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## Neuroeconomics: The Shadow of the Future

**Humans and other animals tend to disregard future benefits and costs when choosing between immediate and delayed gratification. This tendency can lead to the choice of options that are not in one's own long-term interest. A new study looks at the neurophysiological basis of this self-defeating behavior.**

Veit Stuphorn

*The future is purchased by the present*

Samuel Johnson (1709-1784)

*I would gladly pay you Tuesday for a Hamburger today*  
Wimpy (early 20<sup>th</sup> century)

You used to be a smoker. Just recently you decided, like millions of other smokers each year, that you wanted to quit. The reasons seemed obvious: future health problems, avoiding the disapproval from your family and coworkers and the nagging feeling that you were not in full control of your own behavior. You are sitting in a pub with a friend who smokes. He has just lit a cigarette and offers you one too. This is the moment to tell him about your new plans. Or is it? Suddenly, you have second thoughts. You are reminded how much you like the aroma of tobacco and the pleasure you get from your first puff. After all, what is one cigarette? If you stop smoking tomorrow, it does not matter what you do tonight. You accept the offer and start smoking. Like 81% of others that tried, your attempt to quit failed within the first month [1]. What went wrong?

We often choose alternatives that are tempting in the short-term

over alternatives that are more optimal in the long run. This self-defeating behavior is even more perplexing, as we are almost always aware of the fact that our choice is not in our own best self-interest. Traditionally, it has been assumed in the behavioral sciences, especially in economics, that decisions are perfectly rational, in other words that we choose the alternative that has the most value for us [2]. This assumption is clearly wrong. We are persistently tempted by immediate gratification. The resulting behavioral problems are ubiquitous and range from the mildly dysfunctional, such as procrastination, to the clinically relevant such as overeating and addiction. We do not seem to choose what we value most. How is this possible?

A new paper by Kalenscher *et al.* [3], in this issue of *Current Biology*, reports a first, pioneering step towards an understanding of this phenomenon. The authors decided to study impulsivity and self-control in the pigeon, an animal model with a long history of study in delayed-reward choice tasks [4]. These experiments on pigeons have an identical structure to experiments that have been done with human subjects [5]. So for comparison, the pigeon experiment will be translated into the conditions faced by a human

in a similar experiment. In a typical experiment a hungry pigeon is placed into a box, where it is faced with two different keys in one side of the box. It has learned that pecking of a key will lead to the opening of a shutter in the wall of the box, which allows access to food. Pecking one of the keys results in access to food after only a brief waiting time, but the shutter also closes faster, so that the total amount of food that the pigeon can get is small. Pecking the other key results in longer food access, but the bird has to wait longer. (In the case of humans this would be equivalent to a choice between, for example, \$1 today or \$10 at some later point.)

To find out how pigeons handle the trade off between reward amount and delay, the experimenter varies the longer delay period. First, let's start with equal waiting times for both rewards. (We would ask our human subject "Would you prefer \$1 or \$10 today?") Naturally, the pigeon will exclusively choose the key leading to more food. Next, we slowly lengthen the waiting time of the large food amount option. ("Would you prefer \$1 today or \$10 tomorrow, in a week, in a month, in a year....") The option where the gratification is delayed becomes less and less attractive, until the pigeon switches its preference and chooses the smaller, sooner option instead of the larger, later option. The length of the waiting time that the pigeon or the human is willing to accept is related to its impulsiveness. Typically, a hungry pigeon is not willing to wait longer than a few seconds; humans are less impulsive and are willing to wait from days to decades, depending on the reward. Nevertheless, the principal

structure of the discounting is the same in humans, pigeons and all other animals that have been tested in this kind of experiment [6].

Discounting the future in itself is not irrational; after all “the best-laid plans of mice and men often go awry”. Taking into consideration the risk that a future reward might not manifest itself comes down to estimating the total probability of this unfortunate outcome. This implies that we should reduce the value of a future reward by a constant factor per time unit that reflects this probability. The resulting discount function is an exponential function similar to the one used by financial markets. Exponential discounting implies a constant preference over time. The preference between a smaller sooner and a larger later reward does not change as the smaller sooner reward becomes imminent. However, empirical studies in humans [5] and animals [4] have not supported an exponential discounting function. Instead these studies show a clear tendency to discount expected outcomes proportionate to their delays. This results in a hyperbolic discounting function as first suggested by Mazur [4]. Kalenscher *et al.* [3] also report that the behavior of their pigeons is best described by a hyperbolic function. In contrast to exponential discounting, hyperbolic discounting leads to a preference reversal between the immediate and the delayed reward in the period just before the immediate reward is due [7]. This explains the temptation to choose the smaller reward if it becomes immediately available.

Kalenscher *et al.* [3] recorded from neurons in the Nidopallium caudolaterale, a nucleus in the forebrain of birds that receives input from multiple sensory systems. They found a small group of neurons that were active after the pigeon had made its choice and while it waited for the food to become available. This indicated that the neuronal signal might be related to the expectation of reward in the future. The intensity of the neuronal discharge increased with

the length of access to the food that the pigeon could expect and therefore reflected the amount of reward. Cells of this type have been described before [8]. Critically, Kalenscher *et al.* [3] found that, for a given amount of reward, these cells also decreased their activity the later the reward was delivered. Thus, the neurons integrate information about the size of the expected reward and how far in the future it will become available. This is a new finding in this study [3]. Strikingly, these cells behave in the same way as the hyperbolic value functions that can be derived from behavior. The best way to interpret these new findings is that this newly described group of cells in the pigeon brain carries information about the subjective expected value of a recently executed goal-directed action.

