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A Neuroscience Approach to Optimizing Brain Resources for Human Performance in Extreme Environments

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Abstract

Extreme environments requiring optimal cognitive and behavioral performance occur in a wide variety of situations ranging from complex combat operations to elite athletic competitions. Although a large literature characterizes psychological and other aspects of individual differences in performances in extreme environments, virtually nothing is known about the underlying neural basis for these differences. This review summarizes the cognitive, emotional, and behavioral consequences of exposure to extreme environments, discusses predictors of performance, and builds a case for the use of neuroscience approaches to quantify and understand optimal cognitive and behavioral performance.

Extreme environments are defined as an external context that exposes individuals to demanding psychological and/or physical conditions, and which may have profound effects on cognitive and behavioral performance. Examples of these types of environments include combat situations, Olympic-level competition, and expeditions in extreme cold, at high altitudes, or in space. Optimal performance is defined as the degree to which individuals achieve a desired outcome when completing goal-oriented tasks. It is hypothesized that individual variability with respect to optimal performance in extreme environments depends on a well "contextualized" internal body state that is associated with an appropriate potential to act. This hypothesis can be translated into an experimental approach that may be useful for quantifying the degree to which individuals are particularly suited to performing optimally in demanding environments.

Introduction

Extreme environments are characterized as those situations which place a high demand on the physiological, affective, cognitive, and/or social processing resources of the individual. Extreme environments strongly perturb the body and mind, which in turn initiate complex cognitive and affective response strategies. Performance in different types of extreme environments may share some optimal characteristics, but specific environments can also have unique demand characteristics. For example, exposure to the cold and isolated environment of an Antarctic expedition may result in extreme social and sensory deprivation, whereas exposure to military combat operations may entail extreme sensory overload. It is clear that there are many different types of extreme environments or situations, but it is less clear that an individual's cognitive and affective responses are as varied as the variation in different types of extreme environments.

There is substantial evidence from studies of expedition members, military operators, and elite and extreme athletes that exposure to extreme situations, i.e. conditions that impose a significant cognitive, emotional, and/or physical stress on the individual, has profound effects on performance. Optimal performance can be defined as the degree to which individuals achieve a desired outcome when completing goal-oriented tasks. It is important to note that in an environment that does not impose significant physical or psychological stresses, a task may not be considered demanding and can be performed adequately by individuals with average abilities. In contrast, an individual may have great difficult in performing the same task in an extreme environment. For example, an individual may be quite a good marksman at a practice shooting range, yet not be able to optimally perform as a marksman in combat. Another individual may be excellent at performing an athletic task in practice, but not able to perform to a similar degree in an international competition. An extreme environment may make the completion of specific tasks much more challenging, and thus fewer individuals may be capable of optimally performing the specific tasks. Here we aim to 1) summarize our current understanding of the effects of exposure to extreme environments on cognitive, affective and psychosocial aspects of human performance, 2) discuss key predictors of human performance in extreme environments, and 3) develop a conceptual framework to understand performance effects within the context of cognitive and systems neuroscience.

The effects of extreme environments on performance

Cognitive Effects

Previous research has established that exposure to extreme environment can affect cognitive performance related to logical reasoning, learning, memory, vigilance, and reaction time. For instance, when exposed to extreme environments during military training, both Navy SEALS and Army Rangers experienced significant cognitive decline relative to baseline performance in every aspect of cognitive function assessed (Lieberman.et al., 2005). Simple reaction time and vigilance were impaired as well as higher brain functions such as learning, memory, and reasoning. The degree of these deficits was greater than the deficits typically produced by alcohol intoxication, treatment with sedating drugs, or clinical hypoglycemia. Interestingly, these experienced military cohorts did not show the expected increases in cortisol, which is typically used as a measure of stress, as a result of exposure to extreme environments. Thus cognitive degradation can occur in extreme environments even with normal cortisol levels and presumably normal levels of stress.

Maruff and colleagues (Maruff.et al., 2006) measured cognitive performance in healthy volunteers exposed to desert heat compared to unexposed individuals. Psychomotor speed, attentional and executive functions, but not performance accuracy, decreased as the expedition progressed. However, these impairments resolved completely once the expedition was completed. In contrast, extended exposure to extreme environments, such as deployment during the war in Iraq, has been shown to alter cognitive functioning beyond tour completion. Specifically individuals deployed to Iraq, compared with non-deployed controls, showed performance decrements on tasks involving sustained attention, verbal learning, and visual-spatial memory, but performance improvement on simple reaction time (Vasterling.et al., 2006).

Inter-individual variability in deterioration of cognitive functioning as a consequence of exposure to extreme environments depends upon the task at hand. For instance, in a study on isolation and confinement, participants were instructed to focus on minimizing error. Although not all individuals managed to maintain a low error rate throughout the study, those individuals who did maintain a low error rate experienced the highest fatigue levels (Hockey and Sauer 1996). This suggests that task demands and performance level contribute to the individual differences observed with exposure to extreme environments.

In a meta-analysis of 22 studies, Pilcher and colleagues (Pilcher.et al., 2002) reported that cognitive performance does not deteriorate uniformly over time when individuals are exposed to extreme environments. Specifically, experimental sessions of less than 2 hours had stronger adverse impact on performance than longer duration sessions. These findings are consistent with the idea that cognitive performance of individuals initially deteriorates but then may reach a steady state, and even improve over time, during prolonged exposure to extreme environments. Two studies examined the effects of exposure to extreme temperature, one examining long term effects and another examining short term effects. Reed et al. (Reed.et al., 2001) found a significant decline of cognitive performance over a period of four months during Antarctic residence. However, Marrao et al. (Marrao.et al., 2005), examining exposure to cold during a 9 day survival course, found no significant change in cognitive performance. In a different extreme condition (long distance running), when examining cognitive performance over three days, runners showed best performance after a short nap on day two, which was followed by a progressive cognitive decline until the end of the study (Doppelmayr.et al., 2005).

