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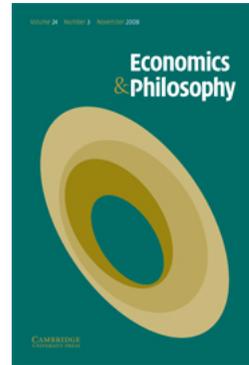
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NEUROECONOMICS, NEUROPHYSIOLOGY AND THE COMMON CURRENCY HYPOTHESIS

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We briefly describe ways in which neuroeconomics has made contributions to its contributing disciplines, especially neuroscience, and a specific way in which it could make future contributions to both. The contributions of a scientific research programme can be categorized in terms of (1) description and classification of phenomena, (2) the discovery of causal relationships among those phenomena, and (3) the development of tools to facilitate (1) and (2). We consider ways in which neuroeconomics has advanced neuroscience and economics along each line. Then, focusing on electrophysiological methods, we consider a puzzle within neuroeconomics whose solution we believe could facilitate contributions to both neuroscience and economics, in line with category (2). This puzzle concerns how the brain assigns reward values to otherwise incomparable stimuli. According to the common currency hypothesis, dopamine release is a component of a neural mechanism that solves comparability problems. We review two versions of the common currency hypothesis, one proposed by Read Montague and colleagues, the other by William Newsome and colleagues, and fit these hypotheses into considerations of rational choice.

1. INTRODUCTION

The ideal for causal-mechanistic explanation in the cognitive and behavioural neurosciences is the capacity to systematically manipulate behaviour by manipulating brain components. Prediction, of course, is part of this enterprise, hence it is *systematic* manipulability with which

explanations in neuroscience are concerned. Other epistemic goals (besides explanation) also motivate neuroscientists. These include at least the articulation of new phenomena to be explained and the development of new tools to facilitate manipulation and measurement (Silva 2008; Silva and Bickle forthcoming). Thus the gains of a new field of neuroscience, such as neuroeconomics, can be measured in terms of the contributions made to this triptych of scientific goals: the articulation of new phenomena, the achievement of systematic manipulability (i.e. explanation), and tool development.

But neuroeconomics is not just a field of neuroscience. It is also supposed to converge with economics. Thus if the triptych of goals listed above are also pursued by economists, we should be able to count the gains to economics along the same dimensions. But this counting depends critically on the goals of economists. And not being economists, neither of us knows what those goals are.

The contributions of neuroeconomics to neuroscience, while nascent, are substantial. Toward articulating new and interesting phenomena for explanations, work in neuroeconomics drew attention to aspects of dopamine signals previously unrecognized, suggesting a specific learning architecture to be explored (see Section 2 below). In the provision of manipulability, headway is being made into the specific roles that each component of that architecture contributes to the production of behaviour. And toward the development of new tools, neuroeconomics has given us hyperscanning for studying brain activation during actual social interactions. These are obvious gains to neuroscience. Are these likewise gains for economics?

Hyperscanning is not an obvious tool for doing economics in the way that it is an obvious tool for doing neuroscience. The resulting brain activation data can hardly be regarded as new economic phenomena and the behavioural methods applied in hyperscanning have been available to economists for far longer than neuroeconomists have made use of them (see Harrison 2008). Thus when neuroeconomists approach the standards of manipulability demanded by neuroscience, they might be doomed to failure in articulating new economic phenomena, explaining economic phenomena, or in creating new research tools of interest to economists.

In fact, it seems to be the case that neuroscientists and economists view neuroeconomics with distinctively different goals. Compare, for example, both McCabe's (2008) and Harrison's (2008) stress on the discovery of new economic phenomena and explanations as a mark of the field's success with the following goal stated by neurophysiologists Sugrue, Corrado and Newsome: "To make adaptive decisions, animals must evaluate the costs and benefits of available options. The nascent field of neuroeconomics has set itself the ambitious goal of understanding the brain mechanisms that

are responsible for these evaluative process" (2005: 363). Ambitious as this goal is, it does not appear to require revolutionizing economics.