Finding cells with this property is exciting, because it takes a theoretical concept from economics and makes it a variable that can be measured directly. This should allow us to reverse the traditional logic. Instead of inferring value from the behavioral choices, we could use the neuronal value signal to predict choices. This links the current study with the emerging field of neuroeconomics. The mathematical assumptions that form the basis of current rational choice theory do not adequately describe how humans make decisions. Neuroeconomics promises a new perspective on this and other problems in decision theory by opening the ‘black box’ [9,10]. Understanding the neuronal mechanism underlying choice will allow economics to be built upon an empirical model of decision-making.

Like all stimulating scientific work the Kalenscher *et al.* [3] paper not only gives new insights, but it also opens up new questions. One of them is how the findings of this study in a bird relate to the situation in the primate. The brains of birds and mammals are separated by approximately 286 million years of evolution [11]. Nevertheless, the

fact that the hyperbolic discounting function is shared between pigeons and humans makes it likely that we will find similar neuronal signals in primates. It is not clear though, what part of the mammalian brain is functionally equivalent to the part of the avian brain where the subjective value signals were found. In earlier work, the authors of this study [12] have presented evidence that point towards a functional similarity between the Nidopallium caudolaterale and the prefrontal cortex. We will need further studies to see how far this similarity goes and which part of the primate prefrontal cortex, if any, is the closest analog to this nucleus in the bird forebrain.

Another important question relates to the decision itself. The neuronal activity that Kalenscher *et al.* [3] describe starts only after the choice has already been made. Clearly, the two alternative outcomes and the value that the animal attaches to them must be represented during the decision stage. Otherwise no comparison is possible. Likewise, it is unclear at this point what the actual mechanism of decision-making is in this paradigm. At least three different mechanisms are possible. First, the decision could be the result of direct competition of expected reward signals that are associated with the two options. This mechanism would simply select the option associated with the highest expected reward value. Secondly, the decision could be the result of competition between two different neuronal systems. One system would support impulsive choices and is mainly driven by the limbic system. The other system would support rational choices and is mainly driven by the cognitive system. It is not clear how realistic this possibility is in the pigeon, but it might play a role in primates and in particular in humans [13]. Third, the decision might be guided by an evaluation of past reward. If a choice leads to less reward than expected, the pigeon switches to the other option. This suggestion draws on models of reinforcement learning that were developed to explain the response

of dopaminergic neurons in the midbrain [10]. These neurons are thought to represent the mismatch between expected and actually delivered reward. In this scheme the newly discovered neurons would provide one of the compared signals.

Lesion studies would allow exploring the exact causal role of this avian brain area in the delayed reward choice task. Studies in rats have shown that the lesion of the Nucleus accumbens, a part of the mammalian basal ganglia, leads to more impulsive choices [14].

We started with the question how humans can behave irrationally. The fact that both pigeons and humans discount future reward in a hyperbolic fashion turns this original question around. Because of the nature of our reward discounting we would expect to always prefer immediate gratification to what is in our long-term interest. In this sense, the smoker did the most natural thing. What needs explanation is the existence of rational behavior. If not pigeons than at least humans are sometimes able to overcome their temptations and to exert self-control. It is this that needs an explanation. Pigeons, which are rather impulsive, might not be the best subjects to study these

control mechanisms. Primates with their well-developed frontal cortex might offer a better chance to understand voluntary control of behavior, a cognitive ability that is of central importance in our life as human beings [15]. This will allow us to development better treatments for substance addiction, gambling, obesity, lack of exercise and a whole host of other important behavioral problems in our modern world.

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## Sex Chromosome Inactivation: The Importance of Pairing

In mammals, the process of making sperm is marked by inactivation of sex chromosomes. Why and how does this happen? The answer apparently lies in whether a chromosome finds a pairing partner. Similar mechanisms in mold and worms reveal a surprising and recurrent theme throughout evolution.

Jeannie T. Lee

The phenomenon of sex chromosome inactivation presents one of the most fascinating problems in biology. It is best known in mammals, where inactivation occurs in several situations. In the female soma, inactivation of a single X chromosome ensures that XX and XY individuals have equal X

chromosome dosage even though they inherit an unequal number of X chromosomes [1]. A second, though less-recognized form of inactivation takes place in males: known as ‘meiotic sex chromosome inactivation’ (MSCI), the phenomenon silences both X and Y during meiosis (Figure 1A) [2]. Why this happens at all remains mysterious, but in recent years there have been

considerable advances in our understanding of its evolution, mechanism and potential biological relevance. Most recently, two papers from the Burgoyne group [3,4] have revealed intriguing new rules that govern MSCI. The trigger, it seems, is unpaired DNA at pachytene, the stage of meiosis when homologous chromosomes normally synapse (pair).

This is a startling discovery, as it implies that the MSCI mechanism may originate in a most improbable biological progenitor — a moldy fungus called *Neurospora*. As in other organisms, meiosis in *Neurospora crassa* is marked by pairing of homologous chromosomes in preparation for segregation to haploid gametes. A few years ago, Metzberg and colleagues [5] made the surprising