Neuroeconomics: Cardinal Utility in the Orbitofrontal Cortex?

Modern economics no longer uses the concept of cardinal utility, which describes the value of a good independently of a comparison with another good. New electrophysiological recordings in primates performing economic choices suggest a neurological substrate for cardinal utility, a finding that economists should perhaps take note of.

Veit Stuphorn

Economics holds that the ultimate goal of human behavior is to increase pleasure, or 'positive utility', and to reduce pain, 'negative utility'. In this view, the outcomes of all possible activities can be translated into a common currency — their 'utility' — and be compared along this dimension to identify the course of action that leads to the greatest increase in utility.

Early theoretical economists (for example [1]) assumed that the concept of 'utility' described a real underlying psychological phenomenon, and that it was possible to measure the absolute utility value of a good on a cardinal scale in the same way as distance, temperature or time. For example, an individual might get 150 units of subjective utility value from one good (Chinese food) and 145 and 50 units from competing goods (French and fast food, respectively). Thus, measuring cardinal utility would allow one to predict the chosen good, in this case Chinese food, and the magnitude of the difference between them (the individual likes French food almost as much as Chinese, even though it was not chosen).

This original concept of utility was first questioned by Pareto, who took the view that utility can only be measured on an ordinal scale. Such a scale only allows the ranking of goods according to their value, but gives no information about the magnitude of the difference between them. Thus, we would expect a person only to be able to reliably express a preference of Chinese over French food, but not how much more he or she prefers one over the other. The new concept of ordinal utility became dominant, when Hicks and Allen [2] and subsequently Samuelson [3] showed that the entire theory of economic choice can be derived in a purely behaviorist fashion from the observation of choices among different groups of alternative goods (the 'revealed preference'), without any reference to a preexisting set of preferences measured on a cardinal utility scale. Thus, the cornerstone of modern microeconomics became the ordinal utility as measured behaviorally in indifference curves.

While this approach works within economics, the new concept of 'utility' is devoid of any psychological meaning. This leaves open the question of the brain mechanisms of value assignment and choice between goods of different value. To answer these questions we need to study directly the internal neuronal representations within the brain of humans and animals that give rise to economic behavior. In an important new experiment, Padoa-Schioppa and Assad [4] have done just that and have provided an important first insight into where and how the utility of economic goods is represented.

In their experiment, Padoa-Schioppa and Assad [4] used the behavioral approach of economics by observing the preferred choice of a monkey among varying amounts of two alternative types of juice. The two offers were indicated by groups of squares on the two sides of a computer screen. The color of the square indicated the juice type and the number of squares the amount. The monkeys clearly preferred some juice flavors over others. For example a monkey might always choose water over Kool-Aid, if equal amounts were offered. At the same time, the monkeys were thirsty and preferred bigger amounts of fluid. Thus, if more Kool-Aid than water was offered, the monkey had to weigh his preference for the taste of water against the bigger amount of Kool-Aid. With bigger and bigger offers of Kool-Aid the monkey was more and more likely to pick the Kool-Aid. At a certain ratio of water against Kool-Aid, the monkey was indifferent between the two offers and picked each liquid half the time. For example, this might happen at a level of one drop of water against four drops of Kool-Aid. This tells us that for the monkey one drop of water is worth four drops of Kool-Aid.

The critical point of the experiment was to record the activity of neurons in the brain of the monkey, while he worked in the behavioral task. Padoa-Schioppa and Assad [4] chose to record from the orbitofrontal cortex, a region in the cortex of humans and other primates that lies directly above the orbit of the eyes and has long been implicated in the representation of value [5,6]. Neurons in this region represent the type of expected juice reward and the relative ranking of such juice rewards [7]. In their experiment, Padoa-Schioppa and Assad [4] found three different cell types in the orbitofrontal cortex of their monkeys. One group encoded the type or flavor of the chosen offer. This is a straightforward representation of an objective attribute of the juice. On the other hand, for two other groups they showed that the neuronal activity was not influenced by the objective physical properties of the goods, such as their flavor or amount. Instead, they represented a subjective value, namely the value of one of the two offers and the value of the chosen offer. Since an offer could be presented on either side of the computer screen the monkey had to look half the time to the right and half the time to the left. Critically, the neuronal activity was the same in each case.

Thus, this paper [4] demonstrates the existence of neurons in the orbitofrontal cortex that represent the subjective utility of an economic good independently of the action necessary for its acquisition. These findings suggest that the orbitofrontal cortex might contain a map of cardinal utility. The activity of a set of neurons in this map encodes the subjective utility of a particular option and allows predicting the choice of the monkey. Note that this is the reverse of the reasoning that actually was used in the experiment to find these neurons, but now that they are identified they could be used to explain economic choices. Finding a candidate for the neuronal representation of the cardinal utility distribution for economic goods is a very important step and opens up a number of questions about this system.

