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Review

Stress revisited: A critical evaluation of the stress concept

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ABSTRACT

With the steadily increasing number of publications in the field of stress research it has become evident that the conventional usage of the stress concept bears considerable problems. The use of the term 'stress' to conditions ranging from even the mildest challenging stimulation to severely aversive conditions, is in our view inappropriate. Review of the literature reveals that the physiological 'stress' response to appetitive, rewarding stimuli that are often not considered to be stressors can be as large as the response to negative stimuli. Analysis of the physiological response during exercise supports the view that the magnitude of the neuroendocrine response reflects the metabolic and physiological demands required for behavioural activity. We propose that the term 'stress' should be restricted to conditions where an environmental demand exceeds the natural regulatory capacity of an organism, in particular situations that include unpredictability and uncontrollability. Physiologically, stress seems to be characterized by either the absence of an anticipatory response (unpredictable) or a reduced recovery (uncontrollable) of the neuroendocrine reaction. The consequences of this restricted definition for stress research and the interpretation of results in terms of the adaptive and/or maladaptive nature of the response are discussed.

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1. Introduction

The present paper is the result of a workshop on conceptual issues in stress research held in spring 2009 in Göttingen (Germany), organized by Eberhard Fuchs and Jaap Koolhaas. The workshop brought together a number of scientists that are actively involved in preclinical stress research. They intensively discussed the current use of the stress concept in various scientific disciplines and the lack of consistency of scientific results across laboratories and stress models. The group felt it important to revitalize the view that stress should be considered as a cognitive perception of uncontrollability and/or unpredictability that is expressed in a physiological and behavioural response. Moreover, one needs to be aware that the reverse is not always true: the physiological response by itself does not necessarily always indicate a state of stress. We propose that the use of the terms 'stress' and 'stressor' should be restricted to conditions and stimuli where predictability and controllability are at stake; unpredictability being characterized by the absence of an anticipatory response and loss of control being reflected by a delayed recovery of the response and the presence of a typical neuroendocrine profile. This definition will be discussed in the following sections and we argue that this more narrow definition will avoid confusion with normal physiological reactions that are mandatory to support behaviour.

The concept of stress has been subject of scientific debate ever since its first use in physiological and biomedical research by Selye (1950). Stress was originally defined as the non-specific response of the body to any noxious stimulus. Later, the concept was refined by distinguishing between 'stressor' and 'stress response'. A stressor is considered a stimulus that threatens homeostasis and the stress response is the reaction of the organism aimed to regain homeostasis (Chrousos, 2009). The term "homeostasis" was originally coined by Cannon (1932). In his work, he conceived that many physiological variables such as blood pressure, blood glucose and intracellular osmolarity have a certain preferred set-point and that a deviation of this set-point is counteracted by physiological responses which are aimed at restoring the optimal level. Several authors have emphasized the ambiguity and circularity of the definition of stress in terms of a threat to homeostasis in general (Levine and Ursin, 1991; McEwen, 1998; Day, 2005; Levine, 2005; Romero et al., 2009). Virtually all activities of an organism directly or indirectly concern the defense of homeostasis. Hence, the definition of stress as a threat to homeostasis is almost meaningless and needs critical consideration in the light of the current knowledge of the systems involved.

Levine and Ursin (1991) emphasize the view that stress should be considered as a process that includes the stimulus, the perceptual processing of this input and the behavioural and physiological output (Levine, 2005). Many studies seem to neglect the aspect of cognitive, higher level cortical processing of information leading to the risk of circular reasoning. In fact, many studies interpret the presence of a stress response as an indicator of stress exposure, without an independent definition of either the stressor or the stress response (Armario, 2006). Conversely, other studies define their stimulus as aversive, often from an anthropomorphic line of reasoning, and interpret the response as a stress response. Hence, there is a need for indices that allow an answer to the question whether a stimulus is indeed perceived as a stressor in the sense that it is considered as a serious threat to homeostasis and thus to physical and psychological health.

Apart from this definition problem, there is the question of the adaptive and/or maladaptive nature of the stress response. In the formulation of the General Adaptation Syndrome (GAS), Selye (1936, 1950) has emphasized the adaptive nature of the stress response. Only after prolonged exposure to stressors might adaptation fail and the organism reach a phase of exhaustion with adverse consequences. Research has always struggled with this dual nature of the stress response. The terms 'distress' and 'eustress' were introduced by Selye in 1976 to distinguish between the maladaptive and the adaptive consequences of the stress response, respectively (Selye, 1976). Despite the fact that several authors have emphasized both the adaptive and maladaptive aspects of the stress response (McEwen and Wingfield, 2003; de Kloet et al., 2005; Korte et al., 2005; Dallman, 2007), it appears to be extremely difficult to dissociate these two sides of the coin. This may lead to a certain degree of interpretation bias of the experimental results in either the maladaptive or adaptive direction.

In the present paper, we will argue that the stress terminology should be limited to uncontrollability and/or unpredictability of stimuli. To illustrate this, we want to follow a less biased line of reasoning by starting from the wide range of both causal and supporting physiological processes required for the performance of behaviour.

2. Physiological support of behaviour

The hypothalamic pituitary adrenocortical (HPA) axis and the sympathetic adrenomedullary (SAM) system are generally considered to be the two key players in the stress response. These systems are well recognized to have a main role in energy mobilization and redistribution of e.g. oxygen and nutrients to active organs and tissues, a metabolic function that goes beyond stress *per se*. Therefore, from a more neutral point of view, one might say that both the HPA and the SAM system have a crucial function in the metabolic and cardiovascular preparation of the body to perform behaviour (Sapolsky et al., 2000). These two master systems can be considered as integrated communication systems aimed to coordinate and synchronize the peripheral physiology at the level of cells, tissues and organs in interaction with the environment. Metabolically more demanding behaviour will be accompanied by a higher activation. To illustrate this point, we will compare the HPA axis activity during several types of behaviours, some of which are not generally thought of in the context of stress. The HPA axis activation of rats in response to aversive (painful) stimuli as well as appetitive (rewarding stimuli) is summarized in Fig. 1, expressed as area under the curve for plasma corticosterone. Although there may be species and/or strain differences in the magnitude of these responses, it is clear that a stress-related framework of interpretation fails to explain the activation of the HPA axis shown in Fig. 1. Appetitive and rewarding situations such as sexual behaviour (Bronson and Desjardins, 1982; Woodson et al., 2003; Bonilla-Jaime et al., 2006) and winning a social interaction elicit HPA responses that are similar in magnitude as highly aversive situations like social defeat.

In many cases, the magnitude of the response seems to be a direct reflection of the behavioural activity and hence of the metabolic requirements of activated tissues. It is important to notice that the stimulus that triggers the behaviour may not necessarily present a direct challenge to homeostasis. Behaviour and hence the physiological response can be self-initiated or be trig-

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