizontal bar and then measured the resulting struggle using an accelerometer. Being hung upside down naturally induced occasional bursts of rapid movements. Surprisingly, these high vigor movements accompanied high serotonin activity. In this context, stimulation of serotonin neurons increased vigor of the escape movements.

Thus, under low-threat conditions the release of serotonin reduces vigor, but under high-threat conditions the same release enhances vigor. How the possibility of threat and loss is represented by the brain, and how that representation interacts with serotonin and dopamine release to affect vigor, are fascinating topics that remain to be better explored.

R4. Building roads that connect communities of science

In the lovely analogy drawn by **Matsushima et al.**, Roman roads were the core infrastructure that brought together various nation-states, leading to exchange of goods and ideas. In *Vigor*, the mathematics of optimal foraging acts as a road that connects neurophysiology of decision-making, energetics of biomechanics, and kinematics of motor control. To continue this road-building, let us summarize some of the questions raised by the reviewers, and suggest experiments that might address them:

1. How does probability of reward affect vigor of movements? Decreasing probability should lower the expected value of a certain reward and correspondingly reduce vigor.
2. The effort required to attain a reward can discount its value. When the brain is deliberating a decision between two options, does the effort-discounted value of each option affect the vigor of movements toward the stimulus that represents the option?
3. As reward value increases, a level of difficulty (effort expenditure) that previously was too steep of a cost to pay may now become affordable. Thus, although the value of the stimulus can be discounted by its effort requirements, it is also affected by the probability that the expended effort will acquire the reward. Does vigor reflect this interplay between effort requirements and probability of incentive acquisition?
4. Does vigor reflect absolute reward and effort costs, or rather is vigor a measure of reward and effort costs relative to an aspiration level?
5. Do individuals infer another individual's subjective valuation of an acquisition by observing the vigor of their movements? If so, how does this affect their own valuation and hence the vigor of their own movements? In other words, does vigor serve as a social cue reflecting and driving valuation in ourselves and others?
6. How does scarcity of resources influence vigor? Scarcity can lead to competition for these resources; if vigor increases the probability of reward, then scarcity should lead to greater vigor. The subjective value of a scarce resource may also be greater than the subjective value of the same resource when more abundant. In this case as well, scarcity should lead to greater vigor.
7. What is the influence of threat on vigor? How do these effects interact with risky decision-making and what roles do dopamine and serotonin play in determining these effects?

Although the roads that we have built in *Vigor* have pitfalls, if they are to have a lasting effect, they must facilitate exchange of ideas between the fields of neuroeconomics, decision-making, and motor control. A most encouraging sign is the broad spectrum of science reflected in the reviewer comments, suggesting that this exchange has begun.

Financial support. This study was supported by grants from the National Institutes of Health (1R01NS096083 and 1R01NS078311).

Conflict of interest. None

References

Barnard, C. J., & Brown, C. A. J. (1985). Risk-sensitive foraging in common shrews (*Sorex araneus* L.). *Behavioral Ecology and Sociobiology*, *16*(2):161–164, doi: 10.1007/BF00295150.

Bautista, L. M., Tinbergen, J., & Kacelnik, A. (2001). To walk or to fly? How birds choose among foraging modes. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(0027–8424 (Print)):1089–1094, doi: 10.1073/pnas.98.3.1089.

Hunter, L. C., Hendrix, E. C., & Dean, J. C. (2010). The cost of walking downhill: Is the preferred gait energetically optimal? *Journal of Biomechanics*, *43*(10):1910–1915.

Jonikaitis, D., & Deubel, H. (2011). Independent allocation of attention to eye and hand targets in coordinated eye-hand movements. *Psychological Science*, *22*(3):339–347.

Lovejoy, L. P., & Krauzlis, R. J. (2010). Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgments. *Nature Neuroscience*, *13*(1097–6256 (Linking)):261–266, doi: 10.1038/nn.2470.

Rolfs, M., & Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. *The Journal of Neuroscience*, *32*(40):13744–1352a, doi: 10.1523/JNEUROSCI.2676-12.2012.

Seideman, J. A., Stanford, T. R., & Salinas, E. (2018). Saccade metrics reflect decisionmaking dynamics during urgent choices. *Nature Communications*, *9*, 2907. https://doi.org/10.1038/s41467-018-05319-w.

Seo, C., Guru, A., Jin, M., Ito, B., Sleezer, B. J., Ho, Y. Y., … & Warden, M. R. (2019). Intense threat switches dorsal raphe serotonin neurons to a paradoxical operational mode. *Science*, *363*(6426), 538–542.

Shadmehr, R., Reppert, T. R., Summerside, E. M., Yoon, T., & Ahmed, A. A. (2019). Movement vigor as a reflection of subjective economic utility. *Trends in Neurosciences*, *42*:323–336, doi: 10.1016/j.tins.2019.02.003.

Yoon, T., Geary, R. B., Ahmed, A. A., & Shadmehr, R. (2018). Control of movement vigor and decision making during foraging. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(44):E10476–E10485.

Yoon, T., Jaleel, A., Ahmed, A. A., & Shadmehr, R. (2020). Saccade vigor and the subjective economic value of visual stimuli. *Journal of Neurophysiology*, *123*(6):2161–2172, doi: 10.1152/jn.00700.2019.

https://doi.org/10.1017/S0140525X20000667 Published online by Cambridge University Press