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Review

Coping with change: A framework for environmental signals and how neuroendocrine pathways might respond

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ABSTRACT

The Earth has always been a changeable place but now warming trends shift seasons and storms occur with greater frequency, intensity and duration. This has prompted reference to the modern era as the Anthropocene caused by human activity. This era poses great challenges for all life on earth and important questions include why and how some organisms can cope and others cannot? It is of heuristic value to consider a framework for types of environmental signals and how they might act. This is especially important as predictable changes of the environment (seasonality) are shifting rapidly as well as unpredictable changes (perturbations) in novel ways. What we need to know is how organisms perceive their environment, transduce that information into neuroendocrine signals that orchestrate morphological, physiological and behavioral responses. Given these goals we can begin to address the questions: do neuroendocrine systems have sufficient flexibility to acclimate to significant change in phenology, are genetic changes leading to adaptation necessary, or both?

1. Introduction

One of the greatest issues of our time is global change and its implications for environment, food, health and energy. Humans have now visited virtually all regions on Earth and products of our industry have infiltrated every square millimeter of the Planet's surface. This prompted Crutzen and Stoermer (2000) to name the modern era as the "Anthropocene". Humans have now modified over 50% of the land surface of the world and much of that has been severely degraded (Hooke et al., 2012). It is arguable that the Anthropocene began as early as the first agriculture thousands of years ago, whereas others suggest it started with the industrial revolution in the 1800s (Zalasiewicz et al., 2008, 2010). Nonetheless, large scale urbanization, desertification, de-forestation, population increase and pollution are all major components of global change (Travis, 2003; Zalasiewicz et al., 2008, 2010; Hooke et al., 2012). Add to this global climate change and large scale shifts in geographical ranges of some habitats accompanied by changing phenology (seasons), and the increasing frequency, intensity and duration of unpredictable events such as storms, El Niño Southern Oscillation events (see also Field et al., 2012). It is becoming abundantly clear that organisms in general, including ourselves, need to cope with change in our predictable environment, e.g. seasons, as well as the unpredictable such as perturbations.

To cope with global change all organisms must respond to environmental events that signal when change is happening, or is about to happen, in the future. This presents challenging questions of how organisms respond to changing environments during their daily, annual and life cycle routines as well as cope with perturbations of the environment. To investigate the potential control mechanisms, e.g. neuroendocrine pathways, by which animals respond to environmental events and make appropriate adjustments of morphology, physiology and behavior, it is important to have a framework that allows a classification of the types of environmental signals, what information they convey and what responses are most appropriate. It is important to bear in mind there are proximate and ultimate (genetic) components underlying these changes (Visser et al., 2010; Schaper et al., 2013) but the focus here will be on the former – mechanisms by which organisms acclimate to climate change.

Some processes triggered by changing environments act facultatively to maintain constant conditions internally (classic homeostasis). Others anticipate change of environmental conditions so that a new internal state with its own homeostatic set points is generated (termed allostasis) and better suited to the new conditions (e.g. McEwen, 2002; Schulkin, 2003, 2004). The latter includes progression through life history stages such as reproduction, migrations, and molting. To make these adjustments, individuals must first perceive environmental conditions, then integrate this information with homeostatic state, age, social status and other internal variables such as infection. These are regulated

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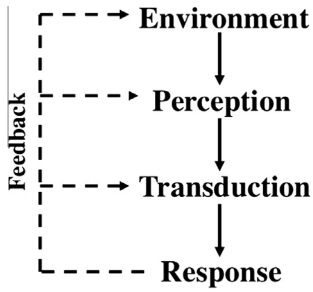

Fig. 1. A working model of how organisms cope with changes in their environment. As conditions change in the physical, social and internal environments, there must be some mode of perception of that change. This could be through a variety of sensory modalities or possibly directly by neuroendocrine and endocrine cells (see Fig. 2). Following perception of the environmental change that information is transduced, in most cases, by the nervous systems into a response that eventually affects behavior and/or morphology and physiology. Note that feedback systems must also exist to at various levels to prevent the response systems getting out of control. After Wingfield and Mukai (2009).

