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EDITORIAL

Ordinaries 8

Thaler, cashews & Tinbergen: biological mechanism and behavior

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Ordinary: "With no special or distinctive features; normal. Not interesting or exceptional; commonplace."
- Oxford English dictionary.

Abstract
The "cashew conundrum" is a seminal event in the history of economics. Professor Richard Thaler observed that his guests were happier not having the option to consume pre-dinner cashews. The fact that people can be happier with fewer options directly contradicts core assumptions in neoclassical economics, and is labeled an "anomaly" by behavioral economics. Far from being surprising, the cashew phenomenon is predicted by biological methods for understanding behavior. The cashew conundrum is not an anomaly, but rather an ordinary.

1 Richard Thaler's cashews launched 1,000 anomalies

'"Newton had his apple," [Professor Richard] Thaler said in an interview, with the bit of mischief he's known for in the classroom. "I had my cashews."'(Chicago Booth Magazine, 2015). In this article, we analyze Richard Thaler's cashew epiphany, which led to the creation of the field of behavioral economics and Professor Thaler's Nobel Prize.

Behavioral economic scholars focus on situations where human behavior diverges from that predicted by neoclassical economics. Behavioral economics utilizes the framework of Thomas Kuhn's *The Structure of Scientific Revolutions* (1970), labeling these divergences as "anomalies."

"An empirical result is anomalous if it is difficult to "rationalize," or if implausible assumptions are necessary to explain it within the [neoclassical] paradigm."

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(Thaler, 1987, p. 198). Behavioral economics is built on a foundation consisting of these anomalies.

Here is the seminal anomaly that created behavioral economics:

> "Some friends come over for dinner. We are having drinks and waiting for something roasting in the oven to be finished so we can sit down to eat. I bring out a large bowl of cashew nuts for us to nibble on. We eat half the bowl in five minutes, and our appetite is in danger. I remove the bowl and hide it in the kitchen. Everyone is happy." (Thaler, 2016, p. 34).

The dinner party anomaly, which we label the "cashew conundrum," is contained in the last sentence: "Everyone is happy." Neoclassical economics assumes that more options are always better than fewer. Accordingly, a guest should be unhappy to have the cashews removed. The notion that a person might eat a cashew and be unhappy is antithetical to the concept of "revealed preference," the bedrock of neoclassical economics (Samuelson, 1938).

The cashew conundrum is the parent of all the subsequent behavioral economic anomalies. Thus, we focus our attention on this key event in the history of economics. Why do people sometimes regret eating cashews? This article explores the cashew conundrum within the mission of this series (Burnham & Phelan, 2019):

> The Ordinaries column will interpret economic behavior from the perspective of evolutionary biology. From this view of life, the anomalies of behavioral economics will disappear into a coherent biological framework that incorporates elements of neoclassical maximization.

2 Economic views of the cashew conundrum without natural science insights

We suspect that every person reading this article has overeaten before a meal and regretted it subsequently. "Please take the chips and salsa away!" How can identifying such an ubiquitous human experience lead to a Nobel Prize? Here is how Richard Thaler explains the relationship between the cashew conundrum and economic theory (Thaler, 2016, p. 110):

> We want to eat just a few more nuts, but are worried that if the bowl is left on the table, we will submit to temptation.
>
> This distinction between what we want and what we choose has no meaning in modern [neoclassical] economics, in which preferences are literally defined by what we choose. Choices are said to "reveal preferences." Imagine the following conversation between a Human who just removed a bowl of cashews with an Econ looking on. [Econ articulates neoclassical theory.]
>
> *Econ:* Why did you remove the cashews?
> *Human:* Because I did not want to eat any more of them.
> *Econ:* If you did not want to eat any more nuts, then why go to the trouble of

removing them? You could have simply acted on your preferences and stopped eating.
Human: I removed the bowl because if the nuts were still available, I would have eaten more.
Econ: In that case, you prefer to eat more cashews, so removing them was stupid.

The human feels an internal conflict of wanting and not wanting the cashews simultaneously. This feeling is common to humans, yet not part of neoclassical economics. Actually, far from not being part of neoclassical economic theory, the incorporation of this ambiguity in preferences would destroy much of standard economic theory. So, what seems like a trivial and obvious statement about human nature is, in fact, very serious for economic theory.

Is the cashew conundrum something new? No. Internal conflict is an essential part of the human experience. Every person has been similarly conflicted. More than 2,000 years ago, Plato wrote, “And might a man be thirsty, and yet unwilling to drink? Yes, he said, it constantly happens. And in such a case what is one to say? Would you not say that there was something in the soul bidding a man to drink, and something else forbidding him” (Plato 360 BCE, Jowett 1888 translation).

Similarly, Sigmund Freud’s theories are based on a three-agent view of the mind. Ego, superego, and id frequently clash (Freud, 1923). So, the idea of internal conflict for people is not new. It has been documented by some of the most famous historical intellectual figures, long before Richard Thaler’s dinner party.

Should we condemn Richard Thaler because his cashew conundrum is obvious and has been well-articulated for thousands of years? Of course not. Many people had observed apples falling before Sir Isaac Newton, and this does not diminish Newton’s accomplishments.

Nonetheless, what is the state of economics today, roughly 50 years since the dinner party that launched a thousand anomalies?

Table 1 contains a summary of economic views of the cashew conundrum. Neoclassical theory argues that eating cashews before a meal, even to the point of nausea, reveals an optimal choice. Behavioral economics sees overeating before a meal as one of thousands of mistakes that people make.

A similar situation extends beyond cashews to all human economic behavior. Neoclassical economics stands, Thermopylae-like, unwavering in defense of revealed preference theory and optimal decision-making. Standard textbooks and curricula

Table 1 Economics of the cashew conundrum without insights from biology

Phenomenon	People eat too much at the wrong time and sometimes regret their overeating behavior.
Neoclassical economics	Eating cashews before dinner, even when it leads to an inability to eat the main course, is optimal. People know what they are doing and their behavior is optimal.
Behavioral economics	People suffer from heuristics and biases. These behavioral tendencies lead to suboptimal outcomes. Eating too many cashews is one of countless human foibles documented by behavioral economists.

remain frozen in time from a period before the cashew conundrum. The foundational theorems of neoclassical economics are unaltered.

Meanwhile, behavioral economics has proceeded to document hundreds, if not thousands, of anomalies. Many of these anomalies capture real, important aspects of human nature like those described by Plato, Freud and other scholars. In any particular circumstance, behavioral economic predictions of human behavior are likely to be more accurate than neoclassical predictions.

Behavioral economics, however, has important shortcomings. The anomalies are imprecisely stated, so they make no clear prediction of behavior. Moreover, the anomalies can be inconsistent with each other. The ambiguities and lack of precision stem, we argue, from the absence within behavioral economics of any underlying theory explaining human behavior.

We argue that the organizing theory for human behavior lies in biology and evolutionary theory. The current state of economics, without the natural sciences, is exactly what is expected for a field without any foundation.

A century ago, much of biology consisted of theory-free observation and cataloging of behavior. The evolutionary scholar Theodosius Dobzhansky (1937, 1973) observed that biology "without the light [of evolution] it becomes a pile of sundry facts, some of them interesting or curious but making no meaningful picture as a whole." Subsequently, the modern synthesis (Dobzhansky, 1937; Huxley, 1942; Mayr & Provine, 1980) transformed biology into a field where observations of behavior are grounded in theory.

Biology is no longer a pile of sundry facts.

Economics still awaits its equivalent of the modern synthesis. Until such a revolution, economics will remain a field divided upon itself. Neoclassical economics is fatally flawed. It fails to incorporate obvious, universal human behaviors that have been known and described for thousands of years. Behavioral economics is a pile of sundry anomalies, some of them interesting or curious, but making no meaningful picture as a whole.

3 Natural selection is the foundation for understanding behavior

Neoclassical economics assumes that people are very good at making decisions, while behavioral economics points out human foibles. Richard Thaler summarizes the disagreement as, "humans are dumber and nicer" than assumed by neoclassical economics.

Who is right? Are humans excellent decision-makers or are we filled with behavioral heuristics and biases? What do the natural sciences say?

The natural science perspective on this question is based on the work of Niko Tinbergen for which he shared the 1973 Nobel Prize in Physiology or Medicine. Animal behavior is studied within a framework which states that the behavior is best investigated from four distinct, but complementary, perspectives (Tinbergen, 1968, p. 1412; see also Tinbergen, 1963).

(1) In what ways does this phenomenon (behavior) influence the survival, the success of the animal?
(2) What makes behavior happen at any given moment? How does its “machinery” work?
(3) How does the behavioral machinery develop as the individual grows up?
(4) How have the behavior systems of each species evolved until they became what they are now?