Taken together, most studies show that cognitive performance deteriorates as individuals are exposed to extreme environments; however, there are a multitude of factors that may influence the degree of deterioration. For example, experimental conditions regarding types of task, task duration, level of training on the task, severity of the extreme environment, and the duration of the exposure play a role in the degree of cognitive deterioration. Moreover, other moderator variables such as acclimatization to the environment, level of personal arousal, and motivational factors can also affect cognitive performance. Thus, studies so far do not support the conclusion of a uniform deterioration of cognitive performance in extreme environments.

Affective / Emotional Effects

In addition to influences on cognition, exposure to extreme environments has substantial repercussions on affective processing, which in turn can have profound effects on human performance. A considerable body of research has been conducted to examine affective responses to extreme polar environments, which combines extreme environment and substantial social isolation. A significant subset of individuals who spend extended periods of time in polar settings experience depression, insomnia, irritability, and hostility (Gunderson 1966). Together with cognitive impairment, these behavioral and emotional changes have been termed the "winter-over syndrome" (Strange and Youngman 1971). During the process of further refining the characterization of this syndrome, Palinkas and other researchers made several new and unexpected findings. Generally, individuals reported a lower self-rated level of vigor , but also reported counterintuitive fluctuation in mood states (Palinkas.et al., 1995;Palinkas 2003;Palinkas.et al., 2000b;Palinkas and Houseal 2000). For example, at times mood states actually improved during the course of the study. To explain these results, Palinkas and colleagues (Palinkas.et al., 1995;Palinkas 2003;Palinkas.et al., 2000b) proposed that the individual's appraisal of the exposure to isolation, confinement, and harsh physical environment plays a critical role of their effects on subjective experience. For example, a positive experience can result if the exposure is viewed as part of personal growth, enhanced self-sufficiency, and learning of stress coping strategies. Therefore, exposure to extreme environments does not necessarily result in non-adaptive affective changes but can result in resilient adaptation with positive mood changes.

Affective responses have also been studied during extreme military environments ranging from simulated training, through actual training, to full deployment to war zones. For instance, lab-based simulations of multi-stressor situations have incorporated continuous physical activity, food deprivation, and sleep loss. These simulations reveal that such situations lead to a significant deterioration of soldiers' mood states characterized by decreased vigor, and increased tension, depression, anger, fatigue, and confusion (Lieberman.et al., 2006). Similarly, Bardwell et al. (Bardwell.et al., 2005) showed that mood states in Marines during cold weather, high-altitude field training exercise changed significantly and that reported fatigue, anger, and vigor scores reached clinically significant levels. Moreover, numerous soldiers deployed to Iraq experienced longitudinal increases in negative state affect, usually expressed as confusion and tension (Vasterling.et al., 2006).

Across the spectrum from training to war, these various studies support the assertion that exposure to extreme environments can result in profound changes in mood which may vary considerably from one individual to another. In turn, negative moods are generally acknowledged to decrease performance, thus suggesting these mood changes can negatively impact the performance of critical tasks and readiness for military duty. Similar mood changes have also been observed in elite athletes when required to perform at optimal levels in extreme environmental conditions. Lane and colleagues (Lane.et al., 2004) have shown that athletic performance at altitude and during extreme heat or cold often produces stress responses that include increased negative mood.

To summarize, exposure to extreme environments can alter mood and result in depression, anxiety and/or irritability. However, as with cognitive effects, affective responses to this exposure may depend on the type of activity, the characteristics of the individuals, and the nature of the extreme environment. Therefore, instead of examining affective responses in isolation, future studies will need to examine the interaction between the extreme environment, the subject's baseline characteristics, and the activity or task that the subject has to carry out. Moreover, much work needs to be done to develop predictive models that take into account biological and psychological factors that are likely to make certain individuals more susceptible to adverse changes in cognition, emotion and behavior.

Social / Interpersonal Effects

Apart from cognitive and affective effects of exposure to extreme environments, individuals also exhibit significant social and interpersonal changes. Palinkas (Johnson.et al., 2003) emphasized that participants on polar expeditions are physically isolated from the outside world, with darkness and weather conditions exerting severe restrictions on travel, and are separated from their families and friends. In addition, there is little separation between work and leisure during such expeditions because living and working spaces are close to one another, and each individual interacts with the same group of individuals during both activities. This constant interaction is reported to often create increased social conflict between workers and supervisors, coworkers, cliques, and people with conflicting personalities. Moreover, absence of privacy and constant gossip are frequent, and often have a negative effect on social relations, especially between men and women (Palinkas 1992). Another source of interpersonal tension and conflict identified during polar expeditions is that of problematic social interactions, which are associated with formation of isolative groups (Palinkas 1992), ostracism of crewmembers who do not adhere to group norms, and emphasis on group differences such as gender (Rosnet.et al., 2004;Leon 2005) or occupation (Palinkas 1992), and may include poor or ineffective leaders (Johnson.et al., 2003;Schmidt.et al., 2004)

Other studies have examined interpersonal exposure effects during long-term space flight (Palinkas 2001;Kanas.et al., 2007;Kanas 2004;Kanas and Caldwell 2000). Kanas and colleagues (Kanas.et al., 2007;Kanas 2004;Kanas.et al., 2000) identified a number of interpersonal factors that can disrupt performance during manned space flight missions. These include crew tension, cohesion, leadership, language and cultural differences. Interestingly, these scientists compared American astronauts to Russian cosmonauts during several space shuttle/Mir space station missions and reported more dissatisfaction with the interpersonal environment among the

Americans compared with their Russian counterparts. Similarly, Palinkas et al. (Palinkas 2001) observed factors that affected interpersonal relationships during the Shuttle-Mir Space Program and other long-duration Russian/Soviet missions such as crew diversity and leadership styles, adaptive and maladaptive features of ground-crew interactions, and processes of crew cohesion, tension and conflict.