Nevertheless, in our discussion we will focus on an issue arising in neuroeconomics that could make a contribution to economics on its own terms – or at least to any research programme requiring an accurate representation of decision processes. The issue concerns whether the brain uses a "common currency" to rank outcomes and actions in its decision-making mechanisms. The common currency hypothesis has been expressed in some of the most high profile neurophysiological research in neuroeconomics, e.g. in the work of Read Montague and Gregory Berns, and of William Newsome and his colleagues. Our focus in this short paper is thus of interest to this special issue for another reason. To read both McCabe's and Harrison's target papers, despite their disagreements, one could come away with the idea that functional neuroimaging exhausts neuroeconomists' neuroscientific research methods. Or one might conclude that functional neuroimaging results (can) stand on their own, without the support of research using more invasive methods. Those impressions, widespread as they are across cognitive science and philosophy, are simply false. Electroneurophysiology in nonhuman primate models, a standard technique in neuroscience for decades, is a technique of choice in numerous labs tackling problems in neuroeconomics. We will emphasize this point primarily through brief descriptions of ongoing research.

To motivate the "common currency" issue we must first describe one of the bridges that have been built between rational choice and neurophysiology. This bridge uses the reinforcement learning framework, and is at the foundations of experimental neuroeconomics. As we will see, this bridge links optimizing choice behaviour to a learning function via midbrain dopamine activity. After crossing this bridge, we will be able to set up the issue whose solution will likely provide important insights for discussions of value and rationality.

2. THE BRIDGE BETWEEN RATIONAL CHOICE AND NEUROPHYSIOLOGY

At the foundations of neuroeconomics resides a thesis with a long history in psychology: humans (and many other living things) pursue rewards and avoid punishments. In experimental psychology, this proposal dates back explicitly at least to Thorndike's formulation of the law of effect, but it no doubt has been part of our folk psychology for as long as psychological hedonism has been around.

The basic idea is as simple as it sounds. Our behavioural propensities are shaped by the outcomes of our actions. Those outcomes that affect our propensities are called 'reinforcers'. In neuroscience, no other factor has

been more consistently associated with reward and reinforcement than the monoamine neurotransmitter, dopamine. As Read Montague (2006) stresses, a pivotal moment in dopamine research came about in the mid-1990s accidentally, when Wolfram Schultz was searching for evidence that dopamine is associated with specific movements. What Schultz found instead was that transient (or “phasic”) dopamine responses were more closely associated with “important” events, such as food rewards. Yet Schultz knew that dopamine was unlikely to encode the reward signal itself. It was Peter Dayan, a post-doctoral fellow in the Computational Neurobiology Lab at the Salk Institute, who first connected Schultz’s discovery to reinforcement learning models.

‘Actor-critic’ models proved to be the most fruitful reinforcement learning resource for characterizing midbrain dopamine activity. (By midbrain dopamine, we mean dopamine released from cells located in the ventral tegmental area and the substantia nigra pars compacta.) In their most basic form, these models have two components, the Actor and the Critic. The Actor is, appropriately, the component that performs actions, while the Critic is the component that learns which actions are predictive of reward outcomes. The predictive component of the Critic is called its “value function”, which assigns states of the agent to predicted rewards. The Critic thus trains the Actor to maximize rewarding outcomes. The Critic accomplishes this by emitting a training signal, δ . Different reinforcement learning models build different details into their definitions of δ , but all share the feature that δ is a calculated *difference* between actually delivered rewards and expected rewards. Thus, in searching for mechanisms that govern the timing of midbrain dopamine release, the reinforcement learning paradigm offers a useful strategy: Look for components that encode reward returns, components that encode expected rewards, and a convergence of those signals on dopamine-producing neural structures (i.e. the substantia nigra and the ventral tegmental area), so that those structures can calculate the difference signal δ .

