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Letter to the Editor

How useful is the appetitive and consummatory distinction for our understanding of the neuroendocrine control of sexual behavior?

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In a recent paper that has appeared in Hormones and Behavior, Professor Benjamin Sachs (Sachs, 2007) has written a stimulating and scholarly essay on the concept of sexual arousal. In the course of his very useful discussion about the complexities associated with this concept he expresses his quite general strong reservations about the use of the terms "appetitive" and "consummatory" but in this context he discusses them as applied to considerations of male sexual behavior. In this critique he reviews well known concerns about the ability to assign clear category boundaries to these two classes of behavior and he reminds us that some authorities such as the ethologists Niko Tinbergen and Konrad Lorenz closely identified these terms with specific energy models of motivation that have been strongly criticized and are no longer considered useful in trying to understand the proximate control of behavior. We are among the authors noted by Sachs who continue to use these terms, especially in the context of the control of male sexual behavior. Although we find Professor Sachs's overall discussion of how one might think about sexual arousal to be very valuable indeed, we disagree with his critique of the use of the terms "appetitive" and "consummatory". In this essay, we would like to explain our perspective on the continuing use of these terms. We will focus our discussion on the use of these terms in relation to studies of sexual behavior but as we note later in this essay, these terms are employed by behavioral neuroscientists investigating the causes of other behaviors. Because many students trained today in contemporary behavioral neuroscience may not be familiar with the background behind these terms, we have placed our discussion in a historical context.

The origins of the appetitive/consummatory distinction

First and foremost it is important to recognize that the appetitive/consummatory distinction was not proposed to support a particular model or metaphor for the functioning of the nervous system. Rather these terms were proposed as a way to capture variation in species-typical behavior that puzzled many comparative psychologists and ethologists. As noted by Sachs (2007), the specific terms "appetitive" and "consummatory" were first coined by Craig (1917). However, we agree with Marler and Hamilton (1966) that in the modern era the behavioral distinction that the appetitive/consummatory nomenclature captures was first clearly articulated by Sherrington (1906). Sherrington distinguished between "anticipatory" or "precurrent" reactions and "final" or "consummatory" ones. Craig (1917, 1918) later made a similar distinction but substituted the word "appetitive" for "precurrent". As noted by Marler and Hamilton (1966, p. 17 and p. 726), the main reason that this distinction was first proposed by Sherrington was based on behavioral observations, not on a theory or metaphor of nervous system functioning. The key issue that behavioral scientists were grappling with in the early 20th century was how to resolve conflicting observations about the species-typical stereotypy of many behaviors, dubbed Fixed Action Patterns by Lorenz (1937, 1950), with the highly variable and almost unpredictable attributes of other behaviors. Craig's distinction of appetitive vs. consummatory helped resolve this issue. Appetitive behaviors are the more variable, searching phase of a behavioral sequence. Consummatory behaviors are the stereotypic phase and tend to result in the termination of a behavioral sequence (see Fig. 1).

With the articulation of this distinction, enduring conflicts related to the mechanistic-vitalist controversy could be resolved. Appetitive behaviors do indeed appear to be more "spontaneous" and less dependent on a clear external triggering stimulus but this does not make their control mechanisms less subject to a mechanistic analysis of their regulation (Marler and Hamilton, 1966, p 18).

Relationship between the appetitive/consummatory distinction and energy models of motivation

The pioneers of modern ethology Konrad Lorenz and Niko Tinbergen both embraced the appetitive/consummatory distinction as a useful first step in behavioral description (Lorenz, 1950; Tinbergen, 1951). A careful reading of their early discussion of this concept reveals that they found it useful precisely because it provided a terminology to organize many behavioral phenomena for a causal analysis. However, both Lorenz and Tinbergen adopted models or metaphors of nervous system function that were designed to explain the control of species-typical behavior (see Fig. 2).

These models tied the occurrence of consummatory behavior specifically with the release of an action specific energy. Lorenz (1950) proposed a hydraulic model to explain how the

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management of action specific energy can be linked with the occurrence of fixed action patterns (Fig. 2A). According to his view, a consummatory behavior would release the reservoir of energy and thus lead to the termination of the behavior in question. Tinbergen's model stressed a hierarchy of neural "centers" that organized behaviors with the control of appetitive behaviors being just prior in the hierarchy to the occurrence of consummatory behaviors (Fig. 2B) (Tinbergen, 1951). These ethological models of motivation were criticized (e.g., Hinde, 1956, 1970) based on several criteria. It was pointed out, for example, that several aspects of the Innate Releasing Mechanisms conceived as a "block" or a "key-lock" structure in the models of Lorenz and Tinbergen involved properties that were presumably not present in the central nervous system (Hinde, 1956). As stated by Hinde (1956, p. 330) problems arose mostly "*when the properties of the model were not clearly differentiated from those of the original*". What he means is that one must remember that a model tries to capture properties of a genuine physiological process to facilitate research but when one starts to think of the model as synonymous with the physiological process under investigation one actually can have "…retarding influences on research" (Hinde, 1956, p. 330). When appropriately understood, these models were helpful in guiding research but the length of time that they would serve a useful function was limited. These models certainly no longer guide research on the mechanisms of behavior and one can argue that they are not even widely known today. But because these terms were associated by some authors with models of nervous system that are no longer relevant, as noted by Sachs (2007), many authors such as Manning and Dawkins (1998) have argued against the use of the terms appetitive and consummatory because they were in the past so closely linked to these models.