Taken together, social effects of exposure to extreme environments can result in isolation, clique formation, and inefficient information transfer among group members. However, as with cognitive and affective effects, the determinants, the degree, and the specificity of the deterioration need to be investigated further. In the next section we summarize some of the key findings regarding predictors of performance which may provide insights into approaches to moderate cognitive, affective, and social changes observed during exposure to extreme environments.

Predictors of Performance in Extreme Environments

Due to the diversity of extreme environments and the many different types of challenges they impose on cognitive, affective, social and experiential processing, it may be difficult, if not impossible, to identify one set of factors that could be utilized across the spectrum of extreme environments as a general predictor of optimal performance. Moreover, optimal performance may not be a unitary variable across both subjects and environments. Nevertheless, identifying the basic personality characteristics and the cognitive, affective, and social processing skills that are critical across different types of environments may facilitate the development an optimal processing model, and may result in a deeper understanding of the critical factors required for optimal human performance.

One useful approach to better understand the characteristics that underlie optimal performance is to examine members of military Special Operations teams who are frequently exposed to a wide variety of extreme environments. A recently conducted systematic review (Taylor.et al., 2006) and qualitative assessment (Taylor.et al., 2007) provide important insights into which factors influence the degree to which individuals successfully complete Basic Underwater Demolition /SEAL (BUD/S) training, which is known to be among the most challenging of military training programs. During the qualitative investigation, 8 BUD/S instructors served as subject matter experts (SMEs) in two semi-structured group meetings designed to establish face validity for 64 characteristics hypothesized to influence attrition in BUD/S trainees. These characteristics were derived from the systematic review of military records (Taylor.et al., 2006). SMEs completed questionnaires to assess whether each characteristic was (1) important for BUD/S trainees to possess, and (2) the extent to which each characteristic differentiated trainees who successfully completed the training program from those who did not complete one of the three training phases [Indoctrination Phase, Phase I (Pre-Hell Week), and Hell Week]. During a second meeting, SMEs were presented with the aggregated questionnaire data and engaged in a discussion of factors believed to influence attrition. Key characteristics most consistently reported to differentiate successful completion of the three phases of training from those who dropped out, included mental toughness, the will to win, physical strength, and physical endurance. Several characteristics increased substantially in perceived importance across the three successive phases of training, most notably mental toughness, achievement motivation, physical strength, physical endurance, emotional stability, and team orientation. Based on the mixed qualitative and quantitative feedback from these SMEs, it was concluded that the successful BUD/S trainee is a mentally and physically tough and achievement-focused individual who is an emotionally stable team player. Although there is strong face validity among these predictors, much less is known about the neural basis and stability of these characteristics, or whether they can be modified by targeted interventions. Thus although clearly identify face-valid constructs have been established to identify individuals who perform well in extreme conditions, there is virtually no established cognitive, affective process model or biological basis for these constructs.

In other Special Operations-specific studies, Hartmann (Hartmann.et al., 2003) examined the predictive validity of several paper and pencil tests in 71 male Norwegian Naval Special Forces candidates. These researchers found only weak correlations between ability tests, personality scales and optimal performance. In comparison, Rorschach approaches to measuring stress tolerance, reality testing, cognition, and social adjustment significantly predicted optimal performance (Hartmann.et al., 2003). These findings suggest that tests which may not be immediately transparent to the participants may provide a more useful approach to selecting optimal performers than do standard questionnaires.

In other military research, Bartone et al. (Bartone.et al., 1998) performed a longitudinal descriptive study of key sources of stress and their effects on performance and readiness within a US Army medical unit performing a peacekeeping mission in the former Yugoslavia. These researchers found that specific correlates of operational stress included depression, psychiatric symptoms, and low reported morale. Furthermore, it was suggested that there are five underlying dimensions which have a profound effect on the variability of performance in extreme environments, which are: 1) degree of isolation; 2) ambiguity about the mission; 3) degree of powerlessness; 4) feelings of boredom; and 5) degree of danger and threat. Other scientists have investigated factors influencing performance in military aviation. Siem and Murray (Siem and

Murray 1994) examined 100 US Air Force pilots to rate importance of 60 traits relative to effective performance in aviation skills and crew management. Results suggested that the personality trait “conscientiousness” was the most important determinant of performance across a spectrum of performance dimensions. Similarly, Martinussen (Martinussen 1996) performed a meta-analysis of 50 studies to identify predictors of pilot performance. The best predictors of pilot performance were previous training experience, cognitive and psychomotor information processing abilities, extent of aviation knowledge, and biographical inventories. Interestingly, personality, academic achievement, and intelligence measures accounted for little variance in pilot performance. These studies show that individual characteristics, perception of the task at hand, and social factors all contributed to predicting optimal performance. Although many of these characteristics have good face validity, almost nothing is known about their underlying neurobiology. Developing neuroscience approaches to predict optimal performance may help to quantitatively assess ongoing levels of performance, to optimize performance prior to exposure, and to remediate performance deterioration post exposure.