For our purposes, ultimate (#1 above) and proximate (#2) causation are the most relevant. They are explained below and at greater length in Ordinaries 3 (Burnham & Phelan, 2020b).

3.1 Tinbergen's ultimate causation: Natural selection favors optimal behavior

In many, perhaps even most, cases animals exhibit incredibly sophisticated behavior that can be thought of as optimal. There are tens of thousands of empirical, experimental studies—across the entirety of the animal kingdom—which document this.

What do we mean by “optimal”? Within the natural sciences, this has a precise and quantifiable meaning (Hamilton, 1964; Parker & Smith, 1990). Optimal behaviors (whether relating to choosing foods, selecting mates, avoiding predators, etc.) cause the individual to produce more offspring, over the course of their life, than if they used a different behavior.

Optimal, of course, comes with a whole set of caveats and nuances. An important twentieth century clarification is that selection favors not just an organism's offspring, but also genes that are likely to be contained in genetic relatives such as nephews and cousins (Hamilton, 1964). There are other qualifications and nuances that we do not describe here (see Parker & Smith, 1990, for a fuller discussion).

We understand why animals engage in the behaviors that maximize their reproductive success. It is simply the numerical outcome of natural selection.

Each animal can be viewed as a little machine. What makes a rodent eat one seed type rather than another? Why does a deer choose a mate with the biggest rack of antlers? Why does a lizard remain motionless to avoid detection when a predator is nearby?

In each case, the animal has instructions that cause these behaviors. The instructions are segments of the DNA—genes—that specify how to build structures and generate behaviors. Different individuals within a population can have different versions of the instructions, causing them to look or behave differently.

Depending on which version of the instructions an organism has, they may produce more or fewer offspring. Biologists say that the instructions (alleles) leading to more offspring are higher “fitness” instructions.

In the next generation, there will thus be more individuals born with the higher-fitness instructions. Those instructions have increased their market share within the population. Conversely, the lower-fitness instructions have decreased market share.

Every so often, new instruction sets may crop up. Mutations in the DNA generate these new instruction sets. Those new instruction versions, like all the other versions in play within the population, will increase or decrease their market share based on their impact on the relative number of offspring produced by individuals carrying those instructions.

Ultimately, the most common behaviors and physical structures and physiological processes that we see in a population are those generated by the (currently) winning instruction sets. We don't tend to see behaviors that cause little or no reproductive success, because the instructions responsible for generating those behaviors are, by definition, no longer present in any individuals.

The result of this process is that the behaviors we see are neither random nor mysterious. They're the optimal behaviors. They are generated by the instruction sets that confer the highest fitness and the individuals carrying those instructions are optimal in the sense that they are maximizing their reproductive success. In other words, as we said at the outset: "In their natural habitat, animals tend to behave optimally."

3.2 Tinbergen's proximate causation: Animals don't necessarily optimize—especially in novel environments

One very important clarification is needed. The instructions that are best in one environment aren't necessarily the best in another. (Why would they be?).

This biological perspective on behavior provides an accurate predictive framework for which behaviors should occur when the organisms are in their native environment. This is true for all animal species, including humans.

Further, this biological perspective directs us toward the physiological mechanisms which generate those behaviors. For example, in Ordinaries 6 (Burnham & Phelan, 2021b), we discuss the receptors in the body that respond to eating dietary fat by releasing dopamine in the human brain's pleasure center.

As in other animals, humans have specific neural architectures that are inflexibly active in particular situations. Shine a light in a person's eyes, the pupils shrink. Place ice on the neck, and the person recoils. Put a Big Mac bite in the mouth and stomach, dopamine floods the dorsal striatum, etc.

When we understand the mechanisms that generate a behavior, and when we are able to identify novel environmental features that make it different from the organism's native environment, we can make sense of (and even predict) apparently anomalous behaviors.

Relatedly,

(1) Some key features of the current environment of modern humans make it different from our native environment (Bowlby, 1969; Tooby et al., 1992).
(2) We have a detailed understanding of many mechanisms underlying human behavior.

Together, this understanding of past and present human environments, and of the mechanisms underlying our "preferences," allows us to predict human behavior across a wide-range of behaviors. It is helpful—and often simpler—to explore this approach in animals, too, so we begin there.

4 "Anomalies" in animals

We will examine three "anomalies" of non-human animal behavior. (Humans are animals, but from now on we use animal to mean non-human.) The goal of the Ordinaries series is to use natural science approaches to improve economics.

Because behavioral economic anomalies are central, we focus on natural science techniques for understanding animal behaviors that may be similar. We then apply general lessons to humans, including the cashew conundrum and other behavioral economic anomalies.

Biologists do not use the term anomalies because biological theories of behavior predict the specific types of situations in which non-maximizing behaviors are expected. Furthermore, the nature of the biological anomalies differs from behavioral economic anomalies. The biological anomalies we discuss focus on mortality and morbidity.

For reasons that we articulate in the first Ordinaries article (Burnham & Phelan, 2019), behavioral economic anomalies focus primarily on inconsistencies. For example, a person may want a cashew now, but *regret* the cashew in fifteen minutes, whereas our biological anomalies are more akin to *dying* from eating (or not eating) the cashew.

4.1 Animal Anomaly 1: suicidal sea turtles

Sea turtle hatchlings frequently die because they mistakenly crawl away from the ocean and toward highways (this discussion of sea turtle misorientation was inspired by Lloyd et al., 2014). This incorrect orientation frequently results in death. We begin with an anecdote and then more on sea turtle anomalies.

E.O. Wilson, the great biologist, was giving a Harvard lecture on "taxis," the movement toward or away from cues. Female natterjack toads, for example, exhibit "positive auditory taxis" by moving up a sound gradient in search of a relatively larger male toad able to produce loud sounds, and, presumably, healthy offspring that will be similarly attractive.

As Professor Wilson was lecturing to the 300 students in the auditorium, he stopped, looking perplexed. He pointed to a student in the front row, named Darrell. Addressing the student, E.O. said, "I can't help but notice that you have a chicken in your lap" (which was indeed true). This appeared to be part of some finals club initiation ritual, and E.O. looked uncomfortable in the situation.

Darrell replied, "If you are so smart Professor Wilson, why did the chicken cross the road?" E.O. smiled and looked relieved, "That's easy. That is positive road taxis." The crowd roared, and Darrell slinked out of the lecture hall (with his chicken).

But, joking aside, many sea turtles actually do exhibit positive road taxis, with disastrous consequences.

Although they live most of their lives in water, sea turtles must lay their eggs in nests on land (Miller et al., 1997). The sea turtle hatchlings then must immediately crawl to the water and swim away from the shore as directly as possible (Lohmann & Lohmann, 1996). Historically, the hatchlings execute these critical behaviors successfully. One study documented that 92.4% of hatchlings reached the water (Erb & Wyneken, 2019).

Today, however, most sea turtle species are in decline and many are endangered (Swindall et al., 2019). Why? Because in much of their habitat today significant numbers of hatchlings behave in a sub-optimal manner. Some hatchlings, for example, stay in shallow water along the shore instead of moving out to the safety of deeper water (Truscott et al., 2017). More strangely, though, is the fact that many sea turtle hatchlings crawl away from the water, which leads to near certain death, from motor vehicles or dehydration or predation (McFarlane, 1963).

Animal Anomaly 1: Sea turtle hatchlings exhibit "positive road taxis," which leads to death.

4.2 Animal Anomaly 2: fat, unhealthy orangutans

In the early 2000s, one of us (Terry) answered his phone in his Cambridge, Massachusetts apartment.

Caller: Hello, is this Terry Burnham?
Terry: Yes.
Caller: I am unhappy because you called my baby "fat."
Terry: What? Who are you?

The caller was, in fact, not correct. We—Terry and Jay—had not called her baby fat; we had called him "really fat." The caller was the famous anthropologist, Dr. Lyn Miles. Her "baby" was the orangutan Chantek (also very famous) that she raised in a human environment. Here is the text from Mean Genes (2000) that offended Dr. Miles.

> Chantek is a smart, lovable orangutan who lives at the Atlanta zoo. Trained in sign language, he has a vocabulary of more than 150 words, and he is considered a decent artist. Now in his twenties, he was born at the Yerkes Primate Center in Atlanta and then spent nine years being raised like a human – complete with diapers and infant formula.
>
> Growing up in this human setting, Chantek became *really fat*, weighing in at five hundred pounds, roughly three times his ideal size. Afraid that the massive bulk would collapse his lungs, scientists placed him on a strict diet. Formerly five hundred pounds of fun, he became four hundred pounds of anger. During the diet, his favorite sign language symbol became "candy." He refused to draw and instead ate the crayons given for his artistic use.
>
> While on his diet, Chantek even pulled off an escape. He threatened and could have easily killed a janitor, but chose instead to attack a 55-gallon drum of food. He was eventually found sitting next to the up-ended food barrel, using all four limbs to stuff monkey chow into his mouth.