First, every sensory system participates in the identification of features that are perceived as more or less pleasant. Sounds, tastes, temperature, touch or visual images can all be judged to be either pleasant or unpleasant. How the brain learns to integrate all these sensory stimuli is not well understood at the present time. Again the present experiments represent a first step, because the monkeys needed to integrate and compare both juice type and amount. It is important to test these cells with a whole range of different features that affect utility. These tests should also include more complex non-sensory factors such as time and risk. The utility of goods is affected by the time it takes until they become available [8]. Likewise, the likelihood that a good becomes or does not become available affects its utility.

Second, if the orbitofrontal cortex contains a utility map, are there other such maps? In human imaging studies not only the orbitofrontal cortex showed activity related to expected reward, but also the nucleus accumbens [9]. Furthermore, there is evidence that the utility of different actions is represented in the primate striatum [10]. If there are many different utility maps we need to understand if and how these maps interact with each other. One would expect anatomically separate utility maps to form a single internal market place of sorts. Otherwise we would expect to see a behavioral separation in which the utility of some goods cannot be compared.

Third, so far most experiments have mainly explored benefits — positive utility — but what about costs, that is, negative utility? Costs include both aversive features of a good itself that come in addition to its positive features and the effort that has to be extended to acquire the good. Are costs integrated with benefits in the same utility map or are the two aspects of utility represented in different parts of the brain?

Fourth, how are the utility representations translated into actions? The orbitofrontal neurons in the study by Padoa-Schioppa and Assad [4] showed no relationship to the action that was necessary to acquire the good whose utility it represented. Thus, the information contained in these neurons needs to be combined with information about the outcome of possible actions to select the appropriate behavior. There is evidence that neurons in the anterior cingulate cortex represent such action-outcome contingencies [11]. Furthermore, sometimes we do not follow through with plans even though we are well aware of the pleasure we will derive from completing our actions (for example during a diet). Is this a problem of the utility representation or of lack of motivation to act on it?

Lastly, by now we know about a whole range of human behaviors that represent a paradox from the point of view of standard economic theory (for a review see [12]). One prominent example is the ultimatum game. In this game one agent, the ‘Proposer’, makes an offer to split a monetary prize (the ‘ultimatum’). The second agent, the ‘Responder’, can only accept the suggested division or reject it in which case neither side receives anything. Economical theory would predict that the Proposer should offer the smallest possible share to the Responder. For example, in the case of $10 the Proposer should offer only one cent for the Responder. The Responder should accept, because one cent has still a higher utility than no money at all. Of course, that is not what happens. The average offer to the responder is 40% of the prize money and offers of 20% or less are very often rejected.

Such a rejection represents an altruistic punishment, because withholding the money from the Proposer is only possible at a loss to the Responder. As an explanation, extra-monetary rewards have been suggested that would alter the utility matrix of the different outcomes. These other factors include a fairness preference [13] to explain the generous offers and enjoyment from the release of righteous anger in the case of altruistic punishment [14]. While these factors are plausible, they are also purely speculative. A representation of cardinal utility would provide a possible way of testing these suggestions by directly measuring the subjective utility associated with different outcomes of the ultimatum game. These measurements could be compared with the monetary rewards and the factors responsible for any difference could be further explored.

References

1. Marschall, A. (1948). Principles of Economics, Eighth Edition (New York: Macmillan).
2. Hicks, J.R., and Allen, R.G.D. (1934). A re-consideration of the theory of value. Economica *14*, 52–76, 196–219.
3. Samuelson, P.A. (1938). A note on the pure theory of consumer’s behavior. Economica *5*, 61–71.
4. Padoa-Schioppa, C., and Assad, J.A. (2006). Neurons in the orbitofrontal cortex encode economic value. Nature *441*, 223–226.
5. Holland, P.C., and Gallagher, M. (2004). Amygdala-frontal interactions and reward expectancy. Curr. Opin. Neurobiol. *14*, 148–155.
6. Rolls, E.T. (2004). The functions of the orbitofrontal cortex. Brain Cogn. *55*, 11–29.
7. Tremblay, L., and Schultz, W. (1999). Relative reward preference in primate orbitofrontal cortex. Nature *398*, 704–708.
8. Roesch, M.R., and Olson, C.R. (2005). Neuronal activity in primate orbitofrontal cortex reflects the value of time. J. Neurophysiol. *94*, 2457–2471.
9. Knutson, B., Taylor, J., Kaufman, M., Peterson, R., and Glover, G. (2005). Distributed neural representation of expected value. J. Neurosci. *25*, 4806–4812.
10. Samejima, K., Ueda, Y., Doya, K., and Kimura, M. (2005). Representation of

action-specific reward values in the striatum. Science *310*, 1337–1340.
11. Matsumoto, K., Suzuki, W., and Tanaka, K. (2003). Neuronal correlates of goal-based motor selection in the prefrontal cortex. Science *301*, 229–232.
12. Camerer, C.F. (2003). Behavioral Game Theory (Princeton: Princeton University Press).
13. Rabin, M. (1993). Incorporating Fairness into Game Theory and Economics. Am. Econ. Rev. *83*, 1281–1302.
14. de Quervain, D.J., Fischbacher, U., Treyer, V., Schellhammer, M., Schnyder, U., Buck, A., and Fehr, E. (2004). The neural basis of altruistic punishment. Science *305*, 1254–1258.