With respect to expedition environments, Palinkas and colleagues (Palinkas.et al., 2000a) examined the influence of crewmember social characteristics, personality traits, interpersonal needs, and station environment on performance and behavior of 657 American men during Antarctic wintering-over expeditions between 1963 and 1974. Of note, individuals in crews with a clique structure reported significantly more depression, anxiety, anger, fatigue and confusion than individuals in crews with a core-periphery structure. Interestingly, depressed mood was *inversely* associated with severity of station physical environment, supporting the existence of a positive or "salutogenic", i.e. health-promoting, effect for individuals seeking challenging experiences in extreme environments. In general, this group found that social/demographic characteristics, personality traits, interpersonal needs, and characteristics of station environments collectively accounted for 9-17% of the variance in performance measures. Significant positive predictors of performance were extent of military service, low levels of neuroticism, high levels of extraversion and conscientiousness, and a low desire for affection from others. With respect to space missions, Palinkas and colleagues (Palinkas 2001) summarized several key factors influencing optimal performance in extreme environments. These are: (1) subject-specific factors such as personality, response to stress due to isolation and confinement, susceptibility to deterioration of emotional and cognitive performance, adaptive and maladaptive coping styles, and need for psychological support during the mission; (2) interpersonal factors such as crew diversity, leadership styles, small group dynamics, characteristics of ground-crew interactions, and crew cohesion or conflict; and (3) organizational factors such as the organizational culture, mission duration, and managerial requirements. In other studies, predictors of performance during a polar expedition were found to include high levels of paratelic or “playful” dominance, low levels of neuroticism, and the use of planned problem-solving as a coping strategy more frequently than other coping strategies. (Palinkas.et al., 1995).

These studies show that questionnaires are generally poor predictors of optimal performers, and that tests which enables individuals to identify the desired response, are fundamentally susceptible to perception biases which seriously limit their usefulness. Nevertheless, the degree to which individuals interact with others, basic temperamental styles, and subtle psychological processes, may need to be further explored as means to identify optimal performers.

Approaches to assessment of performance differences in extreme environments

Given the profound physiological, cognitive, affective, and social effects of exposure to extreme environments, it seems obvious that there is a need to develop a more fundamental experimental approach to to assist in predicting how an individual would respond if exposed to an extreme environment. Several research groups have developed rating scales or experimental paradigms in an attempt to predict individual performance under extreme conditions.

Laboratory-Based Simulations

Several strategies have been used to generate laboratory models that simulate extreme environments. For example, thermal heat stress as an extreme environment alters the homeostatic state of the individual and can produce small deficits in working memory, information retention and general information processing (Hocking.et al., 2001). In comparison, short-term cold stress (unlike prolonged cold stress) in healthy fit individuals does not appear to produce serious decrements in cognitive and physical performance (Marrao.et al., 2005). Lieberman and colleagues have developed a brief, intense, laboratory-based simulation of a multi-stressor environment which includes sleep loss, continuous physical activity, and food deprivation. Using this model they have shown that decrements can be obtained in cognitive function and physical activity, similar to those observed in highly stressful field environments (Lieberman.et al., 2006). Similarly, extended periods of effortful activity in simulated extreme environments (e.g. a simulated 12 hour refueling mission) result in significant impairments in visual perception and in complex motor and psychomotor vigilance. These impairments were inversely correlated with measured mission performance (Russo.et al., 2005a). Some research groups have proposed to develop demand-specific cognitive assessment to predict optimal performance, and they have generated a computerized environment to accomplish this goal (O'Donnell.et al., 2005).

Interestingly, a recent study suggests that the individuals most likely to fail under pressure are those who, in the absence of pressure, have the highest capacity for success (Beilock and Carr 2005). These findings suggest that simulations may play an increasingly important role in identifying the potential and training status of optimal performance in extreme environments.

Biomarkers

Another approach that may help to predict performance differences in extreme environments is to identify physiological parameters (i.e. biomarkers) that correlate with performance. For example, some research groups have used surrogate biomarkers of neural activity such as movement activity, oculometrics, heart rate, and voice stress signals to examine cognitive states during performance in extreme environments (Russo.et al., 2005b). Others have developed a Rapid Cognitive Assessment Battery for measuring impaired cognitive performance in extreme environments (Shephard and Kosslyn 2005). Nevertheless, this approach is in its infancy and much more work is needed to better identify which physiological assessments might be useful in predicting optimal performance in extreme environments. The use of biological markers, particularly when they can be linked to relevant underlying physiology or neuroscience, could play an important role in developing better predictors of optimal performance.

Intervention Studies

Some studies have utilized controlled interventions to better understand factors influencing performance in extreme environments. Reed et al. (Reed.et al., 2001) examined the effects of thyroxin supplementation on cognitive and exercise performance and on depressive symptoms during an Antarctic winter-over. In this study 12 subjects were assessed before deployment to an Antarctic residence, and then monthly thereafter. After four months of residence half of the subjects received L-thyroxin supplementation. Prior to the supplementation period, both groups demonstrated declines in cognitive performance as well as increased depressive symptoms, compared with their baseline state. During the intervention period the treated group improved to baseline values, while the placebo group did not. Submaximal exercise performance decrements were not changed with L-thyroxin administration. Cognitive performance, however, was positively correlated with L-thyroxin levels, which may point to a causal role of L-thyroxin in this process. This study is noteworthy in that it identifies an important physiologic process that may underlie the deleterious cognitive effects of extreme exposure, and demonstrates an approach to counteract these effects and thus preserve performance.

In a military environment, Lieberman et al. (Lieberman.et al., 2002) examined the possible moderating effects of caffeine on severe stress-induced cognitive decline during Hell Week of BUD/S training. In this study, 68 SEAL trainees were randomly assigned to receive either 100, 200, or 300 mg caffeine or placebo in capsule form following 72 h of sleep deprivation that coincided with severe operational stress. The results showed that the decline in cognitive tests (scanning visual vigilance, four-choice visual reaction time, a matching-to-sample working memory task, and a repeated acquisition test of motor learning and memory), mood state, and marksmanship that were observed in the placebo-treated trainees were buffered in a dose-dependent fashion by the administration of caffeine (Lieberman.et al., 2002). The greatest positive effect was observed 1 hour post-administration, but significant positive effects persisted for 8 hours. This study demonstrated that even in the most severe military environments, moderate doses of caffeine can help to maintain cognitive function and physical performance.

Unfortunately, the number of interventional studies that are focused on optimal performance is extremely limited so it is not clear how applicable these findings are to other environments. Nevertheless, techniques to assess performance will be very important for determining the efficacy of various interventions and training strategies in optimizing behavioral performance in extreme conditions.

The Case for Cognitive and Systems Neuroscience

In this section we suggest that neuroscience approaches can be helpful in providing basic processing models that can be used to generate better predictions about individual and group performance in extreme environments and to develop more refined interventions to improve performance. Although we have elected to focus on systems neuroscience in general, and neuroimaging in particular, it is quite conceivable that molecular approaches may also yield deep insights that may help to understand why individuals differ in performance when exposed to extreme environments.

Cognitive Theory

Cognitive appraisal theories of emotion emphasize the importance of situational meaning in determining the degree of affective and physiological responses. In general, situational meaning refers to how a person appraises ongoing events (e.g., the immediate situation or one's life in general) in terms of personal relevance and the ability to cope, and to the options available for coping. Specifically, perceived control, evaluation, and encouragement are likely to be important variables for determining situational meaning, and hence to determine the emotional responses in stressful situations. Several studies support this cognitive appraisal view over the peripheralist view, which proposes that cognitive processes are secondary to incoming physiological signals (Tomaka.et al., 1997). Previous work highlights three important dimensions which appear to be critical in mediating stressful task performance and these are task engagement, distress, and worry) . These domains may contribute to several modes of self-regulation, which are abstracted representations of the ecological relationship between person and environment (Matthews.et al., 2002). We propose, in light of the model that is being advanced below, that cognitive appraisals can be viewed as internal states generated by the central nervous system to account for the complexities of the external environment. Therefore, the combination of the cognitive appraisal approach together with systems neuroscience may enable one to develop a more systematic approach in understanding the factors which predict optimal performance, and thus to improving performance.

Systems Neuroscience

From a systems neuroscience perspective, optimal performance under extreme conditions can be conceptualized as goal-oriented task completion during a high demand context. This conceptualization highlights the importance of stress-related neural processing, of cognitive control, and of learning, in the adaptation to extreme environments. Here we suggest that two cognitive processes, which can be examined experimentally and that are critical for top-down control and learning, may be critical for optimal performance. These two cognitive processes are: (1) feedback of an adverse outcome, which is necessary for adjusting behavioral strategies in decision-making; and (2) top-down modulation of ascending sensorimotor information to predict future states, which is an important evolutionary advantage associated with the development of complex cortical circuitry. The top-down modulatory ability is fundamentally related to the cognitive appraisal notion introduced above and to learning associations between stimuli and future pleasant or aversive outcomes. Below we briefly review aspects of stress, the key neural substrates in performing under stressful conditions, and the proposed role of two brain areas that may contribute to optimal performance in extreme conditions.

Neuroendocrine basis of Stress

Stress is a word used to describe experiences that are challenging both emotionally and physiologically (Selye 1956). A hallmark of the stress response is the activation of the autonomic nervous system and hypothalamo-pituitary-adrenal (HPA) axis (McEwen 2007). In contrast to many animal models, human beings are prone to prolonged periods of elevated HPA activity which helps us survive acute challenges, but may also be associated with poor outcomes. To better understand the adverse consequences, the term "allostasis"(McEwen 1998) was introduced, which means the process of maintaining stability (homeostasis) by active means, namely by producing stress hormones and other mediators. Moreover, the concept of "allostatic load" or "overload" describes the wear and tear on the body and brain caused by allostasis, particularly when the mediators are deregulated (such as remaining activated when stress is over) or not adequately activated when they are needed (McEwen 2007)).

It has long been suggested that endogenous corticotropin-releasing factor (CRF) systems in the central nervous system function as a fundamental behavioral activating system to modulate the response to stress (Koob.et al., 1993). CRF, a 41 amino acid-containing peptide, is thought to be important for the autonomic and behavioral responses to stress (Arborelius.et al., 1999), and stress has been shown to increase CRF levels in the locus coeruleus (Curtis.et al., 1999). Interactions of the CRF and noradrenergic systems in the brain may, under some conditions, function as a feed-forward system, leading to the progressive augmentation of the stress response with repeated stress exposure (Koob 1999). The stress-responsive neural circuitry is thought to be organized in a hierarchical fashion and be capable of comparing information from multiple limbic sources with internally generated and peripherally sensed information, and thus participate in tuning the reactivity to external and internal stressors (Herman.et al., 2003). Several lines of evidence support an important role for a CRF-norepinephrine interaction in the region of the locus coeruleus in response to stressors, such that CRF neurons activate the locus coeruleus in a modality-specific manner (Koob 1999). Abnormal signaling at CRFR1 and/or CRFR2 receptors may underlie the pathophysiology of stress-related disorders (Dautzenberg and Hauger 2002). Thus, the CRF system and associated neurotransmitter systems are important candidates for physiological and systems neuroscience biomarkers indexing how well an individual might perform when exposed to extreme environments.

Neural Substrates underlying stress and its modulation

Several neural substrates may play a key role in mediating a stress-related response. These systems are reviewed below from a process perspective to assist in integrating these findings into a preliminary systems neuroscience model of optimal performance in extreme environments. Specifically, some investigators have suggested that reduced CRF gene expression in the central nucleus of the amygdala is associated with fear and anxiety (Hwang.et al., 2004), which is consistent with another study (Kalin.et al., 2004). Recent findings support the notion that CRF1 receptors modulate NMDA neurons and affect calcium-calmodulin-dependent protein kinase II in the basolateral nucleus of the amygdala (Rainnie.et al., 2004). Others have suggested that interaction between CRF and serotonin in the ventral hippocampus are important for the expression of stress-related behaviors (Kagamiishi.et al., 2003). Moreover, there is evidence of CRF-augmented serotonergic modulation of inhibitory GABAergic neurons in the prefrontal cortex (Tan.et al., 2004), which would suggest both limbic and cortical modulation of stress-related behavior. Some have suggested that Neuropeptide Y is a functional antagonist to CRF action via CRFR1 receptor in the amygdala (Sajdyk.et al., 2004). Although CRFR1-immunoreactive neurons are widespread in the brain, the highest concentration of anti-CRFR1 immunoreactivity has been found in insular cortex, pituitary, cerebellum, and in portions of brain stem (Kostich.et al., 2004). Thus, based on the neural systems involved in the stress response, one would hypothesize that the amygdala, hippocampus, prefrontal cortex and insular cortex play a critical role in modulating optimal performance.

Neural substrates underlying optimal performance in extreme environments

It is clearly beyond this review to describe all possible neural structures that may be involved in modulating performance in extreme conditions. Thus, we will focus on two paralimbic structures which play an important role in sensing and in acting to maintain a homeostatic equilibrium in the presence of perturbation.

The insula (reviewed in (Augustine 1996;Augustine 1985) is a paralimbic structure and has been referred to as sensory limbic cortex. The anterior insula is strongly connected to different parts of the frontal lobe, whereas the posterior insula is connected to both the parietal and temporal lobes (Ture.et al., 1999). The insular cortex has been implicated in a wide variety of processes including pain (Tracey.et al., 2000), interoception (Critchley.et al., 2004), emotion (Phan.et al., 2002), cognition (Huettel.et al., 2004), and social processes (Eisenberger.et al., 2003). Relevant to its role in processing how an individual might perform when exposed to extreme environments, the insular cortex is important for subjective feeling states and interoceptive awareness (Craig 2002;Critchley.et al., 2004). Together with the middle and inferior frontal gyri, frontal limbic areas, and the inferior parietal lobe, the insular cortex has been identified as participating in inhibitory processing (Garavan.et al., 1999). Given the fact that the insular cortex receives integrated input from ascending primary afferents and is closely connected to all parts of the cortical mantle and limbic motor cortex, it is obvious that this area is ideally suited to orchestrate affective and cognitive responses to disturbances in homeostatic balance. The information about the interoceptive state processed in the anterior insula is relayed to the anterior cingulate cortex, which, as part of the central executive system, can generate an error signal that is critical for the allocation of attentional resources (Carter.et al., 1999). Thus, interoception involves monitoring the sensations that are important for the integrity of the internal body state and connecting to systems that are important for allocating attention, evaluating context, and planning actions.

In comparison, the anterior cingulate cortex, which has been called the limbic motor cortex (Craig 2003), is reciprocally connected with the anterior insula. The anterior cingulate cortex forms a large region around the rostrum of the corpus callosum that is termed the anterior executive region (Bush.et al., 2000;Vogt.et al., 1992). The affect division of anterior cingulate cortex modulates autonomic activity and internal emotional responses, while the cognition division is engaged in response selection associated with skeletomotor activity and responses to noxious stimuli (Peyron.et al., 2000). Thus, the anterior cingulate cortex plays a crucial role in linking the hedonic experience to the incentive motivational components of reward (Devinsky.et al., 1995).

Integration of neuroscience and optimal performance – a preliminary model

A preliminary model of optimal performance in extreme environments starts with the observation that these environments exert profound interoceptive effects, which are processed via the interoceptive system described above. The interoceptive system provides this information to (1) systems that monitor value and salience (orbitofrontal cortex and amygdala); (2) are important for evaluating reward (ventral striatum/extended amygdala); and (3) are critical for cognitive control processes (anterior cingulate). Moreover, the more anterior the representation of the interoceptive state within the insular cortex the more "textured", multimodal, and complex is the information that is being processed due to the diverse cortical afferents to the mid and anterior insula. We have hypothesized that the anterior insula not only receives interoceptive information but is also able to generate a predictive model which provides the individual with a signal of how the body will feel (Paulus and Stein 2006), similar to the "as if" loop in the Damasio somatic marker model (Damasio 1994). In this formulation, Damasio's theory extends the James Lang theory of emotion because the insula can instantiate body sensation without necessarily receiving peripheral inputs. The interoceptive information is thus "contextualized", i.e. brought in relation to other ongoing affective, cognitive, or experiential processes, in relation to the homeostatic state of the individual, and is used to initiate new or modify ongoing actions aimed at maintaining the individual's homeostatic state. In this fashion interoceptive stimuli can generate an urge to act.