Chantek is not alone in his weight problems. Zoo orangutans tend, like Chantek, to become *really fat*, weighing in at 2–3 times the weight of wild orangutans. Zoo orangutan obesity produces a wide variety of negative health effects including breathing problems, kidney disease, heart disease, and diseases of the gut (Cassella, 2012; Lowenstine et al., 2016; McManamon & Lowenstine, 2012; Hamilla, 2018).

Animal Anomaly 2: Zoo orangutans eat too much, move around too little, and so get unhealthily fat.

4.3 Animal Anomaly 3: primate drug addicts

Rhesus monkeys enjoy drugs so much that, if given access, they die from overuse. In fact, when given the opportunity to self-administer cocaine or amphetamines, 100% of rhesus monkeys in one study consumed cocaine or d-amphetamines until they died. The cocaine-using monkeys all died in less than one week (Johanson et al., 1976).

In a related study, hungry rhesus monkeys were given a choice between food or cocaine (Aigner & Balster, 1978). Before the experiment started, the monkeys had no food for 23 h. During the experiment, every fifteen minutes, each monkey had the option to choose either cocaine or food. The experiment lasted for eight days. In the first few days, the monkeys chose cocaine at nearly every single opportunity.

At this point, the experimenters altered the system to invert the rewards. When the monkeys made the choice that had previously led to cocaine, they were given food instead. After days of binging on cocaine, not eating, and losing weight, what did the monkeys do with the unexpected food? Nothing. They consumed almost none of it. Instead, they quickly learned the new behavior required to obtain cocaine. The monkeys continued using cocaine and ignoring food until the experiment ended.

Animal Anomaly 3: Primates with access to drugs consume them to the point where they harm themselves and/or die. Summarized as, "The animals chose cocaine almost exclusively, which resulted in high cocaine intake, decreased food intake, weight loss, and marked behavioral toxicity" (Aigner & Balster, 1978, p. 534).

In the next three sections, we explain each of these animal anomalies using natural science approaches. For behavioral economists, documenting an anomaly is the end of the path of understanding the behavior. For biologists, however, documenting some puzzling behavior is the beginning of the process.

We aim to illuminate behavioral economic anomalies by understanding animal behavior. We address some of the underlying difficulties in a subsequent section. Are humans animals? Yes. Is human behavior qualitatively different from that of animals? Sometimes. Nevertheless, we argue that the same biological approaches to animal behavior can help resolve the cashew conundrum.

5 Suicidal sea turtles explained

How do biologists make sense of sea turtles that move away from the safety of the ocean and die inland from cars, dehydration, and starvation? Before investigating this anomalous behavior, it is helpful to first discuss a bit of sea turtle behavior and physiology.

5.1 Sea turtle behavior

Sea turtles, as their name suggests, live in water. All life on earth originally developed in the oceans, then certain species evolved to live on land. All turtles are reptiles—sea turtle ancestors were terrestrial, and subsequently returned to the oceans (Evers & Benson, 2019).

Although sea turtles have adapted to an aquatic life in many aspects, they still lay their eggs on land. Adult female sea turtles climb up beaches, dig nests, lay two dozen or more eggs in a single nest, and then swim away.

Sea turtle females are picky about the type of beach they select based on the quality of the beach and the sand, and the location of the nest relative to the waterline and vegetation. Their choices help them to create nests in areas with better than average prospects for hatchling survival.

Sea turtle hatchlings emerge and survive or die on their own. In order to survive, sea turtles must navigate a gauntlet of predators on the way to the ocean, swim away from shallow shore waters, and continue toward deeper ocean areas, where they can grow to maturity (Glen et al., 2005; Tomillo et al., 2010). The survival rates to maturity and reproduction are extremely low, with under 1% of sea turtle hatchlings living to reproduce themselves.

Sea turtle hatchlings perform several behaviors that increase their survival odds. First, hatchlings generally emerge at night. Second, they orient themselves toward water and run, leaving the dangerous beach very quickly. Third, once in the water, hatchlings swim directly away from shore, escaping from the shallow kill zone as quickly as possible. Fourth, the hatchlings are able to swim long distances to reach development zones. The hatchlings are able to navigate across open ocean in quite direct routes in both daytime and nighttime.

5.2 The ultimate cause of sea turtle behavior

How do tiny newborn sea turtles perform so many complex, but essential, behaviors? The ultimate cause of such sophisticated behavior is natural selection, which favors gene variants that increase survival and reproduction.

Consider, for example, two gene variants that can influence the timing of sea turtle emergence out of the nest and on to the beach. One gene variant produces turtles that emerge both in the day and the night, while the second produces exclusive nighttime emergence. To the extent that predation is greater in the day, fewer of those gene variants will make it into the next generation. After all, they cause individuals possessing them to die before they can reproduce. This is natural selection acting to favor the genetic variant that produces more nighttime emergence.

A similar logic underlies each of the behavioral attributes listed above, as well as myriad other sea turtle adaptations not discussed here. Genes that improve orientation toward the water, thus reducing beach transit times are favored over competing genetic variants that produce less effective transit to water. Genes that create swimming directly away from the shore are favored, too, as are genes that facilitate efficient ocean navigation.

So, at one level, we can explain sophisticated sea turtle behavior as the product of natural selection. Over nearly-impossible-to-comprehend lengths of evolutionary time, natural selection has produced elegant solutions to the challenges faced by sea turtles and sea turtle hatchlings.

Perhaps the most quoted sentence from *The Origin of Species* is, “There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.”

Darwin highlights that the products of natural selection often are “beautiful and wonderful.” Sea turtle hatchlings emerging in darkness, running to the water while their siblings are eaten, then moving their tiny bodies out to sea with frenetic paddling before embarking on an epic voyage are indeed beautiful and wonderful.

The ultimate explanation for behavior lies in its evolutionary consequences. However, as we introduced above, biologists, most famously Niko Tinbergen, detail multiple different, and yet consistent, causes for behavior (Tinbergen, 1963).

5.3 The proximate cause of sea turtle behavior

For our purposes, proximate causation—that is, the mechanistic explanation for how a behavior occurs—is the most important of Tinbergen’s complementary explanations for behavior. (See Ordinaries 3 for a longer discussion of proximate and ultimate explanations of sex ratios.) Behavior is produced by specific physiologic machinery, often in combination with environmental cues, to produce flexible behaviors.

To understand the proximate cause of behavior, consider how sea turtles manage to preferentially emerge in the night. Anthropomorphizing sea turtles in the manner of animated movies, one can imagine the hatchlings emerging and waiting, buried in the sand, for their optimal moment to streak to the ocean. “Hold the line brothers and sisters, hold, hold, hold, … Now! Run for your lives!”

Obviously no such conversation takes place. The explanation is much simpler. Sea turtle hatchlings emerge from their eggs inside the nest in both daytime and nighttime. Without any conscious plan, and without any consideration of the time of day, the hatchlings crawl toward the surface.

If the temperature of the surface is too high (above 93° Fahrenheit, for example, in one species), the hatchlings become immobilized. This is the consequence of a physiological mechanism, requiring no conscious thought on the part of the hatchling (Spotila, 2004).

In the daytime, the beach tends to be hotter and exceed the threshold for inducing hatchling torpor. Once the sun sets, the sand temperature declines, and as it drops below some critical threshold, the hatchlings become energetic again and re-commence digging upward until they emerge.

There is between-species variation regarding mechanisms to favor nighttime emergence (Drake & Spotila, 2002). Some species, for example, have mechanisms that are not based on absolute temperature (93° in the example above), but rather on the temperature gradient (Gyuris, 1993). These differences between species are important for their individual conservation, but they are identical from the perspective of mechanisms creating behavior.

What appears indistinguishable from strategic, conscious behavior, is just produced by specific, biological machinery. This machinery was produced by natural selection over evolutionary time because the gene variants that create this physiology were more successful than competing variants.

A similar mechanistic explanation underlies every one of the complex sea turtle behaviors that we noted above. Consider the ability of sea turtles to travel thousands of miles in the open ocean on quite direct routes. This incredible navigation ability is produced by systems that orient the turtle relative to light rays. Moreover, some sea turtles are able to navigate even in complete darkness. In addition to systems that navigate based on visual cues, sea turtles have internal compasses that guide the organisms based on the earth's magnetic field (Lohmann & Lohmann, 1993, 1996).

When sea turtles emerge from the nest, their internal compass is built to direct them to travel at a fixed angle to the earth's magnetic field, relative to their growing sites. How could such a system arise? At first glance, it may appear to be similar to other adaptations. Turtles that swim in the correct direction win the evolutionary contest.