So the reinforcement learning paradigm takes midbrain dopamine activity to encode not reward, but “error in predicted reward”. And rewards are essentially things that we want. Thus studying the neural mechanisms of reward (and punishment) representations should reveal our preferences.¹

One of the more interesting and powerful features of reinforcement learning systems is that they can learn to treat predictors of reward as though they were rewards themselves. These predictors have been

¹ Here we disagree with McCabe’s (2008) characterization of wants (Landreth 2007; Schroeder 2004). Wants are not behavioural tendencies. Rather they are neural mechanisms that encode reward values.

called “reward proxies” (Montague and King-Cassas 2007; Landreth forthcoming). This capacity is beautifully reflected in the responses of midbrain dopaminergic neurons. When animals learn to predict the occurrence of a reward, the phasic dopamine response shifts from the reward event itself to the presentation of the predictor. This shift in dopamine response to a predictor of reward could thereby enable an agent to treat the predictor stimulus as a desirable outcome, so long as the predictor continues to be reliable.

One last important feature of midbrain dopamine that should be mentioned is its association with response disinhibition. When dopamine is released following behaviour, it can update the probability of future action choices. When it is released prior to behaviour, it is believed to facilitate gating functions that unleash cognitive and behavioural mechanisms to, e.g. update goals in working memory or enable movement itself (Hazy *et al.* 2006). Thus, the timing of the dopamine response is relevant, not just for learning about action outcomes but for causing actions to take place.

As McCabe (2008) points out, evidence suggests that more than one Actor-Critic system can be found in the brain. These systems likely divide into fast learning systems that generate δ signals through the offline simulation of actions and outcomes, and slow learning systems that generate δ signals based on real feedback from trial and error learning. The latter kind of system is more closely associated with decisions made out of habit, the former with decisions based on planning. While the distinction between these two kinds of reinforcement learning systems is important, there is another important question regarding systems, namely: how many distinct instances of these systems can be localized in the brain? To put this second question more simply: how many distinct kinds of reward(s) and punishment(s) are represented in the brain?

If each kind of reward defines a distinct value function (which would in turn uniquely determine δ), we must ask: How is it that we choose to pursue the rewards that we in fact pursue? Rather than asking, “how do we rank potential courses of action with respect to valued outcomes?” we must ask, “how do we rank our values?” or “how does our brain determine which value function will make a contribution to δ at a given time?” This question gets us to the heart of the common currency issue and in section 4 we’ll turn directly to it. But first we need a deeper grasp on the brain’s reinforcement learning mechanisms.

3. THE BRAIN’S VALUATION MECHANISMS

It will not surprise many to learn that neuroscience has not uncovered a complete, or even near-complete, characterization of basic decision-making mechanisms. But neuroscientists have a grasp of some of these

mechanisms, at least by the tail. As we described in the previous section, midbrain dopaminergic neuron responses are now known to be a key player, but they are not the only ones. Dopamine has different effects at different receptors, and the cells in which those receptors are embedded have different effects on other cells depending on the circuit structure of the region in which they are found. These facts enable us to flesh out, in causal-mechanistic terms, the distinctions suggested at the end of the previous section between fast-learning and slow-learning systems, and the specific forms of goal-orientation in those systems.

The reinforcement learning paradigm allows us to carve neural systems into actor networks, networks that represent reward predictions, networks that represent reward returns, and networks that generate an error signal based on feedback. Evidence suggests that reward and expected reward signals can be found in orbitofrontal cortex, and that expected reward signals are also found in parietal cortex. These signals likely perform different functions in distinct neural systems. For example, posterior parietal cortex has long been associated with vision involved in basic actions, such as reaching, grasping, and the direction of gaze. Information encoded in posterior parietal networks is formatted in an egocentric frame of reference. Reward preference information associated with reach and gaze-direction has been decoded from electrodes inserted into posterior parietal cortex in a nonhuman primate model (Musallam *et al.* 2004).

Interestingly, the action-oriented character of posterior parietal processing is not reflected in orbitofrontal physiological measurements. Orbitofrontal neurons seem less attuned to actions than to the prediction of outcomes. The kinds of rewards tracked by activity in orbitofrontal cortex have proven to be diverse. These include erotica, food, drinks, brand names, monetary gains, pleasant touch, pleasant music, attractive faces and orgasm (Holstege *et al.* 2003; Rolls 2005; Zald and Rauch 2006). This diversity has been uncovered using a variety of techniques ranging from functional neuroimaging in humans through electroneurophysiology in nonhuman primates.

We've limited our discussion to just a few of the neural systems where expected value signals have been found. The differences in the way these systems encode value information suggests that they specialize in distinct outcome and action valuations. Through their interactions with working memory mechanisms in dorsolateral prefrontal cortex, these systems likely drive action planning, based on a fast simulation-based form of learning.

Cortical valuation systems also stand in contrast to subcortical slow-learning systems. The latter are likely more relevant for understanding the performance of habitual or over-learned behaviour. As other authors in this volume emphasize, our current understanding of brain function is not of a unitary decision-making mechanism, but rather of a system

of competing mechanisms, each vying for behavioural control. This fact highlights the common currency issue.

4. A COMMON CURRENCY FOR DECISION MAKING?

Concerning neuroeconomics' impact on economics, Vernon Smith writes that

Neuroeconomics will not achieve distinction in a focus confined to correcting the 'errors' believed to pervade professional economics of the past ... neuroeconomic achievement more likely will be determined by its ability to bring a new perspective and understanding to the examination of important economic questions that have been intractable for, or beyond the reach of, traditional economics. (2007: 313; cited in Harrison 2008)

We agree, and despite our lack of serious training in economics see a specific way that neuroeconomics might contribute to economics: by providing new information about the structure of valuation processes. (Though as we mentioned above, a singular focus on the use of functional neuroimaging techniques in neuroeconomics will miss this potential contribution.) Particularly, neuroeconomics might allow us to reconsider questions of subjective value that have otherwise been rendered moot by our incapacity to acquire the relevant information.

Before we launch this discussion, however, we stress that we are aware that psychological conceptions of utility, such as the hedonic conception, were abandoned in economics long ago, due largely to the inaccessibility of information regarding hedonic states. We know that a behavioural conception, regarding utility as revealed choice, took the hedonic conception's place. The behavioural conception of utility could be used to predict economic behaviour. But there remained a fundamental economic task that it could not accomplish – namely, representing the intrinsic values governing preferences.

How many values are there? Ultimately do they all collapse into one? Some neuroeconomists have hinted at a stance on this issue, but they have been less than clear about what that stance actually is. The hints come from discussions of the common currency hypothesis. For example, in their groundbreaking article Read Montague and Gregory Berns (2002) write:

A currency is an abstract way to represent the value of a good or service. For our purposes ... it possesses an important property: it provides a common scale to value fundamentally incommensurable stimuli and behavioral acts. For example, suppose we want to understand the relative value of 17 coconuts and 41 sips of water. There is no natural way to combine coconuts and sips of water; however, each can be converted to their valuation in some currency, and the values can be combined in any number of ways. This kind of abstraction is so common in our everyday world that its biological

substrates go virtually unnoticed. Without internal currencies in the nervous system, a creature would be unable to assess the relative value of different events like drinking water, smelling food, scanning for predators, sitting quietly in the sun, and so forth. To decide on an appropriate behavior, the nervous system must estimate the value of each of these potential actions, convert it to a common scale, and use this scale to determine a course of action. This idea of a common scale can also be used to value both predictors and rewards. (2002: 276)

More recently Montague and King-Cassas write:

the impact of reward prediction error signals on behavior (on the choice tasks) along with their prominent neural correlates qualifies them as a kind of 'differential neural currency'. Such differential currencies are ideally suited to compare the relative value of different behavioral options available to each subject given the task at hand. (2007: 518)

Notice that Montague and King-Cassas suggest that there are "currencies" (plural), "available... given the task at hand"—indicating that each task domain may have its own value function.

Based on neurophysiological findings, substrates other than dopaminergic neuron activity have been proposed as a *common* currency for decision making. For example, Sugrue *et al.* describe activity in the lateral intraparietal cortex as a common currency "for information that is pertinent to the selection of future shifts in gaze or attention" (2005: 367) Their claim harks back directly to some of the results we described in Section 2. Setting aside the matter of who is correct about the neural currency of decision-making, the reinforcement learning framework is neutral on the compass of values combined in that currency. This neutrality is important for the way neuroeconomics tasks are typically formulated.