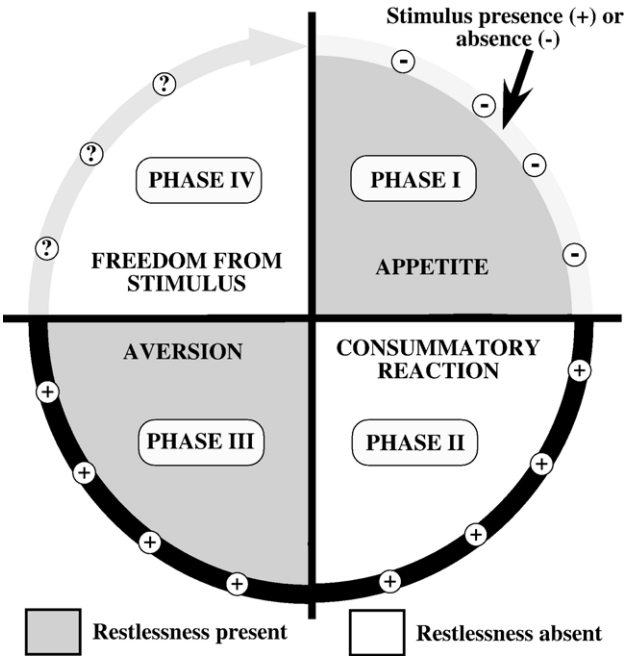

Fig. 1. Model of « instinctive » behavior involving a 4-phase cycle according to Craig. In phase I, the relevant stimulus is absent and subjects show an appetite for that stimulus as indicated by restlessness (grayed quadrant), varied movements, effort and search. During phase II, the stimulus is present and releases the expression of the more stereotyped consummatory reaction to that stimulus. In phase III, the surfeit of that same stimulus becomes disturbing. The animal is in a state of aversion and expresses restlessness (grayed quadrant) and effort directed toward getting rid of the stimulus. Finally, during phase IV, the animal reaches a state of rest and freedom from the stimulus, which can be present or absent at that stage (question marks on figure). Figure drawn based on ideas in Craig (1917).

The current utility of the appetitive/consummatory distinction as a description of behavior related to an analysis of the mechanistic control of behavior

Modern training in neuroethology and behavioral neuroscience no longer devotes much attention to the models of drive proposed by Tinbergen and Lorenz. A survey of relevant textbooks in behavioral neuroscience and neuroethology reveals little consideration of such models outside of a historical context (e.g., Carew, 2000; Rosenzweig et al., 2004; Zupanc, 2004). We would argue that the linkage of the terms appetitive/consummatory with these now defunct motivational models is not an impediment to the appropriate use of these terms by modern students of behavior. Other terms in behavioral science have endured despite the fact that they have been linked to a particular mechanistic theory. For example, the term "imprinting" was coined by Lorenz to describe the selective learning by a gallinaceous chick to follow a moving stimulus encountered shortly after hatching and for this following response that endures until the chick reached sexual maturity. Many investigators have tied this description of a very particular behavioral phenomenon to different theories about neural mechanisms. The theories of control have changed over the years but the term has remained useful. This is also the case for the appetitive/consummatory distinction.

However, there have been criticisms of the appetitive/consummatory distinction related to its utility as a way to describe behavior. The most obvious and commonly stated problem is that the distinction between the two categories is not always clear. In regard to this problem, we would like to make the general observation that many biological categories have poorly defined boundaries. One need only consider the challenges associated with the definition of a species or a gene to realize how difficult it can be to definitively define the boundary of a biological category. In the case of the appetitive/consummatory distinction it is not always apparent when the transition between these categories occurs.

This problem can be discerned when one considers the organization of male sexual behavior. In Japanese quail, the species we have studied for many years, males when alone will produce a vocalization called a "crow" that functions to attract females (Goodson and Adkins-Regan, 1999). Once the male is in the presence of a female, the crow vocalizations declines (Potash, 1974). Subsequently, in the presence of a female, a male will often exhibit a display called strutting. This will be followed by a copulatory sequence of behaviors during which the male will grab the female's neck feathers with his beak, attempt to mount on her back and then eventually succeed in apposing his cloaca to the female's cloaca so that sperm transfer can occur.