The sea turtle internal compass, however, is more subtle and complex than simply swimming in a fixed direction. The earth's magnetic field has changed over time—even as the sea turtles have been making use of it—including more than 100 geomagnetic reversals where the north and south magnetic poles swap (Cox, 1969).

Because the earth's magnetic field is not constant, sea turtle compasses must somehow be able to detect the *current* direction of the magnetic field. Clever studies have demonstrated that this detection process, at least in some species, takes place in the nest before birth, while the turtles are still developing inside their eggs. Experimenters arranged magnets around turtle nests that created magnetic fields that differed in direction from the earth's magnetic field.

Hatchlings that develop when exposed to the earth's natural magnetic field swim in the species' correct direction, from nesting sites to feeding areas that often are quite distant. Hatchlings exposed to artificial magnetic fields that differ from the actual earth's magnetic field, however, do not. In fact, they "had orientation that was statistically indistinguishable from random" (Fuxjager et al., 2014).

Specific mechanisms are responsible for producing all of the other salient behaviors that we had discussed. Adult female sea turtles select productive nest-sites based on a variety of factors including beach slope, width, presence of shells, and proximity to vegetation (Mortimer, 1990, 1995). Sea turtle females are reported to cluster nests near vegetation adjacent to beaches (Hays et al., 1995; Garmestani et al., 2000), and base their nesting choices, in part, on the environment cues, including wind burst and lunar cycles (Barik et al., 2014).

Turtle hatchlings run toward the ocean because there is more light coming from the ocean and the light from the ocean can strike the hatchlings at a lower angle to the earth (Limpus, 1971; Mrosovsky, 1978; Salmon & Lohmann, 1989; Lucas et al., 1992).

In contrast, natural light that comes from inland areas at night is much lower in intensity. It also tends to be at higher angles because trees and other vegetation block some of the low-angle light. Sea turtle hatchlings run toward brighter lights, coming at lower angles. For the entirety of sea turtles' existence as a species—until very, very recently—this mechanism has resulted in them running toward the ocean.

The final behavior we have discussed is the hatchlings ability to swim directly away from shore immediately upon entering the water. The mechanism that produces this behavior is the ability to detect the direction of waves and to swim directly into them (Lohmann et al., 1990). This mechanism has been extensively studied in artificial (i.e., wave tanks) and natural settings (i.e., dropping hatchlings in the ocean).

There is a beauty and elegance to sea turtle hatchlings behavior, owing to natural selection favoring particular genetic variants. These genes produce biological machinery that responds to environmental cues to produce adaptive behavior. Sea turtle hatchlings emerge at night, run directly to the ocean, swim away from shore, and then travel up to thousands of miles in the open ocean to ancestral territories.

5.4 Sea turtle destructive behavior is caused by mechanisms in novel environments

Beauty and elegance notwithstanding, there is a downside to the mechanisms that generate sea turtle behavior. Because behavior is produced by the interaction between mechanisms and specific environmental cues, changing the environment can change behavior. In this case, with catastrophic consequences (Kamrowski et al., 2012).

The primary cause of suicidal sea turtles is human-created artificial light. The same mechanisms that reliably guided sea turtles to the ocean for literally millions of years, can, in the presence of artificial light, produce mis-oriented turtles who seem bent on self-destruction.

Because the hatchlings are disoriented by artificial light, their time on the beach is extended. This increases predation upon them. Further, the extra energy spent finding the water detracts from the limited amount of energy hatchlings derive from their yolk. This has a significant negative impact on their ocean migration (Salmon, 2006; Hamann et al., 2007). On moonless nights, sea turtle hatchlings that have made it to the ocean can even be induced to return to land by artificial lights (Truscott et al., 2017).

What causes sea turtle hatchling anomalous behavior? We know the answer. It is an adaptive, ocean-oriented biological mechanism operating in an evolutionarily-novel environment that includes human-created artificial light. Furthermore, the mechanistic approach does not end with simply identifying the cause of a problem.

The mechanistic approach also provides a path to resolution. For example, experiments show that loggerhead turtles are affected less by low-pressure sodium lights (Witherington & Bjorndal, 1991). Problems caused by mechanisms in novel environments can be mitigated—or resolved completely—by constructing new environments informed by detailed understanding of physiology.

5.5 Summary: suicidal sea turtle behavior is predicted and explained

Sea turtles have evolved to exhibit sophisticated survival and reproduction strategies. These behaviors have allowed sea turtles to successfully persist for tens of millions of years. These adaptive behaviors are produced by a combination of specific biological mechanisms operating in particular environments. For example, sea turtle hatchlings move toward bright light coming toward them at low angles relative to the ground.

The physiological mechanisms that have helped sea turtles for the entire history of the species get fooled by novel aspects of the environment, including human-created artificial light. Solutions to the problems with sea turtle navigation require detailed investigation of the biological mechanisms that produce behavior.

Puzzle: Sea turtle hatchlings die when they fail to crawl toward the water and to swim to deep water.

Explanation: Adaptive mechanism mismatched to a novel environment that includes artificial light.

Solution: Novel ways to illuminate human environments that do not confuse sea turtle hatchling biological mechanisms.

6 Fat, unhealthy orangutans explained

6.1 Orangutan feeding behavior

Orangutans are one of the four groups of primates—known as great apes, or hominids—that include humans and our closest evolutionary relatives. Chimpanzees and bonobos are our very closest relatives among these groups, with gorillas next closest, and then the orangutans (Andrews & Martin, 1987). Orangutans are native to Indonesia and Malaysia, with wild populations today in Borneo and Sumatra (Rijksen & Meijaard, 1999; Delgado & Van Schaik, 2000).

Living mostly in trees within tropical rainforests, orangutans are shorter than humans—with most between 3.5 feet and 4.5 feet tall—and more sexually dimorphic. Adult females average 80 pounds, while the average weight of adult males is 184 pounds (Smith & Jungers, 1997; Rodman, 1984). Their median lifespan is about 30 years in the wild, with a maximum recorded longevity of 58 years (Wich et al., 2009).

If one were to observe a population of orangutans, at first it might appear that they simply eat when they are hungry and randomly consume whatever fruits and leaves they see. But that's far from accurate. Orangutans are, in fact, highly selective about what they eat, with a well-established hierarchy of preferences, and dramatic boom-and-bust dietary shifts across the year, reflecting the annual fluctuations in fruit production (Leighton, 1983; Delgado & Van Schaik, 2000).

During the booming months with highest fruit production, orangutans eat nothing but fruit. Males consume more than 8400 kcal per day and females consume more than 7400 kcal per day (Knott, 1998). But fruit production is mostly over by May, at which point orangutan diets shift. As fruit abundance dwindles, the primary diet component becomes bark, along with large numbers of leaves and some insects (MacKinnon, 1974; Rodman, 1977; Rodman, 1984; Galdikas, 1988). During this "bust" period, male intake is just 3800 kcal per day and female intake is less than 1800 kcal per day (Knott, 1998).

6.2 The ultimate cause of orangutan feeding behavior

Orangutan feeding patterns reveal complex responses to fluctuations in fruit availability. Consistent with optimal foraging model predictions (MacArthur & Pianka, 1966; Charnov, 1976; Krebs et al., 1983; Stephens & John, 1986), orangutans exhibit adaptations for maximizing energy input and storage during times of food abundance, and reduced energy expenditure and efficient utilization of fat reserves when food is limited (Leighton, 1993; Leighton et al., 1995; Knott, 1998).

When fruit is abundant. During times of high fruit availability, orangutans employ a "search-and-find" strategy, actively seeking out locations with high fruit abundance (Knott, 1998; Russon et al., 2009). By only consuming easy calories from high-energy-content fruits, they maximize their caloric intake rate.

When fruit is scarce: During the months of fruit scarcity, orangutans switch to a "sit-and-wait" strategy, exploring less, minimizing activity, and reducing the depletion of their energy reserves (Knott, 1998; Russon et al., 2009). They switch their diet, too, increasing consumption of the inner cambium layer of bark, which is a significantly less-energy-rich food source. (They possess specialized dentition adaptations that improve bark opening and stripping [Martin, 1985].)

Additionally, orangutan ovarian activity and reproduction are suppressed during times of fruit paucity (Knott, 1998). This feedback between energy balance and hormone functioning (Ellison et al., 1993; Ellison, 2009) is an important adaptation, as orangutan reproduction is particularly energetically expensive and they have an 8-year interbirth interval (Galdikas & Wood, 1990).

6.3 The proximate cause of orangutan feeding behavior

Among all of the primates, orangutans experience one of the most extreme cases of alternating feast and famine. Their behavioral and metabolic physiology is characterized by numerous adaptive mechanisms. In response to specific environmental cues, these mechanisms enable orangutans to function within the extreme constraints imposed by the huge fluctuations in the amount and quality of food available to them.