Department of Psychological and Brain Sciences and Krieger Mind/Brain Institute, Johns Hopkins University, 3400 North Charles Street, Baltimore, Maryland 21218, USA.
E-mail: veit@jhu.edu

DOI: 10.1016/j.cub.2006.07.005

Phylogeny: The Continuing Classificatory Conundrum of Chaetognaths

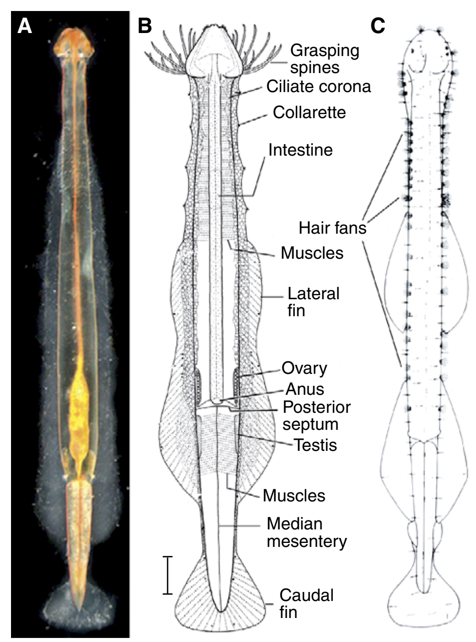
The phylogenetic conundrum posed by the Chaetognatha, a cryptic phylum consisting largely of planktonic predators, is the subject of two short papers in this issue of *Current Biology*. These analyses go some way towards defining the phylogenetic position of the chaetognaths, which possess features apparently spanning the protostome/deuterostome divide.

Eldon E. Ball[1,*] and David J. Miller[2]

It would be difficult to invent a more bizarre group of creatures than the chaetognaths or arrow worms, (literally 'bristle jaws'). The chaetognaths are an ancient lineage of invertebrates that shares some characteristics with just about every other major invertebrate phylum and has consequently puzzled taxonomists ever since its original description in 1769. Darwin described chaetognaths as "remarkable for the obscurity of their affinities" and they have puzzled a succession of eminent zoologists ever since [1]. Though unfamiliar to most biologists, chaetognaths are typically the most abundant planktonic predators, sometimes accounting for more than 10% of zooplankton biomass and being outnumbered only by their major prey, the copepods. Approximately 20 genera have been described, containing more than 100 species ([2], see also: http://academic.evergreen.edu/t/thuesene/chaetognaths/chaetognaths.htm).

Although most chaetognaths are only a few mm in size and planktonic, there are some inshore benthic and deep-water species that may be much larger, up to 12 cm in length. The basic body plan of the chaetognaths (Figure 1A,B) is relatively constant across the phylum, although details may vary considerably. The structure of the nervous system reveals little about the evolutionary affinities of chaetognaths, although it bears some resemblance to the nervous systems of nematodes, kinorhynchs and priapulids [1]. The age of the phylum is borne out by fossils from the Cambrian Burgess Shale which show a remarkable resemblance to modern chaetognaths [3] (Figure 2), suggesting chaetognaths have existed without major morphological change for at least 500 million years. Chaetognaths are unusual among marine invertebrates in that they are direct developers, hatching from the egg essentially as small adults rather than as a distinct larval stage.

Chaetognaths appear to rely mainly on vibrations for information



Current Biology

Figure 1. Chaetognath morphology.
(A) The deep water chaetognath *Eukrohnia* sp. from the Sargasso Sea (Photo courtesy Russ Hopcroft/UAF/NOAA/CoML). In contrast to most shallow water forms, this species is pigmented, making the internal organs easily visible. (B) This labelled drawing of the pelagic chaetognath, *Heterokrohnia*, provides a good introduction to the basic features of chaetognath anatomy. Some authors divide the body into head and trunk, while others add a tail, dividing the trunk at the posterior septum. There are three body cavities, which, together with the cuticle and the longitudinal muscles, form a hydrostatic skeleton. One or two pairs of longitudinal fins provide stabilisation, while the flattened caudal fin provides locomotory power. There is no circulatory system and no specialised excretory system. The anterior grasping spines used in prey capture are shown spread, although they are normally folded under a hood, which presumably serves the dual purpose of protecting them and streamlining the head during swimming. Eggs are released into the thoracic coelomic space and sperm into the coelomic space of the tail. Modified from [20], with permission. (C) Drawing of *Sagitta hispida* showing the closely spaced hair fans which presumably provide the sensory input required for such complex behaviours as mating and prey capture. Modified with permission from [4].