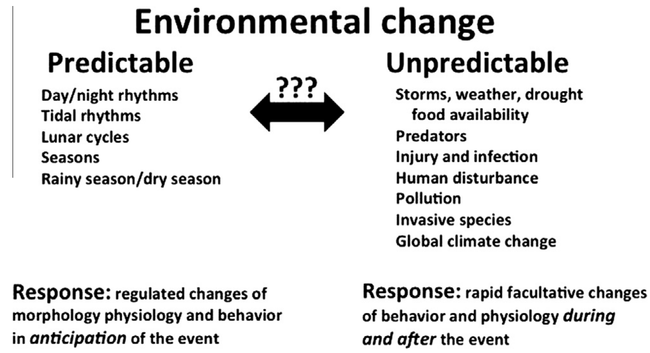

Fig. 2. Responses of organisms to environmental change can be divided into two major components. Predictable changes as part of daily or annual routines (e.g. circadian rhythms, seasonal changes), and unpredictable events that may lead to stress. Neuroendocrinological implications are that responses in physiology, morphology and behavior occur in anticipation of predicable events and thus environmental signals must contain information about those future events. In contrast, responses to unpredictable events require rapid physiological and behavioral changes that occur during and after perception of the change. These two types of environmental change indicate fundamentally different neuroendocrine and endocrine pathways from perception, transduction and response. There is growing evidence for interactions of predictable and unpredictable environmental changes (e.g. global climate change) but how this may affect neuroendocrine control systems remains obscure (Wingfield, 2003; Wingfield and Sapolsky, 2003). Modified after Wingfield (2008b).

in complex central and autonomic nervous pathways, including neuroendocrine systems, and have vital roles in control of responses to environmental change.

Over the past few decades global climate change has had major influences on many aspects of life cycles of vertebrates including patterns of migrations, breeding seasons and coping mechanisms (Berthold et al., 1992; Thomas and Lennon, 1999; Pulido et al., 2001; Both and Visser, 2001; Walther et al., 2002; Travis, 2003). However, the mechanisms by which relevant signals from the environments are perceived, processed and transduced into neural and hormonal signals that then regulate the organism's response remain poorly known (Caro et al., 2013). Relevant questions that arise include "why do some species cope well with global change and others do not?" To fully understand this basic question it is imperative that we also understand the mechanisms underlying responses to the environment especially in the face of very great complexity. As a working model it is useful to consider three main processes (Fig. 1), perception of the environment, transduction of that information, and the response allowing the individual to adjust (Wingfield and Mukai, 2009). There will likely be several levels of feedback from responses to transduction pathways and sensory modalities involved in perception (Fig. 1). To what extent mechanisms underlying these processes contribute to flexibility (Piersma and Drent, 2003) of an organism (able to cope with global change) or inflexibility (unable to cope with global change) is another interesting, indeed fundamental, question.

2. Environmental signals: Perception and pathways of action

Homeostatic processes, social systems, growth, and life history stages require major adjustments of morphological, physiological and behavioral functions in response to environmental demands. These functions are organized into a fixed temporal sequence of life history events (stages), each timed to occur at a time of year that will maximize overall fitness (Wingfield, 2006, 2008a,b). Environmental signals that are indicative of when transitions in life history stages should occur can be used to trigger appropriate responses including termination of the current life history stage and development of the next (Wingfield, 2006, 2008a,b).

Components of the predictable environment (Fig. 2) provide information that the organisms can use to *anticipate* a future event (Farner, 1970). On the other hand, responses to unpredictable events require neuroendocrine control *during and immediately after* the signal is received so the animal can adjust facultatively to the perturbation (Fig. 2; Wingfield, 2003). It is also becoming clear that there are interactions between types of environmental signals. For example, breeding status may affect responsiveness to perturbations and stress (Wingfield and Sapolsky, 2003) and social interactions can influence responses to both seasonality and perturbations (Fig. 2, Ball and Bentley, 2000; Wingfield, 2003, 2008b). These combinations of environmental events have important implications for flexibility of neuroendocrine control systems that regulate complex responses of the individual.

2.1. Types of environmental signals and their roles

Although the sheer complexity of potential environmental information that organisms can use appears overwhelming, it is possible to classify these cues into three major categories (Fig. 3). The organism and its internal condition (homeostasis, sex, age, body condition, disease and infection – Fig. 3) determine how it then responds to relevant signals from the external environment. Predictive information has two sub-types with distinct roles. Initial predictive information triggers onset of the development phase of a life history stage (e.g. migration, reproduction, molt, etc.) and its termination (Farner, 1970; Wingfield, 2006, 2008a). An example of the importance of anticipating future events is the need to develop the reproductive system before the breeding season begins. An example of a type of signal that provides accurate anticipatory (predictive) information is the annual change in day length that orchestrates the correct timing and duration of life history stages (Farner and Follett, 1979; Farner and Gwinner, 1980; Gwinner, 1986, 1996; Wingfield et al., 1999; Dawson et al., 2001; Dawson, 2008). Increasing day length in spring is a classic activator of neuroendocrine signals that regulate gonadotropin-releasing hormone (GnRH) release and onset of gonadal maturation (e.g. Yoshimura, 2004).

The second sub-type, local predictive information, regulates the rate at which initial predictive information acts and when certain components of a life history stage, e.g. final ovarian maturation leading to ovulation, are triggered (Marshall, 1949, 1960; Wingfield et al., 1999; Dawson, 2008). Some local predictive cues accelerate the effects of initial predictive information (e.g. warm temperature, rainfall, increased food supply) whereas others

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