Comments on Steven Quartz

Jackie Sullivan

Dr. Quartz offers two criticisms of "narrow evolutionary psychology". He states, first, that even if cognitive functions can be detected behaviorally, this does not entail that they correspond to distinct brain structures. Furthermore, even if brain functions can be localized, it does not follow that each identified function corresponds to a separate gene. This general strategy of critique is familiar, as it resembles criticisms of adaptive explanations for traits: even if traits can be identified, this does not entail they were selected for independently.

In place of "narrow evolutionary psychology" he offers an alternative positive developmental evolutionary psychology. In articulating this view, he attends to two specific questions:

(1) In an individual's lifetime, how do higher cognitive functions get "built up"? In other words, what are the mechanisms by which higher cognitive functions get "built up"?
(2) How was the program to build up cognitive functions selected for in the course of evolutionary history?

My commentary is directed primarily at analyzing the answers that he provides to these two questions and identifying some specific problems with these answers that I believe put into question the viability of the alternative he offers.

II. Developmental Account

One crucial element of the developmental account is that the human brain undergoes a protracted course of development in so far as cortical growth occurs during an extended timeframe. One feature of this extended period of development is that specific subcortical structures that are operative early in embryonic development play an essential role in determining the course of later cortical growth and development. Dr. Quartz isolates one primary subcortical neurotransmitter system that he deems crucial to determining how the developmental trajectory of the cortex will unfold, namely, the midbrain dopamine system. He provides what I take to be a two-step analysis of this system.

First he tells us about information-processing features of dopamine neurons, based on data that suggests the specific kinds of information these neurons themselves encode and the type of learning mediated by the system as a whole. This data is taken from Wolfram Schultz's single-unit recording work on dopamine neurons in alert behaving monkeys. The data suggests that the dopamine system functions primarily as a reward or "pleasure seeking" system and, more specifically, that dopamine neurons encode information concerning (1) the relationship between stimuli and rewards as well as (2) expectations regarding the delivery of reward. On the basis of this evidence, Dr. Quartz characterizes the dopamine system as an "open biological control system", in so far as it leaves the path from internal goal states to target states open and discoverable via learning" (Quartz 2002, 15), which he claims enables flexible action.

Once he specifies the function of the dopamine system as a reward system, he isolates it as the primary system upon which a variety of cortical areas are built up. I take his hierarchical cognitive developmental story in a nutshell to run as follows:

(1) In the early stages of development, the system directs the infant to interact with its environment, enabling it to develop associations between rewards and goals.

(2) Due to these goal-directed interactions with the environment, activity-dependent cortical growth and activity-dependent changes in synaptic strength occur. This use-dependent activity in conjunction with specific neuronal growth mechanisms results in flexible learning and is indeed essential to such learning.

(3) The cortical areas to which the dopamine system projects appear to realize their cognitive functions based on this early goal-seeking behavior.

While the specific details of this story are far more complex, this reconstruction is sufficient for the particular criticism I wish to make. The main point of this reconstruction is to emphasize just how much of Dr. Quartz's neuroconstructive cognitive account is hinging on the dopamine system. Now let me turn to the data Dr. Quartz uses to support his claims.

Schultz's single-unit recording work in behaving monkeys is suggestive in establishing a role for dopamine neurons in reinforcement and prediction learning. This does not establish, however, what role these neurons play in mediating the types of learning associated with those cortical areas to which the dopamine system projects. As far as I understand the story, it is unclear what inputs to layer V pyramidal cells dopaminergic neurons are mediating. Knowing this is crucial to establishing just how it happens that these systems are "built up" via the dopamine system.

Now, one can cite evidence from developmental studies that implicates the dopamine system in the development of cortical areas subserving specific "higher-order" cognitive functions. Dr. Quartz employs this strategy in asking us to consider the case study of phenylketonuria (PKU). Patients with PKU have deficits in working memory and inhibitory control abilities, which are thought to result due to a lack of the enzyme phenylalanine hydroxylase, which converts phenylalanine to tyrosine, a precursor of dopamine. The specific pathway implicated in this disease is the projection from dopamine neurons to dorsolateral prefrontal cortex. Based on this and similar evidence, Dr. Quartz wants to establish the fundamental role of dopamine in the realization of cognitive functions in this area of cortex.

