

Original Article

Costly Signaling Theory of REM Sleep and Dreams

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Abstract: The function of REM sleep dreaming is still unknown. We situate our approach to understanding dream phenomenology and dream function within that part of evolutionary theory known as Costly Signaling Theory (CST). We contend that many of the signals produced by the dreaming brain can be and should be construed as “costly signals”—emotions or mental simulations that produce daytime behavioral dispositions that are costly to the dreamer. For example, often the dreamer will appear in the dream as handicapped in some way (i.e., no clothes, no ID, no money, is under attack, being chased etc.). The dreamer, during waking life, is then influenced by the carry-over effect of the unpleasant dream content. The informational and affective content of the dream creates a mental set in the dreamer that operates during the daytime to facilitate the signaling of a “handicapped” Self. The subtle signaling effect might be via display of the intense emotions or physical demeanor that had first appeared in the dream. When the dreamer shares his dream with others the dream has a more direct impact on waking life and social interactions. In effect, the dreamer uses his or her dreams to adopt a self-handicapping strategy when dealing with significant others. The increased use of costly signals (the self-handicapping strategy) during the daytime then facilitates some vital communicative goal of the dreamer.

Keywords: REM Sleep, Dreaming, Costly Signaling Theory, Handicap, Emotions

Introduction

The function of REM sleep and dreaming is still unknown. To the extent that some forms of sleep mentation depend on REM sleep physiology it can be said that this mentation is part of that physiology. In this paper we treat dreams that occur in temporal relation to REM sleep episodes as part of the physiology of REM sleep. Not all dreams and not all of the content of REM-related dreams are due to REM physiology alone (see Nielsen, 2000; