Economic, Psychological, and Neural Creatures

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"Perception and choice are the products of context dependent and comparative evaluation mechanisms that can be systematic and predictable, but that do not readily lend themselves to analyses that assume consistency, independence and invariance."

--Eldar Shafir

Eldar Shafir's paper powerfully reinforces the notion that we are indeed different creatures from what much economics supposed. To cite some of Shafir's examples, people are impulsive, myopic, trusting and vindictive, often have faulty intuitions about their own motives and behaviors, exhibit biased judgment and malleable and incoherent preferences. Extending this line of reasoning a bit, perhaps we are not only fundamentally different creatures from the economics viewpoint, but perhaps we are also fundamentally different from what our common sense intuitions about ourselves supposes. That is, despite the impression that we are unitary in our decision-making – that the "me" who decided on a double latte at Starbucks last week is roughly the same "me" who decided on a grande coffee yesterday – this impression could prove to be false. Think of this as the Fundamental Attribution Error directed at ourselves. There is no *a priori* reason why

our common sense intuitions about ourselves should be privileged. It may be that our sense of being a unitary agent is simply a *post hoc* reconstruction, perhaps even a useful illusion evolution has perpetrated on us.

Shafir's paper presents numerous lines of behavioral evidence illustrating the ways in which we diverge from the economic picture of human agency. In this brief commentary, I want to extend Shafir's themes by considering what brain science may have to add to the behavioral evidence he cites, and ultimately, whether our behavior has its roots in a unitary mechanism or in multiple -- perhaps even autonomous -- mechanisms. My aim is to present some lines of evidence from cognitive neuroscience that suggests our behavior has its source in a number of neural systems that do interact, but whose operation can have a high degree of autonomy in many contexts. Contrary to intuition, we are a conglomeration of behavioral systems. To offer a metaphor: we are an evolutionary merger in which the different divisions are still awaiting an integrated communication system – as a consequence, the local offices often do things without the supervision of the home office, whose purview is limited.

The Ubiquity of Reward

One of the most fundamental insights of the molecular genetics of development has been the extraordinary homology of nervous system developmental genes: there is a common genetic toolkit that organisms share. In many cases, this translates into common organizational themes. Perhaps the deepest such common theme is the ubiquity of neural reward systems. A variety of experimental techniques, ranging from

psychopharmacology to neural imaging, has demonstrated the striking ubiquity and conservation of reward structures across species. At virtually all levels of the human nervous system, for example, reward systems can be found that play a central role in goal-directed behavior (Schultz, 2000). Here, I focus on one such system, the midbrain dopamine system. The midbrain dopamine system projects principally from the ventral tegmental area to the nucleus accumbens and the temporal and frontal cortex. Studies utilizing self-stimulation paradigms revealed that activation of this system was highly reinforcing, often with laboratory animals preferring to self-stimulate this system than eat or copulate with a receptive partner (reviewed in Wise, 1996). Most addictive substances involve this system, giving rise to the hedonic theory of dopamine as the signal underlying pleasure (though see Garris et al., 1999). Given what I have previously stated regarding the possibility that control structures are highly conserved, it is interesting to note the striking homology between the dopamine system in humans and a reward system in the bumblebee. The bumblebee suboesophogeal ganglion contains an identified neuron, VUMmx1, which delivers information about reward during classical conditioning experiments via the neurotransmitter, octopamine, which is similar in molecular structure to dopamine (Hammer, 1993).

Both experimental and computational work on the role of VUMmx1 in bumblebee foraging has provided important insights into the signal carried by octopamine and the system's functional significance (Real, 1991; Montague et al., 1995). Rather than simply carrying information regarding reward, it appears that octopamine signals information regarding prediction errors. Whereas reward is traditionally a behavioral notion, prediction is a computational notion. The difference between certain

rewarding outcomes and their predictions can be used to guide adaptive behavior. A system that learns through prediction learning need not have the path from goal to reward specified, in contrast to fixed behavioral patterns, such as stimulus-response learning. Instead, the path from goals to rewards may be left open and discoverable via learning, resulting in flexible action. Evolution, then, may shape the pattern of basic rewards animals are motivated to obtain, but the behavioral path is left open to discovery, as are more complex relations among predictors. In this sense, brains are prediction machines that use information gathered from past experience to predict future events important for survival (reviewed in Montague and Quartz, 1999).

Experiments utilizing neurophysiological recording in behaving monkeys by Schultz and colleagues demonstrate that the midbrain dopamine system plays an important role in prediction learning in the mammalian brain (Schultz et al., 1993). When these monkeys were presented with various appetitive stimuli, dopaminergic neurons responded with short, phasic activations, which typically lasted for only a few repeated presentations. In an important finding, however, Schultz and colleagues found that when the rewarding stimuli was preceded by an auditory or visual cue, dopamine neurons changed their time of activation to just after the time of cue onset. In contrast, when the reward did not follow the conditioned stimulus, dopamine neurons were depressed below their basal firing rate exactly at the time the reward should have occurred. These results indicate that the dopamine signal encodes expectations regarding the delivery of reward. That is, the output of dopamine neurons code for an error between the actual reward received and predictions of the time and magnitude of reward. Like the octopamine signal in the bumblebee, the dopamine signal codes a prediction error that can be used in

learning and in action selection. This mode of action is equivalent to Temporal Difference learning, a thoroughly examined form of reinforcement learning (Sutton and Barto, 1998) that learns the predictive structure of an environment. Simulations demonstrate that despite the apparent simplicity of this model, it is a very powerful learner, capable of learning master level backgammon, for example (Tesauro, 1995).

A variety of evidence supports the notion that this system works in a similar fashion in humans (though it is important to point out that this in no way is meant to be the exclusive locus of behavioral choice). For example, it is possible to design reward functions where the computational model of dopamine will pursue sub-optimal strategies. Montague and Quartz (1999) found that human choice behavior in a simple two-card task followed these sub-optimal strategies when faced with these anomalous reward functions. Berns et al (2001) have recently examined prediction learning directly with functional imaging, essentially replicating Schultz's monkey experiments in humans, and have found activation of the midbrain dopamine system. These results suggest that the midbrain reward system in the human brain shares common functional properties with homologous reward systems across a diverse array of species.

Renovating the Neural Architecture

It is deeply intriguing to note where the midbrain dopamine system projects to in the human brain. In particular, what is most intriguing is the fact that it projects to dorsolateral prefrontal, premotor, and parietal cortex, which are structures believed to mediate goal representations, and the orbitofrontal cortex, which is believed to mediate

the representation of relative reward value and reward expectation (for a review, see Schultz, 2000). A great deal of attention has centered on the dorsolateral and orbitofrontal prefrontal cortex as structures implicated in crucial components of human cognition, particularly social cognition and theory of mind (Stone et al., 1998), symbolic learning (Deacon, 1997), representations of self (Craik et al., 1999), and executive function and behavioral inhibition (Norman & Shallice, 1986).

In an evolutionary context, it is important to ask, what is the functional significance of the fact that a phylogenetically old part of the brain projects to a relatively phylogenetic newcomer? According to the view of developmental evolutionary psychology, these structures constitute a hierarchically organized control structure, where additional layers of control have been added to the evolutionarily conserved dopamine system and where this hierarchical organization is evident developmentally as well. To see how, it is important to examine the developmental links between these components, as I explore in more detail below.

Diamond and colleagues (reviewed in Diamond, 1998) have demonstrated that a functional midbrain dopaminergic system is necessary for normal development of prefrontal functions. The most compelling evidence regarding this developmental dependence stems from studies of Phenylketonuria (PKU). Patients suffering from PKU do not naturally produce a particular enzyme, phenylalanine hydroxylase, which converts the essential amino acid phenylalanine to another amino acid, tyrosine, the precursor of dopamine; when untreated, PKU leads to severe mental retardation. Diamond and colleagues found that lowered levels of tyrosine uniquely affect the cognitive functions dependent on prefrontal cortex because of the special sensitivity of

prefrontally projecting dopamine neurons to small decreases in tyrosine. In a 4-year longitudinal study, they found that PKU children performed worse than matched controls, their own siblings, and children from the general population on tasks that required the working memory and inhibitory control abilities dependent on dorsolateral prefrontal cortex. In contrast, these PKU children performed well on control tasks that were not mediated by prefrontal cortex (Diamond et al., 1997).

The hierarchical organization of the control structures that constitute the human cognitive architecture is apparent developmentally, with human cognition and behavior becoming increasingly mediated by frontal structures. In contrast to the early functional involvement of midbrain dopamine systems, prefrontal structures develop relatively late and exhibit a protracted development that continues into adolescence. Thus, behavior and cognition increasingly comes under the mediation of frontal structures from subcortical structures across development, a process sometimes referred to as frontalization of behavior (Rubia et al., 2000). For example, executive function is a control mechanism that guides, coordinates, and updates behavior in a flexible fashion, particularly in novel or complex tasks (Norman and Shallice, 1986). This requires that information related to behavioral goals be actively represented and maintained so that these representations may guide behavior toward goal-directed activities. In humans, executive function follows a special developmental trajectory, reflecting an evolutionary reorganization of prefrontal structures and their development. Between 7 ½ and 12 months of age, infants show a developmental progresson on A-not-B (Diamond, 1985), delayed response (Diamond and Doar, 1989), and object retrieval tasks (Diamond, 1988). There is substantial evidence that these tasks are mediated by dorsolateral prefrontal cortex and rely on working

memory, neural representations of goal-related information, and behavioral inhibition (Goldman-Rakic, 1990; Petrides, 1995). Further, various sources of evidence indicate that dopamine is necessary for successful performance on these tasks (Sawaguchi and Goldman-Rakic, 1994).

Jack of All Trades, Master of None?

I have briefly outlined two behavioral systems that are central players in generating human behavior. I should point out there is a great deal of cross-talk between these systems, and yet it appears that in many contexts our behavior is dominated by the operation of one or the other. Much of the time our behavior is unconscious and learning implicit—perhaps in contexts whose parameters can be navigated sufficiently by midbrain systems. In other systems, especially novel social contexts that are inherently ambiguous, perhaps behavior shifts over to a more prefrontal locus of control (this dichotomous way of putting it is an obvious oversimplification for illustrating the general point). Humans have prefrontal structures that are specialized for social cognition, which facilitate our capacity to adapt behavior rapidly in the light of shifting social contexts, as my research group is investigating with functional brain imaging. Indeed, we appear to have such proclivity for this context-dependence that it undermines trait models of personality, which stress cross-situational consistency, as does much economic theorizing, and leads to the Fundamental Attribution Error. Rather than view this as a fault, as something that a normative theory strives to overcome even, we should instead see it as perhaps the central capacity that allows us to engage in complex social life. The

demands of navigating complex social contexts and cross-situational (and inter-temporal) consistency are antagonistic, and our brain appears to favor behavioral flexibility. Even then, the contexts we find ourselves in may cue different neural structures for their navigation, some of which reflect ancient behavioral strategies (sometimes we act like bees) while some relatively recent evolutionary innovations. Just as the unity of perception is a constructive act our nervous system performs, so too our sense of being a unitary agent may be the nervous system's way of making our behavior coherent to ourselves, though not reflecting a deep property of the neural systems that actually generate our behavior.

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