6.3.1 During "feast" times, with positive energy balance

Food selection: Although they can eat, digest, and extract energy from a wide variety of easily accessible plant parts, orangutans pass over those items, consuming only fruits, which have a significantly higher energy payoff per unit of time (Leighton, 1993; Galdikas, 1988; Knott, 1998).

Energy usage and storage: In order to assess the physiological energetics of orangutans during feast and famine periods, it is necessary to conduct urinalysis. In humans, such analyses are relatively easy. Collecting urine from wild orangutans living high in trees in rainforests, on the other hand, poses some extreme logistical challenges. Amazingly, dressed in rain gear and armed with plastic sheet collection devices (sometimes resembling inverted umbrellas), intrepid anthropologists have been able to do this (Knott, 1997)!

Ketones are products of fat metabolism and are present in urine. Orangutan urinalysis revealed no ketones whatsoever during feast times (Knott, 1998). This indicates that orangutans are extremely effective at storing dietary fat and excess caloric intake as fat during these periods of high fruit consumption.

6.3.2 During "famine" times, with negative energy balance

Energy usage and storage: During periods of fruit scarcity, significant concentrations of ketones were present in orangutan urine (Knott, 1998). This is an indicator that the orangutans were energetically stressed, not meeting their energetic needs from their food consumption, and so were utilizing stored fat reserves (Robinson & Williamson, 1980). This is consistent with data showing significantly reduced daily caloric intake and large weight loss during this period, even as they spent a significantly greater proportion of their time resting (Knott, 1998).

Food selection: Orangutans switch to lower quality "fallback" foods during times of low fruit availability. During these periods, their predominant food source becomes leaves and bark, which have reduced caloric content (Kanamori et al., 2010).

Even during these times of negative energy balance and weight loss, orangutans don't simply eat whatever plant parts that they can find. In fact, they exert very strong and specific preferences. Out of the 45 species of available plants that they are able to consume and digest, just two species account for more than half of their foraging time (Hamilton & Galdikas, 1994).

Additionally, orangutans were extremely selective about which parts of the plants they consumed. They select young rather than mature leaves, which have higher protein content, with less fiber (Milton, 1979; Oates et al., 1980; McKey et al., 1981). They also carefully separate unripe fruits and flowers, consuming one part and discarding others (Hamilton & Galdikas, 1994).

Importantly, during times of low fruit availability, orangutan food choices are those species and specific plant parts having the highest protein content, while minimizing their intake of the relatively non-digestible chemicals cellulose and lignin (Waterman et al., 1983; Hamilton & Galdikas, 1994). Additionally, they avoid plant parts containing toxic secondary compounds, and condensed tannins, which bind to proteins and reduce their digestibility (Hamilton & Galdikas, 1994; Eori et al., 2019).

6.4 Genetic underpinnings of adaptive physiological and behavioral mechanisms

The mechanisms described here are adaptations to harsh, fluctuating environmental conditions that result from strong selection. Consistent with these observations, researchers using whole-genome sequencing identified numerous genetic changes associated with such mechanisms (Mattle-Greminger et al., 2018).

The genome of Bornean orangutans is characterized by consistent patterns reflecting physiological adaptations to fluctuating and unpredictable food supplies. In particular, the Bornean orangutan genome has an enrichment of genes under positive selection relating to:

* more efficient cardiac usage of restricted energy sources;
* enhanced fat and glucose metabolism and energy storage, potentially allowing buffering against starvation (Morrogh-Bernard et al., 2009; Isler, 2014);
* improved insulin and cholesterol regulation.

6.5 Summary: Fat, unhealthy orangutan behavior is predicted and explained

Behavioral and physiological mechanisms adapt orangutans to environments with fluctuating and unpredictable food supplies. But these same mechanisms are vulnerable to a sort of "environmental hacking." Consider the environmental cues associated with abundant food. These typically trigger mechanisms causing high food consumption, with an almost complete restriction of food intake to food items with the highest energy yield.

This "eat a lot, and only the best foods" approach leads to an appropriate and adaptive outcome when it occurs for the relatively brief period of high fruit availability in tropical rainforests. That's how natural selection works and why organisms become adapted to their environments.

But what happens when parts of rainforests are cut down and replaced with farmland? Nearby orangutans locate those farms and their high density of cultivated fruits. They raid the crops, supplementing their food intake and reducing their activity (Campbell-Smith et al., 2011). As a result, they meet their daily energy needs more easily and quickly.

Now take it one step further. Consider captive orangutans in a zoo environment—in which they are typically provided with year-round diets consisting of a wide-variety of fruits, high in caloric value and requiring little expenditure to obtain and consume, as well as commercial primate feeds, high in protein and calories (Dierenfeld, 1997; Cassella, 2012; Hamilla, 2018).

In zoos with rich food supplies, orangutan behavioral and physiological foraging and feeding mechanisms are triggered continuously, even though such a diet is qualitatively and quantitatively different from what is available in their natural habitat (Choo et al., 2011; Crosby, 2015; Dalimunthe et al., 2021). If cashews were available, the orangutans' feeding mechanisms would likely nudge them to consume them all.

How do their foraging mechanisms lead to the bad outcomes in captivity? Ultimately, orangutans living in these novel-to-them environments exhibit exactly the feeding behavior dictated by their adaptive behavioral and physiological mechanisms. As a consequence, they experience a predictable and wide range of pathologies, including:

* obesity (Jones, 1982; Leigh, 1994; Gresl et al., 2000; Schmidt & Zoo, 2004; Lowenstine et al., 2016);
* hyperthyroidism (Suedmeyer, 1997);

* hypertensive heart disease and stroke (Weisenberg et al., 1991);
* Type II diabetes (Gresl et al., 2000; Kuhar et al., 2013);
* atherosclerosis (Wang et al., 2012; Lowenstine et al., 2016);
* kidney disease, particularly chronic interstitial nephritis and glomerulonephritis (Lowenstine et al., 2008).

To reduce or mitigate a problem caused by a novel environment, natural scientists study the specific mechanisms producing the target behavior. Based on this knowledge, it is sometimes possible to create a new environment that produces a more positive behavior. For example, in the case of some sea turtle species, low-sodium lights illuminate well for humans, and do not confuse turtles.

In his zoo environment, forced dieting was not effective for helping Chantek. However, by understanding orangutan mechanisms, researchers were able to get Chantek to eat less, move around more, and become much healthier. Here is the end of the story as told in *Mean Genes*.

> When we met him, Chantek was dieting, hungry, angry, and dreaming of candy. After his escape and the monkey chow episode, he was moved to a new area with a much larger domain – several acres – where he must walk a bit to get his food.
>
> Furthermore, because wild male orangutans are territorial and spend much of their time patrolling their part of the jungle, Chantek likes (or feels compelled) to walk around to make sure that no males are intruding on his turf. Of course in the zoo there will never be intruders, but his genes don't know that.
>
> As a result, Chantek is much more active and, even though he is no longer on a strict diet, he has lost fully half of his 500 pounds.

Puzzle: Zoo orangutans get sick and die from being sedentary and overeating.

Explanation: Adaptive mechanism mismatched to a novel environment that includes excess, high-calorie food.

Solution: Engineer the environment to motivate increased voluntary orangutan activity.

7 Primate drug addiction explained

7.1 Rhesus monkey behavior

Rhesus macaques (*Macaca mulatta*), known as rhesus monkeys, are a species of primates whose range extends throughout south, central, and southeast Asia (Lindburg, 1971). Less closely related to humans than orangutans are, macaques are part of a group of taxa that includes baboons. Rhesus monkeys are among the most studied of all primates—in the wild, in laboratories, and in human-made research colonies. In google scholar, there are over 100,000 research articles on "*Macaca mulatta*."

Almost every aspect of rhesus monkey behavior, morphology, and genetics has been the subject of extensive study. Some of the important areas include the field study of diverse behaviors (Altmann, 1962; Lindburg, 1971), reproduction (Drickamer, 1974), eating (Marriott et al., 1989), predation (Anderson, 1986; Etting & Isbell, 2014), social dominance (Chikazawa et al., 1979; Bercovitch, 1993), innate mathematical abilities (Cantlon & Brannon, 2007), and genomics (Xue et al., 2016).

While our goal here is not to review the literature on rhesus monkeys, we make two points.

First, natural science investigations of rhesus monkey behavior are extremely detailed, including all the aspects listed above and many more. Natural scientists study the evolutionary payoffs to behaviors, the physiological mechanisms that produce behaviors, phylogenetic relationships between species, ontological development of mechanisms and behaviors, the underlying genes influencing the behaviors, and much more.

Second, rhesus monkeys have been successful at thriving in a complex and dynamic physical and social world for the more than 20 million years since the last common ancestor with humans (Stewart & Disotell, 1998). Survival and replication require avoiding predators, finding food, remaining healthy, retaining sufficient social rank, finding mates, raising offspring, and more.

7.2 The ultimate cause of rhesus monkey behavior and morphology

The process by which natural selection has produced morphology and behaviors in rhesus monkeys is exactly the same as it is for all other organisms, including humans.

Darwin described evolution by natural selection in *The Origin of Species* (Darwin, 1859):

> [in the] Struggle for Existence, we see the most powerful and ever-acting means of selection…More individuals are born than can possibly survive. A grain in the balance will determine which individual shall live and which shall die, – which variety or species shall increase in number, and which shall decrease, or finally become extinct…The slightest advantage in one being, at any age or during any season, over those with which it comes into competition, or better adaptation in however slight a degree to the surrounding physical conditions, will turn the balance.

Rewritten in current biology textbook form (Phelan, 2021), Darwin's seminal insight becomes:

> **Natural selection** is a mechanism of evolution that occurs when there is heritable variation for a trait, and individuals with one version of the trait have greater reproductive success than do individuals with a different version of the trait.
>
> **Adaptation** (which refers both to the process by which organisms become better matched to their environment and to the specific traits that make an organism more fit) occurs as a result of natural selection. (Examples of adaptations abound. Bats have an extremely accurate type of hearing, echolocation, for navigating

and finding food, even in complete darkness. Porcupine quills make porcupines almost impervious to predation. Mosquitoes produce strong chemicals that prevent blood from clotting, so that they can extract blood from other animals.)

Rhesus monkeys are just like all other extant species in having survived (so far) due to adaptations resulting from this process of natural selection. In short, we shouldn't be surprised at the sophistication and elegance of rhesus monkey behavior and physiology.

7.3 The proximate cause of rhesus monkey behavior

In the cases of sea turtles and orangutans, we have described some details of specific physiologic machinery. In the case of rhesus monkeys, let's zoom out to consider the bigger picture of evolution, and the evolution of behavior in particular.

Do rhesus monkeys make conscious mathematical calculations to maximize reproductive success? For example, do they think, "Is coming to the aid of my sister when she is attacked by a predator—which carries some risk of death—an adaptive behavior? My help will have potential benefits for my sister's offspring, with which I share one-quarter of my genes. But taking the risk also carries potential costs with respect to my own daughters, with which I share one-half of my genes."

No. For monkeys—and for virtually all organisms—behavior is driven by proximate mechanisms. Among vertebrates, these proximate mechanisms usually involve dopamine in the brain's pleasure centers. No conscious thought is required to perform most behaviors.

However, natural selection favors mechanisms that generate pleasure from behaviors that lead to genetic replication. That is, it causes those mechanisms to increase in frequency in a population over time (see Ordinaries 3, Burnham & Phelan, 2020b). Monkeys make no calculation of evolutionary payoffs, but they can be said to behave *as if* they were choosing to maximize reproductive success (see Friedman & Savage, 1948; Friedman, 1953, for the 'as if' assumption in economics).

Rhesus monkeys in their natural setting can behave in an optimal manner by following a simple rule: Do what feels best. Maximize dopamine release in the brain pleasure centers. There is no need for self-control and no need for analysis. Just maximize pleasure.

So, rhesus monkeys and other animals are built to seek pleasure. And in their natural environment, seeking pleasure reliably leads to survival and reproduction.

Eating foods that are nutritious will cause the release of relatively large amounts of dopamine, as will maintaining appropriate temperature by navigating sun and shade. Sex is pleasurable, as is sleeping. Fighting and killing other rhesus monkeys can produce dopamine if it leads to higher dominance rankings. Care and feeding for its offspring, too, will produce pleasure for rhesus monkey mothers.

Put another way, happiness is a genetic incentive scheme to induce animals to survive and reproduce (see Ordinaries 4, Burnham & Phelan, 2020c). Natural selection has forged reward circuits that induce genetic replication. As a consequence, pleasure seeking and genetic payoffs are in sync.

In contrast, genetic mismatch—the situation in which organisms are in novel environments—is the cause of self-destructive animal behaviors and the cause of behavioral economic anomalies. Sea turtles get lost in environments with artificial light, and orangutans become sick and overweight in zoos filled with excess food.

When it comes to mismatch, however, nothing is more destructive than direct manipulation of the very currency of motivation. This is exactly what is occuring when organisms have access to drugs that directly stimulate the pleasure center.

7.4 Primate drug addiction is caused by mechanisms in novel environments

In the wild, animals can perform myriad behaviors. In response to each, they may get punished with pain or rewarded with pleasure. Pain is an effective evolutionary adaptation that causes animals to steer clear of behaviors with negative evolutionary payoffs. Conversely, pleasure is an evolutionary adaptation selected to reward behaviors that redound to the benefit of the organism's genes.

Behavioral punishments and rewards are fine-tuned based on both the environment and the internal state of the organism. Orangutans get more pleasure from eating fruit than bark because fruit is more valuable. Similarly, people get more dopamine from eating when hungry than sated, because the same food has more value when the organism's energy reserves are lower.

Novel environments create all sorts of problems for organisms. This has been a persistent theme of Ordinaries. Fish out of water die. Astronauts in space must learn how to sleep. Birds in laboratories "impatiently" choose a more-immediate-but-smaller food reward, even when they will just cache it for the future (Burnham & Phelan, 2021a). People eat Big Macs even as they want to weigh less. Sea turtles walk toward artificial lights. Orangutans eat too much in zoos. The list is endless.

The most fundamental mismatch occurs in an environment in which organisms can directly produce pleasure, bypassing the peripheral behavioral mechanism usually needed for such a reward. Rhesus monkeys do this when they are able to press a lever that gives them access to cocaine or other drugs that increase the levels of dopamine in the brain's pleasure centers.

The brain is built to repeat those behaviors that produce pleasure. But when the pleasure pathways are hijacked, the brain does not know if the monkey has escaped a predator by an elegant leap between trees or by robotically pressing a cocaine-releasing lever. When flooded with dopamine, the brain simply says, "Good job monkey! Do that again, whatever it was."

7.5 Summary: primate drug addiction is predicted and explained

Economists assume that people maximize happiness. Biology agrees that organisms are built to repeat behaviors that produce pleasure. The biological view, however, provides two essential insights beyond the economist's hedonism.

First, the ultimate goal of pleasure-seeking is genetic replication. Over evolutionary time, natural selection favors physiologic mechanisms that reward behaviors that are in genes' interests. Happiness is an incentive scheme. Our genes can push us toward behaviors that appear brave or cowardly, kind or spiteful, energetic or slothful. Underneath each of the apparently disparate influences is the uniform selective pressure to maximize your relative rates of survival and reproduction.

Second, genetic mismatch leads to behavior that is not optimal from any perspective. Rhesus monkeys use drugs until they die. Sea turtles get squished by trucks on highways. Orangutans become sick and die from overeating. Drugs are the most extreme version of mismatch in that they subvert the entire mechanism for creating behavior.

Puzzle: Monkeys die from overuse of drugs, including cocaine and amphetamines.

Explanation: Adaptive mechanism mismatched to a novel environment.

Solution: Remove drugs from the environment. Note, humans can try to minimize drugs in the home or in their local environment. It is much harder for people to remove drugs from the broader community.

8 Is human behavior the same as non-human animal behavior?

In the next section, we explain the ultimate and proximate causes of the cashew conundrum. The summary is that hunger is an adaptation that helped our ancestors survive and reproduce.

An important aspect of our adaptive suite of feeding behaviors is constant surveillance of the environment for opportunities to consume food, particularly in situations like those of shelled cashews in a nearby bowl. Shelled cashews are high-caloric-density food that is accessible with very little effort.

Before we get into the details of how the human nucleus accumbens is flooded with dopamine by the sight and smell of cashews, however, let us address the notion of human self-control and human uniqueness.

It's not hard to find skeptics saying, "humans are not as dumb as lost sea turtles, overeating orangutans, or drug-loving monkeys." The skeptical argument continues, "We humans are able to control our passions and cannot be fooled by our primitive, biological mechanisms in the manner of simple animals."

We—Terry & Jay—do believe that humans are better able to control behavior than non-humans. Ordinaries 4: "The causes and cures of self-control problems," focuses on self-control techniques (Burnham & Phelan, 2020c). Our summary is that humans are indeed better at exerting self-control than other organisms. But such control is far from perfect. We all know this.

Here are three questions that might help illuminate the fact that biological mechanisms do indeed influence human behavior.

Q1. What does "hangry" mean?
Q2. Do you believe the men on steroids are more likely to be violent?
Q3. Have you been scared in a horror movie?

Answer 1: Hangry is defined in the Oxford English dictionary as "bad-tempered or irritable as a result of hunger." Does your partner behave differently when hangry? Your children? Do you? Does human behavior change with eating?

The fact that hangry people behave differently from those who are sated is evidence of the influence of biological mechanism on human behavior. Obviously, people have the ability to control our behavior to some degree. In theory, we can be nice to our families and friends even when starving. In practice, this isn't always the case. The biological response to food is a mechanistic system, akin to sea turtle navigation, that influences our behavior.

Answer 2: 'Roid rage—both the causes and the consequences—is well-documented. A particularly dramatic example of steroid-altering behavior is the case of a man who, while on steroids, purposely drove his fancy sports car into a tree. He was so excited by the prospect of this destructive act, he set up cameras to film the crash (see *Mean Genes* for a longer discussion of steroids).

Most 'roid rage incidents, however, are not funny at all. 'Roid rage is caused by the effects of injections of supraphysiological doses of certain chemical molecules interacting with a set of biological mechanisms.

Answer 3: Horror movies that terrify viewers reveal a mechanistic basis. Fear is an adaptive emotion, selected by evolution to produce appropriate behavior in dangerous situations.

When we sit in a movie theater seeing people in danger from a menacing villain or monster, part of our brain understands that we are safe, but other parts of our brain scream (neurologically), "We've got to get out of here." Horror movies produce their responses because the real-seeming images interact with our adaptive biologic neural machinery.

Even the eminent Richard Thaler acknowledges the importance of mechanism. In an email to one of us some years ago, he defended the non-biological, atheoretic foundation of behavioral economics, writing, "I don't need Darwin to tell me not to go grocery shopping while hungry."

Professor Thaler's note implicitly acknowledges the existence of mechanisms with clear impacts on human behavior. When food hits our stomach and intestine, it changes our brains so that we make different and better decisions in the grocery store and beyond.

Our view is that people are animals. Our behavior is influenced by our biological machinery and its interactions with the environment. We are not lumbering robots destined to carry out some pre-programmed genetic program. We are, however, nudged by our neural machinery in ways that are both subtle and profound.

9 The cashew conundrum from a natural science perspective

Destructive, apparently anomalous, behaviors are caused by a mismatch between a current setting and biological machinery selected to produce adaptive behavior in the ancestral setting. These destructive behaviors include mis-navigating sea turtles, overeating orangutans, drug-addicted monkeys, and Richard Thaler's cashew-consuming dinner guests.

Humans are built to eat because food is necessary for survival and reproduction. Furthermore, ancestral humans developed the ability to store extra calories on our bodies as a biological savings account to survive lean times.

The current wave of obesity is caused by an ancestral set of mechanisms evolved for times of periodic scarcity, functioning in an environment of persistent surplus. We are fat because our ancestors were hungry and faced starvation, but today many of us live in environments with no periodic food scarcity.

The motivational machinery of the human brain is constructed to produce appropriate, adaptive eating behavior for our ancestors, without the need for conscious awareness about the behavior's adaptive value. Hunger is one of the most powerful drives in humans and non-humans. Satiation is accompanied by dopamine, while hunger is produced by its absence, in reward centers deep within the center of the brain (Salgado & Kaplitt, 2015).

Not only are humans built to eat a lot and to overeat in times of surplus, we are also built to be finely-tuned to the costs and benefits of different potential food items. We have specific neural structures that motivate us by producing dopamine when we perceive food. We are built to look out for especially valuable food that is densely packed with calories, while requiring low effort to handle and consume.

A bowl of unshelled and salted cashews is an evolutionary gold nugget. Filled with massive amounts of calories, and available with no food preparation, and not even any energy required to find.

An ancestral human would have been crazy—and acting extremely maladaptively—not to eat cashews of the form presented by Richard Thaler. More than crazy, actually. The humans who did not eat the ancestral equivalent of free, already prepared and delivered cashews, are not our ancestors. Ancestral humans who did not take advantage of free calories lost the evolutionary battle to their contemporaneous competitors who did eat the cashews.

We eat the cashews because they were good for our ancestors. Consequently, the genes that produced smart, efficient eating (and not those that produce disinterest in the face of easy calories) have been passed down through the generations right into Richard Thaler's home.

9.1 The ultimate cause of human overeating

Why are so many people overweight?

In 1987, the anthropologists Peter Brown and Melvin Konner wrote, "Humans are the fattest of all mammals." "Food shortages have been so common in human prehistory and history that they could be considered a virtually inevitable fact of life in the past" (Brown & Konner, 1987).

Continuing their argument, Brown and Konner wrote, "Food shortages suggest a hypothesis of the evolution of obesity. Because shortages were ubiquitous for humans under natural conditions, selection favored individuals who could effectively store calories in times of surplus. For three-fourths of the societies, such stores would be depleted, or at least called on, every two to three years, and sometimes more frequently."

In 2000, we (Terry and Jay) made the same argument—obesity is caused by mismatch between current food availability and biological machinery selected to store extra calories as adaptive behavior in the ancestral setting—in *Mean Genes*. Here is an edited, shortened version of our description of the evolutionary source of modern, human obesity.

> Like zoo orangutans, many of us have trouble staying skinny and healthy. Easy living with plentiful food is the source of weight control problems for humans and captive orangutans alike. Our appetites were built in a world where plentiful food was inconceivable.
>
> Outside the industrialized countries, famine and malnutrition are still common, with half of the developing nations experiencing food shortages in a typical year. Under these conditions, it pays to build up some reserve against the hunger season that often lurks ahead. Indeed, our nearly insatiable appetite was once a survival feature of human biology. A profound love of food helps people to pack on a few extra pounds and thereby survive periods when food is scarce.
>
> Those thrifty genes still drive our behavior. Holdovers from the uncertain times of our ancestors, they function as though our world has not changed. It has. In our zoo-like environment we have continual access to food, and a suburban famine seems to occur when dinner is delayed for an hour or two.
>
> Our ancestors lived off the land by hunting animals and gathering plants. To understand how different our world is, consider the life of people who forage for survival even today. To acquire food, they expend hundreds of calories each day walking and then spend hours preparing meals. Just staying alive requires lots of energy – energy that can be found only in food.
>
> For those who are relatively affluent in industrial societies, a few taps on the accelerator take us to supermarkets brimming with food ready to be cooked or eaten. The garage is only steps from the kitchen, and the supermarket has a parking lot that brings us to within fifty feet of the food. If driving to a market is too taxing, we can use our phones for pizza or Chinese food.
>
> Our lives are filled with machines – remote controls, phones, refrigerators, electric can openers, TVs, computers, and cars – all of which help us get our fill of calories, social contact, and entertainment with minimal effort.
>
> Sitting on our couches, sitting in our cars, sitting at our desks, we are not experiencing any sort of energy crisis. Most of us already have too much stored energy on our bodies in the form of love handles, saddlebags, beer bellies, and other unwanted lumps of flesh.
>
> Powerful, instinctual hunger kept our ancestors going in a tough, energetically demanding world. Imagine a time when the individuals of a population vary in their appetites.
>
> One gluttonous type thinks of food day and night. Another type becomes satiated once their daily needs are met. Of these types, who has the biggest surplus of energy stored in their thighs and buttocks when food is scarce? Who weathers

> the famine with calories left over for reproducing? Who is most likely to be your ancestor? Fatties, fatties, and fatties again.
>
> This hunger was a survival-enhancing feature in our genetic programming. Now it is a bug in that programming. Predictably, we keep gaining weight, both as we get richer as a society and as we age individually. Most of us would reduce our risk of heart disease, stroke, and diabetes if we lost even as little as ten pounds. We know this. That's why so many of us are trying to lose weight – and the rest are eating scared.
>
> Zoo orangutans are fat because their genes are adapted for the wild, where food is scarce and life hard. Our human ancestors lived in conditions more similar to the Indonesian jungles where wild orangutans roam than to modern industrial circumstances.
>
> Obesity was as rare for ancestral humans as it is for wild primates today. Just as dogs and cats often get chubby around the house, zoos are populated with animals that have weight problems. We would be better off if we wore signs that read, PLEASE DON'T FEED THE HUMANS.

What has happened in the 35 years since Brown and Konner's paper and the 22 years since the publication of *Mean Genes*? The hypothesis that genetic mismatch is the cause of obesity has become more widespread and supported by a huge amount of additional evidence (Ulijaszek & Lofink, 2006; Bellisari, 2008). Here are a few salient examples.