Thus we propose the following process hypotheses: (1) individuals who are optimal performers have developed a well "contextualized" internal body state that is associated with an appropriate level to act. In contrast, sub-optimal performers either receive interoceptive information that is too strong or too weak to adequately plan or execute appropriate actions. As a consequence, there is a mismatch between the experienced body state and the necessary action to maintain homeostasis. Therefore, a neural systems model of optimal performance in extreme environments needs to include brain structures that are able to process cognitive conflict and perturbation of the homeostatic balance, i.e. the anterior cingulate and insular cortex. Thus ultimately, engagement of these brain structures is likely to be predictive of performance and may also be used as an indicator of efficacy of an intervention.

The neuroscience approach to understanding optimal performance in extreme environments has several advantages over traditional descriptive approaches. First, once the role of specific neural substrates is identified, they can be targeted for interventions. Second, studies of specific neural substrates involved in performance in extreme environments can be used to determine what cognitive and affective processes are important for modulating optimal performance. Third, quantitative assessment of the contribution of different neural systems to performance in extreme environments could be used as indicators of training status or preparedness. These are just some of the possibilities for utilizing neuroscience approaches to gain a better understanding of what makes individuals perform differently when exposed to extreme environments. The application of this systems neuroscience approach will help to extend findings from specific studies of individuals exposed to extreme environments to the development of a more general theory of human performance under extreme conditions. As a consequence, one can begin to develop a rational approach to develop strategies to improve performance in these environments.

Endnotes

The views expressed in this article are those of the authors and do not reflect the official policy or position of the Navy, Department of Defense, or the U.S. Government. This research has been conducted in compliance with all applicable federal regulations governing the protection of human subjects in research.

