

backwards induction? ESS learning rules for dynamic games await elaboration.

Learnt dynamic ESSs take us to the problem of optimality in the following way. Although we still lack a satisfactory model of the working brain (cf. Anderson & Palca 1988), a promising approach is neuronal Darwinism (Dehaene et al. 1987; Edelman 1987). According to these models, a kind of natural selection is going on in the brain itself, among neuronal groups. Selection of functional repertoires from primary ones is taking place in a manner compatible with the survival needs of the organism as a whole. As Michod (1989) emphasizes, a selection hierarchy is involved: Genetic evolution should lead to innate rules of the brain that ensure that most of the time adaptive behavioural patterns are allowed to emerge through neuronal Darwinism. As in the analogous cases of hierarchical selection ranging from earliest evolutionary units (Szathmáry 1989) to recent genetic ones (Dawkins 1982), the higher level system must be able to constrain the evolution successfully at the lower level; otherwise the higher unit is disrupted. Whereas selfish genes (including those affecting behaviour) have received wide attention, selfish neuronal groups leading to nongenetic and organismically maladaptive behaviour remain largely unnoticed. Inasmuch as these are of importance in the behaviour of (presumably) the most intelligent animals, deviations from optimal strategies as implied by the dynamic programming approach are to be expected. Although it is relatively easy to calculate the frequency of selfish genetic elements in spread-selection balance (Charlesworth & Charlesworth 1983), analogous calculations will, I fear, be very difficult to make in the case of behaviour.

Finally, it should be realized that selection hierarchies imply the simultaneous application of different time scales (Szathmáry 1989). A dynamic inner game and the outer game describing its evolution proceed at two time scales: characteristic times for the former are shorter than the organisms' generation time, whereas those for the latter are markedly longer. Learning through brain dynamics introduces yet another time scale.

Modeling change in biology and psychology

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As Heraclitus observed about 25 centuries ago, all things change in nature (i.e., change is the highest form of invariance). Whether change should be the emphasis of natural theory depends on the speed of alteration relative to the events and structure under study. Clark makes a strong case for dynamics in the instance of behavioral adaptation. Because I am a psychologist, I will parallel remarks that are specific to the present topic with comments on dynamics in psychology. It seems to me that many of the concerns and problems are the same in psychology and biology.

William James observed that consciousness is like a stream, ever changing and continuous. Many great psychologists have neglected that notion. Dynamics have primarily been seen in learning theory (now again on the ascent, particularly in connectionism) and certain sensory and information processing oriented approaches. By and large, however, most areas of psychology (including cognitive, clinical, psychobiological, and developmental) have tended to view their phenomena as separate states with little concern for how one gets from one state to the other. Formal decision theory was an example of this neglect of change and process, with an overemphasis on static utilities and subjective probabilities. (Recently Jerome Busemeyer and I have been attempting to develop a more dynamic yet still quantitative theory of decision making: Busemeyer 1982; Townsend & Busemeyer 1989). (Because of the ubiquity of

change and process in psychology and biology, I would go so far as to suggest a course in dynamic systems theory and process modeling for all Ph.D. candidates in these disciplines).

There was some slight confusion in the target article between qualitative versus quantitative and dynamic versus static. These are not the same and it is important not to confuse them.

One parallel between behavioral adaptation and psychology is the use of optimal modeling. Optimal modeling can serve not only as a substantive theory as suggested by Clark, but also as a useful base point against which to compare real behavior (e.g., as in signal detection theory, cf. Green & Swets 1966). This may be even more important in natural biological settings, where laboratory research is often precluded, than in psychology, where many phenomena can be explored in laboratory settings.

Now for more specific comments and questions:

1. Even though *BBS* is not the place for a detailed theory presentation, it is important not to gloss over critical facets. Consider the claims about convergence and the independence of $A^*(x)$ in Section 6, paragraph 3. There are always important conditions on which convergence depends. In what sense is $A^*(x)$ independent of the terminal fitness function? The reader may imagine circumstances where it should not be, or where the theory would be trivial if it were.

2. On the capturing of the past through the present state: There may exist systems where the present state is not sufficient to specify the conditional probability distribution on the next state. In this case, one may expand the notation to include past states and their even their associated times, thus generating a higher order Markov process.

3. I agree with the remarks about too much complexity vis-à-vis the amount of, and information in, the data. For instance, causal modeling in psychology and in other behavioral science areas suffers from a combination of sophisticated models with a paucity of data. This can also be a problem with an over-reliance on multidimensional scaling in the absence of substantive theory. The result is an unfortunate lag in scientific progress using those procedures.

4. The matching phenomenon may be a good example of a different variety of optimality, but then it is incumbent on the dynamic theorists to develop a new model in which matching is optimal (does the cited work by Stephens (1987) accomplish this goal?).

5. The argument concerning the size of the advantage of optimal versus nonoptimal behavior is a slippery one. Unless there is a solid theory/methodology of measurement bridging data and theory, such reasoning can and will often be used for theory rescue rather than theory testing.

6. Finally, the particular avenue taken by Clark and his colleagues appears to be more *immediately* fruitful than those placing too much emphasis on the modish but risky chaos-dynamic approach (see, e.g., Townsend, in press).

Using models of behavior in optimal fashion

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1. Introduction. Clark argues persuasively for the usefulness of the dynamic approach to the modeling of behaviors. Dynamic models represent a more sophisticated mathematical treatment of behavior but the level of sophistication of a model is not necessarily the criterion by which its usefulness should be judged. The usefulness of this class of models for understanding patterns of animal behavior arises from two attributes. First, dynamic models can be used to examine situations that cannot be adequately addressed by static models. Second, for many