> "Changes in the global food system together with increased sedentary behaviour seem to be the main drivers of the obesity pandemic." – Blüher, 2019
>
> "Our genes have not changed appreciably over the past several decades, implying that environmental changes must have caused the current obesity epidemic." – Hall, 2018
>
> "For the past 200 millenia, most people barely eked out enough food to stay alive … As the spread of agriculture and domesticated animals made food more available, our waistline spread." – Regestein, 2018

This last article presents the mismatch argument as fact with no citations. In the biology, anthropology, and medicine literature, it now is considered to be so obviously true that no citations are needed.

9.2 The proximate cause of human overeating

Evolution has selected for genes that push many people to overeat in modern, affluent settings. As with the other behaviors that we have discussed, specific physiologic machinery produces eating and overeating in some settings. Here is a scientific summary of some of the research on human eating behavior.

Dopamine plays a key role in a wide range of behaviors (see Ordinaries 4, Burnham & Phelan, 2020c, for more details). In fact, dopamine is centrally involved in most goal-directed actions in both humans and non-humans (Wise, 2004).

The dorsal striatum is a brain region centrally-involved in decision making, with a particularly important role in mediating the choosing and initiating of actions (Balleine et al., 2007). The nucleus accumbens, part of the ventral striatum, is one of the primary brain structures involved in both behavior and emotion (Salgado & Kaplitt, 2015).

"The drive for food is one of the most powerful of human and animal behaviors" (Volkow, et al., 2002). As with other behaviors, dopamine is involved in regulating food consumption through modulation of the rewarding properties of food (Martel & Fantino, 1996).

When people consume food that they like, dopamine is released in the dorsal striatum (Small et al., 2003). The dopamine responses to eating food like cashews—energetically dense and easy to digest—"elicit similar responses in reward-related brain regions that mimic those of addictive substances" (Burger & Stice, 2011, p. 182).

Furthermore, it isn't necessary to actually eat food in order to initiate dopamine release in the motivation and pleasure centers of the brain. Experimenters placed human subjects into brain scanners, exposed the subjects to the sight, smell and taste of food, and recorded significant dopamine release in the dorsal striatum in all three cases (Volkow, et al., 2002).

Additional studies investigating the impact of visual food cues alone (without smell or taste) in humans also revealed activation of the ventral striatum (Wiers et al., 2021). A review article entitled "Eating with our eyes," states, "Contemporary neuroscience demonstrates just what a powerful cue the sight of appealing food can be for the brain" (Spence et al., 2016). Not only is the brain built to find food, this article notes that foraging using visual cues to the presence and availability of nutrition, is one of the 'primary functions' of the brain.

One brain scanning study almost solves the cashew conundrum by itself. "The increased incidence of obesity most likely reflects changes in the environment that had made food more available and palatable. Here we assess the response of the human brain to the presentation of appetitive food stimuli during food presentation using PET and FDG" (Wang et al., 2004). In just the abstract, this paper explains the ultimate cause of obesity, and the mechanistic drive to eat cashews when exposed to their sight and smell.

Our summary of this extensive research is that humans are built to enjoy eating. That enjoyment is reified as the release of dopamine in the motivation and pleasure centers of the human brain. The proximate cause of our eating behavior is a motivational system where we get pleasure from eating. This mechanistic approach is also built to find food in the environment. Merely seeing food is enough to flood the human brain with dopamine and create a powerful desire to eat.

This extensive research on the neural architecture of hunger explains why simply moving the cashews out of sight, along with increasing the foraging effort required, reduces the temptation to eat among Professor Thaler's dinner guests. The guests may still know, in part of their brain, that the cashews are available in the kitchen. The proximate mechanisms that detect food in the immediate environment, however, are no longer screaming at the guests to eat.

9.3 The cashew conundrum is predicted and explained

When people see and smell cashews, huge amounts of dopamine are released in the motivation and reward centers in the brain. People are built to eat food, particularly calorically-dense foods that require little effort to consume.

Companies that sell food spend enormous amounts of money on advertisements. All these food advertisements share one feature—they include images of delicious, tasty, calorically-dense, low-effort-to-eat foods. Why? Because these images release dopamine in the motivation centers of the brains of viewers. Cues to readily-available food items change human behavior.

Companies measure the response to advertisements, and they show images because beautiful images of food lead to purchases and profits. The powerful role of photographs in food advertising has been documented in academic studies (Kusumasondjaja and Tjipton, 2019; Septianto et al., 2019; Vermeir & Roose, 2020). Not only do we know that food images change human behavior, there is even a body of academic literature on what types of images are most effective (Vermier & Roose, 2020).

Eating is an essential human survival behavior. The brain produces a powerful drive to consume food. This drive takes place in the dorsal striatum and the sub-portion labeled the nucleus accumbens. Consuming food leads to increased dopamine in the dorsal striatum.

The drive for food is so powerful that eating "energy dense, palatable foods" like cashews produces a dopamine response as powerful as addictive substances. The sight, smell, and taste of food, even without eating, produce dopamine in human subjects.

So, we argue, the case of the cashew conundrum is solved.

Puzzle: The sight and proximity of cashews exacerbates affluent human overeating.

Explanation: Adaptive mechanism mismatched to a novel environment.

Solution: Move the cashews into the kitchen. Or see Ordinaries 4: The causes and cures of self-control struggles (Burnham & Phelan, 2020c).

10 Biological economics

The anomalies of behavioral economics are produced by the interactions of genetically-created biological mechanisms with novel environments (Burnham, 1997, 2013, 2016; Burnham & Phelan, 2000, 2020a).

The Ordinaries column seeks to improve economics through the use of natural science approaches (for a summary of articles to date, see Burnham & Phelan, 2021c). When biologists observe behavior that is self-destructive or puzzling in some other manner, they begin their research.

Biologists study the mechanistic causes of behavior in the context of natural selection favoring maximizing in the ancestral environment. The mechanisms that produce behavior are analyzed from multiple perspectives including the genetic basis, neural architecture, behavior in natural settings and in experimental settings designed to elucidate details of physiology.

Behavioral economics should, in our view, use the natural science approach to understanding human behavior. Two main benefits stem from using biology to understand human economic behavior. First, non-maximizing behavior in novel contexts is not surprising. Quite to the contrary, it is expected. Second, documentation of some non-maximizing behavior is the beginning of research, not the end.

Using the natural science perspective, Richard Thaler's cashew conundrum is both predicted and explained by the mechanisms for human feeding behavior. Humans have sophisticated mechanisms for locating and performing cost–benefit calculations about food alternatives.

Cashews are calorically-dense food packets. In the sight and smell of cashews, specific neural mechanisms in human brains nudge us to eat. The firing of these neural pathways biases us in one direction. In this case, toward eating more cashews than we will have wanted to have eaten 30 min later.

There is a similar explanation for all the "anomalies" of behavioral economics. This is why we chose the title of "Ordinaries" for this series of papers. We expect people to eat delicious, readily-digestible food because this type of behavior redounded to the evolutionary benefit of our ancestors, while the alternative behavior of not consuming such food when available, was an evolutionary route to extinction.

There are literally thousands of studies documenting animal behavior that is far from optimal. Animals get lost, starve to death amidst plenty, are fooled by predators and get eaten, migrate to the wrong location, roast to death in the sun, mate outside their species, etc.

Among this panoply of non-human anomalies, which do you think is the most famous among biologists? What is the biological equivalent of eating too many cashews, which Richard Thaler likened to Isaac Newton's apple?

The answer? None.

There is no equivalent documentation of behavioral anomalies in biology. Recall the definition of an anomaly used by Richard Thaler: "An empirical result is anomalous if it is difficult to "rationalize," or if implausible assumptions are necessary to explain it within the paradigm." (Thaler, 1987, p. 198).

The biological paradigm predicts that organisms will fail to maximize in circumstances of evolutionary mismatch. Thus, the thousands of examples in the biological literature are not surprising. They each represent the beginning of an investigation, not the end via cataloging.

The cashew conundrum is not an anomaly, but rather an ordinary (Table 2).

Table 2 Economic views of the cashew conundrum with insights from biology

Phenomenon	People eat too much at the wrong time and sometimes regret their overeating behavior.
Neoclassical economics	Eating cashews before dinner, even when it leads to an inability to eat the main course, is optimal. People know what they are doing and their behavior is optimal.
Behavioral economics	People suffer from heuristics and biases. These behavioral tendencies lead to suboptimal outcomes. Eating too many cashews is one of countless human foibles documented by behavioral economists.
Biological economics	Human neural mechanisms monitor the environment to evaluate the cost/benefit of foraging behavior. Shelled cashews that can be seen and smelled light up human motivational brain circuits. In the evolutionarily novel circumstance of persistent caloric excess, our biological mechanisms tend to cause overeating both in the short term (i.e. "spoiling" dinner) and in the long term (producing obesity).

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