

Where's the example?

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Abstract: Lewis has missed an excellent opportunity to concisely demonstrate that a dynamical system can provide a bridge between emotion theory and neurobiology.

Lewis proposes constructing a bridge between emotion theory and neurobiology by using concepts from dynamic systems (DSs). Our major criticism is that the author has missed an excellent opportunity to concisely demonstrate what he has tried to explain with pages of words. First, we observe that nowhere in this target article are there any examples of a DS. Second, the diagrams given are very schematic, usually consisting of several boxes with lines and arrows connecting them in all possible manners and directions, and yet they lack the specificity needed to construct a DS. Thus these diagrams do not clarify, but rather simply say that “anything is possible.” Third, there are no quantitative comparisons given anywhere, so the mathematically oriented reader is left without any means for judging the validity of the ideas presented.

This target article would have been much improved by the inclusion of just one example of a DS. Ideally, the exemplary DS would model some simple feature of emotion theory, which could then be bridged to some feature of neurobiology. Nothing close to this is given in the article. Instead of demonstrating with an example, the author has spent his effort, and pages, attempting to convince others of the workability of his idea. This may be convincing to readers with a strong neuropsychological background, but practitioners of DS would be, like us, mathematically oriented and would find a quantitative example much more convincing.

Although we are willing to believe that it may be possible to use DS to bridge emotion theory and neurobiology, until a specific DS is proposed and is validated as at least somewhat workable by comparison with observations in the real world, there is no assurance that the proposed theory is useful. See Perlovsky (2002) for an example of a step in this direction.

Anything can be modeled by the use of mathematics. Mathematics is arguably nothing more than the use and manipulation of symbols to test ideas and hypotheses. This target article proposes a hypothesis. Any hypothesis could be tested or demonstrated by mathematics. What is needed is demonstration and verification of the hypothesis by comparison with observation.

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On the relationship between rhythmic firing in the supramammillary nucleus and limbic theta rhythm

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Abstract: Lewis emphasizes the role of theta oscillations in emergent coupling among neural subsystems during emotionally relevant tasks or situations. Here I present some recent data on the relationship of rhythmic neuronal discharge in the supramammillary nucleus and the large-scale theta oscillations in the limbic system which provide support to many of his ideas regarding vertical integration in dynamic systems.

There are two structures in the posterior hypothalamus which exhibit theta rhythmic neuronal discharge. The mammillary body nuclei, which only receive descending input from the hippocam-

pal formation, have been characterized in detail in Lewis's target article. I will add some recent observations regarding the other, the theta-generating diencephalic structure, which has direct bidirectional connections with the septohippocampal system. As mentioned in the target article, in rats anesthetized with urethane the majority of neurons in the supramammillary nucleus (SUM) fire rhythmically in synchrony with hippocampal theta rhythm (Kirk & McNaughton 1991; Kocsis & Vertes 1994). As these neurons project to the septum and hippocampus it is generally assumed that their role is to mediate ascending activation leading to hippocampal theta rhythm. The connections between SUM and the septohippocampal system are reciprocal, however, and there is strong evidence that both septum and SUM are capable of generating theta rhythmic activity. It has been shown that theta rhythm may persist in the septum-hippocampus after large lesions in the posterior hypothalamus (Thinschmidt et al. 1995), as well as in the SUM after pharmacological suppression of the septal generator (Kirk et al. 1996).

Activation (electrical or pharmacological stimulation) of the SUM always results in hippocampal synchronization, but SUM neurons may also be synchronized with hippocampal theta when the rhythm does not originate from the SUM. Few data exist regarding the natural behaviors in which SUM activation significantly contributes to limbic theta rhythm. Pan and McNaughton (2002) used a variety of experimental paradigms to study the effect of partial lesions of the SUM on different behaviors in defensive and learning tasks, and tested whether these effects can be related to the known role of SUM in frequency modulation of the theta rhythm (Kirk & McNaughton 1993). They found that SUM lesion and the resulting small decrease in theta frequency did not change the performance of rats in a spatial learning task (water maze), as hippocampal damage would, but the pattern of changes in motivated-emotional behavior (hyperactivity in defensive and operant tasks) appeared, in general, to be similar to those after hippocampal lesions (Pan & McNaughton 2002). This indicates that although SUM discharge may be generally synchronized with hippocampal oscillations during all theta states, including, for example, moving around in the water maze, its functional contribution to limbic theta is limited to emotional behaviors.

The dynamics of coupling between rhythmic discharge in the SUM and the “global” theta rhythm represented by hippocampal field potentials was further examined in urethane anesthetized rats by comparing the direction of influence during theta states occurring spontaneously and evoked by sensory stimulation (Kaminski & Kocsis 2003). The direction of the theta drive between the two structures and its temporal dynamics was analyzed using the method of directed transfer function (DTF). This measure is derived from short-time spectral estimates based on an autoregressive model (Kaminski & Blinowska 1991) and it provides information about the direction of propagation of neuronal activity and its spectral content. It makes use of the asymmetry of the transfer matrix which describes connections between channels. A larger DTF between two signals in one direction as compared with that for the opposite direction indicates an influence of one structure on the other. We found that DTF values were consistently higher for the descending than the ascending direction in the majority of SUM neurons. Significant SUM-to-hippocampus DTF at theta frequency only appeared for short periods, on the background of a dominant descending drive. Only in a few experiments was the ascending SUM-to-hippocampus theta drive found to dominate the relationship between the two structures, but the asymmetry in these cases was also limited to episodes of sensory stimulation (i.e., tail pinch).

During theta states the oscillations in the two structures are coupled so that each SUM neuron fires at a certain phase relative to the hippocampal rhythm. The phase is different for different SUM neurons but when single cells are recorded over several theta episodes their phase is always the same (Kocsis & Vertes 1997). Thus, every time the two oscillators get engaged – that is, switch from non-coherent activity to coherent rhythm – they do