Now, it is interesting and quite relevant to note that tyrosine hydroxylase is a precursor not only for dopamine, but also for all catecholamine neurotransmitters, including norepinephrine and epinephrine. In other words, if one does not naturally produce the enzyme that converts phenlalanine hydroxylase to tyrosine, he/she lacks all of the catecholamine neurotransmitters. Presumably in PKU patients, these neurotransmitter systems are similarly affected. In turn, it seems reasonable to argue that it is not dopaminergic projections to the dorsolateral prefrontal cortex alone that are responsible for the production of the types of cognitive deficits that we see in PKU patients. In other words, the explanation as to why we see these cognitive deficits in PKU patients is probably far more complicated than Dr. Quartz leads us to believe. I want to suggest that this puts into question the fundamental role he assigns to the dopamine system as the primary base upon which higher-order cognitive functions are built-up.

The moral of the story is that when we individuate distinct neurotransmitter systems and attempt to isolate how they function developmentally as "behavioral control structures", we might miss how these distinct systems act in concert in the process of what Dr. Quartz terms "hierarchical cognitive development". My worry is that if we begin with incomplete or fragmented developmental stories, in so far as we prematurely assign functions to specific brain areas without considering how they interact with other areas to enable cognitive functions, we wind up telling similarly fragmented adaptationist stories, which make it unclear as to how much better off we are than the "narrow evolutionary psychologist". In fact, we may only better off in so far as we are taking our analysis one step lower and beginning to look at the biology. Yet this introduces a specific element of complexity. Dr. Quartz certainly appreciates this complexity, but the question is: how might it be worked into his current account?

This second criticism regarding the evolutionary story that Dr. Quartz articulates is based on a specific tension that I find with respect to his position on the units upon which selection can act. At one point in the paper he suggests that selection can act potentially upon phylogenetic variations in heterochrony, namely,

variations in the trajectory of "developmental programs" that coordinate brain development. However, he also seems to suggest that selection can act upon variations in biological control structures, the dopamine system being one instance of a biological control structure. To get clear on the tension, allow me to very briefly restate Dr. Quartz's adaptationist account.

III. Evolutionary Account

Dr. Quartz first suggests that selection can potentially act upon heterochrony, namely, phylogenetic variation in the relative timing of major developmental events. Such phylogenetic variations in the trajectory of developmental programs correspond to specific mechanisms--arrays of regulatory genes, or genomic regulatory systems. In humans, the duration of neurogenesis in the course of a lifetime is protracted, this protraction to some extent mirrors the spatial organization of the neuraxes of the neural tube from which the nervous system develops.

During the last 600,000 years, a period of enduring ecological instability occurred. The dopamine system was an evolutionary precursor to specific cortical regions, so at some point in this timeframe it was already on-line. This period of ecological instability coincided roughly with hominid encephalization, namely, (1) the development of higher cortical structures situated at the anterior and ventral ends of the neuraxis as well as (2) the protracted development of these structures.

Dr. Quartz's claim is that selection acted upon heterochrony, and progressively more and more layers of cortical control were added on top of the subcortical dopamine system, the dopamine system playing a crucial role in their development much like the role it plays more modernly in cognitive development. The entire system evolved to comprise a hierarchical control structure that bestowed upon the species increased flexibility for dealing with an ever-changing environment.

A tension in this story arises, at least in my mind, because it appears that the dopamine system as a behavioral control system was selected for prior to the selection of the developmental program. A plausible adaptationist account may be offered as to why the dopamine system was selected for; indeed this account appears to be implicit in Dr. Quartz's story. My question is whether he maintains that selection acts upon what appear to be two distinct kinds of units.

IV. Conclusion

If I am correct with respect to this interpretation, I think there are certain problems for Dr. Quartz's adaptationist account. He has taken a system and separated it off from other systems that seem equally as important to the modern developmental story, and given it pride of place in an evolutionary context in so far as establishing a separate heritability for it, and has suggested that it is functioning in a similar way as it functions in current development. Yet, as I mentioned previously, there are variety of systems which contribute to higher-order cognitive development currently, these different systems are not all reward systems, and how the details of how they interact in concert with the dopamine system in the realization of higher-order cognitive functions is not well worked-out. So, in essence my claim is that there is little evidential support for the developmental story and this poses a problem for the evolutionary story. Both stories have to be far more complex than Dr. Quartz's account leads us to believe.

These criticisms aside, I cannot stress enough my sentiments on the value and importance of Dr. Quartz's novel and interesting contributions to this literature. If we want to move beyond "narrow evolutionary psychology", this is the ultimately the direction in which we want to move and I wholeheartedly thank him for setting the ball rolling.