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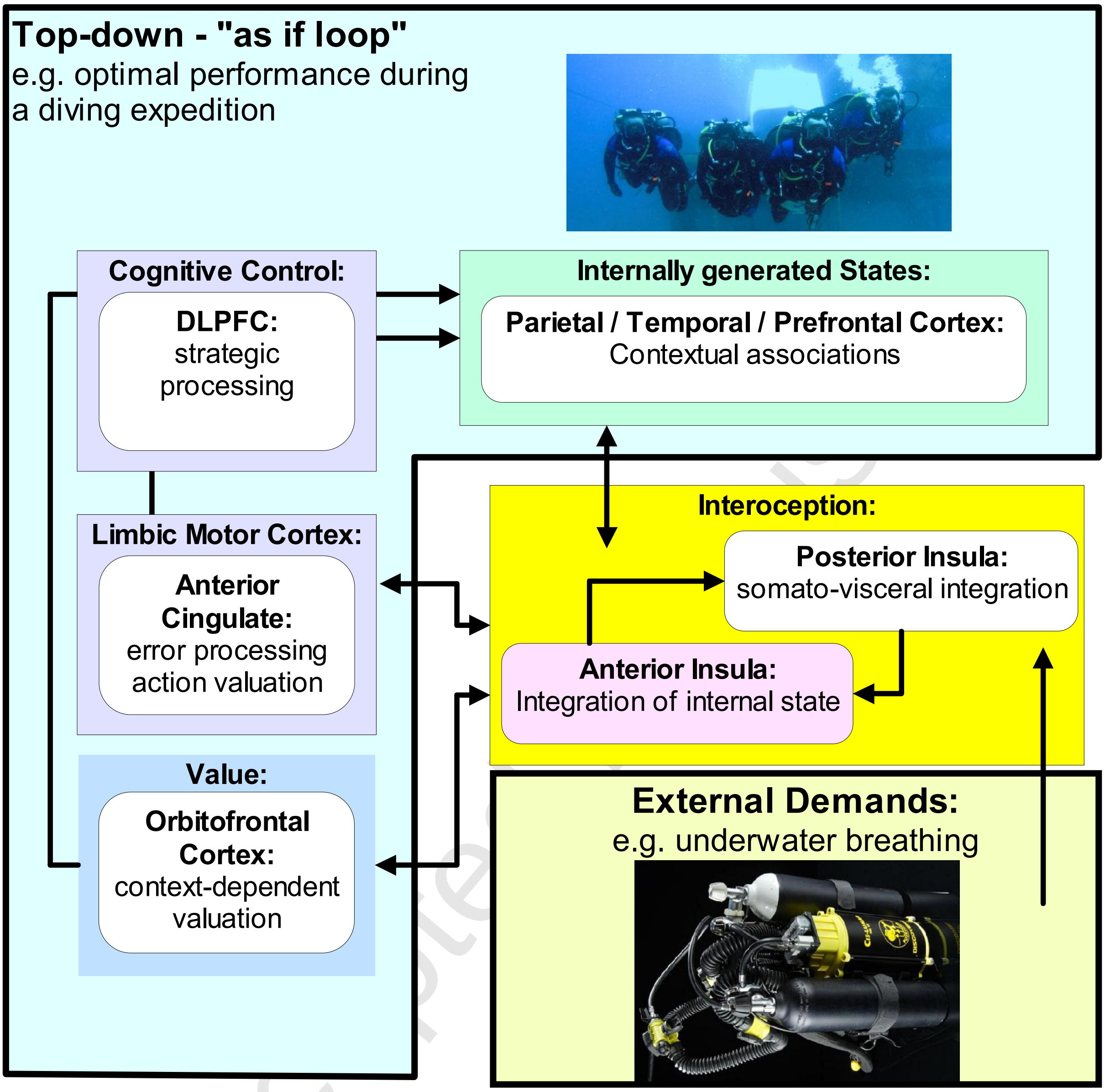
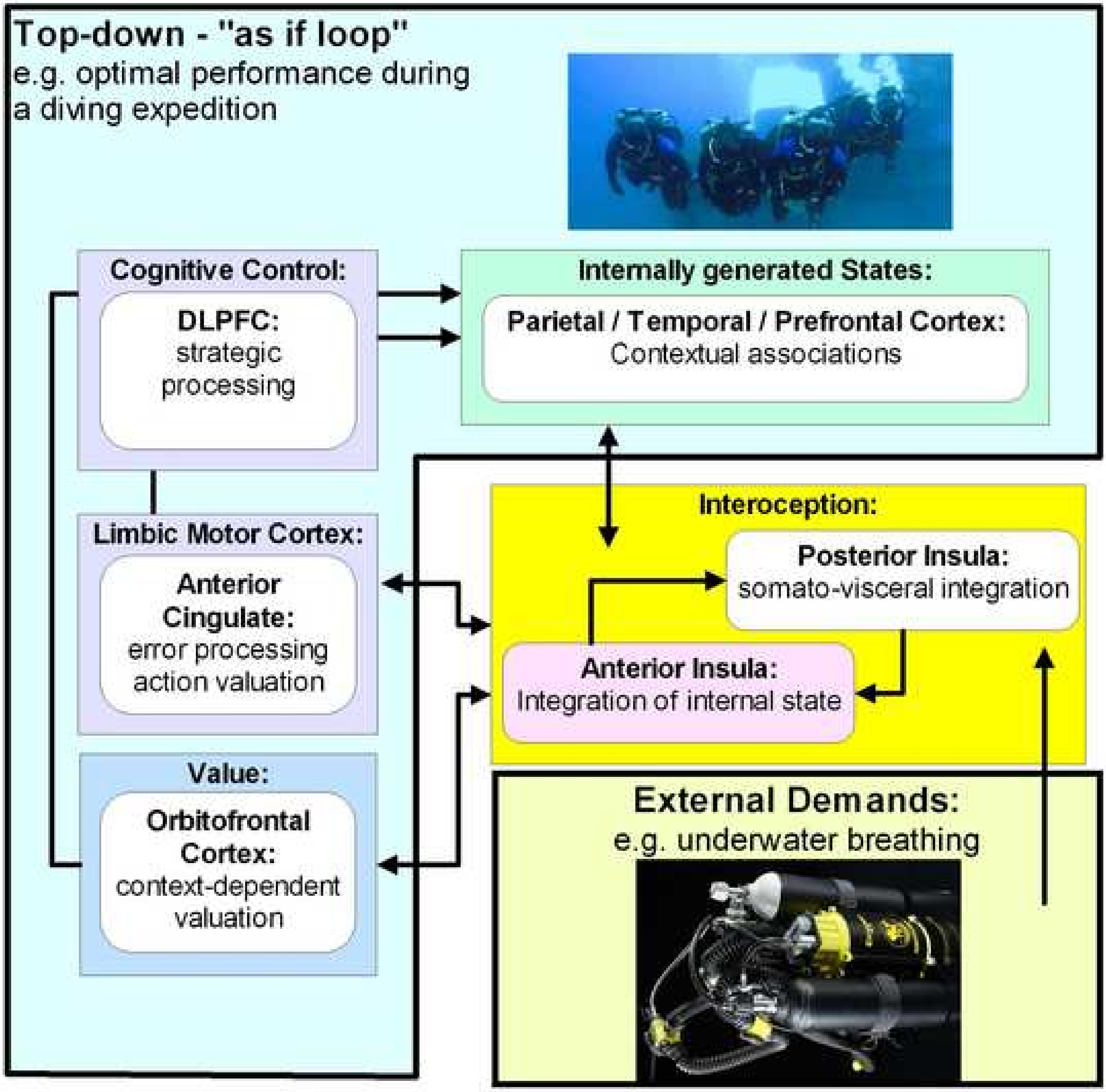
Figure 1 shows the extended limbic circuitry and the top-down control circuitry involved in optimal performance in extreme environments. The individual is thought to maintain a homeostatic steady state in the presence of top-down performance demands and bottom up physiological challenges to the body. The anterior insula is critical for the integration of an internal state, which, in turn, is the association of affect to a stimulus. Optimal performance is hypothesized to occur if the peripheral challenges are optimally contextualized by top-down modulatory areas, i.e. when there is minimal discrepancy between what the top-down system is predicting the body should feels like and what the peripheral afferents signal that the body is feeling.


Top-down - "as if loop"
e.g. optimal performance during a diving expedition
Cognitive Control:
DLPFC:
strategic processing
Internally generated States:
Parietal / Temporal / Prefrontal Cortex:
Contextual associations
Limbic Motor Cortex:
Anterior Cingulate:
error processing
action valuation
Interoception:
Posterior Insula:
somato-visceral integration
Anterior Insula:
Integration of internal state
Value:
Orbitofrontal Cortex:
context-dependent valuation
External Demands:
e.g. underwater breathing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Anterior Insula:
Integration of internal state
Value:
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