Typically these tasks involve rewards and punishments that are intuitively of the same kind. Lettuce, raisins, and apple slices are all primate foodstuffs. Water, saline, and juice are all potable liquids. Presumably, these rewards can be ranked because there is some complex internal setpoint (or need) and some of these items more closely approximate the demands of the need than others. Distinct needs define distinct scales of value along which reward outcomes can be ranked. Thus the currency the brain uses to rank outcomes and actions is a function of the need that motivates task behaviour. This raises a question: Is there some more comprehensive currency in which needs themselves are ranked?

It is with respect to this question that the reinforcement learning framework appears neutral. However, this is also the question that Sugrue *et al.* (2005) seem to propose an affirmative answer to. They claim that need signals and sensory signals interact to generate value representations in a common currency. Presumably, the convergence of needs in the determination of value representations generates a motivational ranking

of needs. Little experimental work has been done to assess the tenability of this notion.

When reviewing the neuroeconomics literature, one typically encounters tasks with food or liquid rewards, or monetary rewards in the human neuroimaging literature. The rewards will almost never be mixed. Subjects will not have to choose between money or food, or food and sexually arousing material. And yet in our daily lives tasks with mixed rewards seem to dominate. We are confronted with decisions concerning which *kinds* of rewards to pursue, e.g. food rewards or sexual rewards. We also seem to be able to combine these pursuits on some occasions, e.g. a seductive dinner date. So in describing the common currency of value in the brain, we can pick out need- or task-relative currencies, where outcomes or actions are ranked with respect to a particular need. But we can also ask whether there is a need-general currency, enabling needs themselves to be ranked.

Economists might take note that this latter question is not so different from one that arises in welfare economics, namely: How many kinds of values must our economic arrangements maximize? To explore this question, we could develop hypotheses regarding hierarchical relations between reward systems, and test them using the myriad methods of neuroscience (e.g. tracing studies, pharmacology, electrophysiology, immediate early gene expression, and of course, neuroimaging). For example, needs might be ranked on a scale of expected net need satisfaction and δ signals calculated on the basis of discrepancies between net need reduction and actual need reduction. Thus, pursuing food might take priority because energy is needed to satisfy so many other needs. Once food is obtained, it would be momentarily devalued and another need would take precedence, based on the expectation of net need satisfaction, given the new need's prioritization. It is interesting to consider where the pursuit of pleasure might fit into this picture or how the mechanism of such a need-general currency might fit with habit-based action selection systems (Landreth 2007 for detailed discussion).

Of course, the common currency hypothesis (at least in the need-general formulation) might be false. There might be no need-general common neural currency. Or, there might be several. In either case, in answering these questions, we would learn more about which values are our most fundamental, and how we truly come to value actions and outcomes. This information could then be taken back into debates on the proper representation of utility functions. Surely this result would impact economics.

Developing the capacity to count the brain's reward (and punishment) functions would also provide information for assessing the rationality of human choice. If we can determine, *independently of what is professed in self-reports*, which values a person's brain is geared to optimize, abandon, and

adopt, we would no doubt have more satisfactory constraints on assessing the rationality and irrationality of choice behaviour than economists now possess. Or so say we two non-economists.

5. CONCLUSION

Our discussion has focused on puzzles regarding the causal structure of decision processes as they arise in neuroeconomics, especially in research that employs standard neurophysiological techniques in nonhuman primate models. There is no guarantee that resolution of these puzzles will benefit economics. Neuroeconomists pursuing this research from different disciplines seem to have different experimental goals. Even if an accurate characterization of the neural mechanisms of decision processes becomes available, realistic representations of phenomena are thankfully unnecessary for some predictive purposes. Yet it would be surprising that such characterizations would be uninformative for explaining a number of economic phenomena, such as self-defeating behaviour, or for constraining assumptions regarding the nature of human welfare. If they wound up being treated as uninformative for these concerns, non-economists might rightfully wonder if economics was committing itself to a stubborn sense of autonomy – the same sense that hindered brain-influenced developments into cognitive psychology for nearly two decades, and still lingers in some fossilized segments of that discipline.²

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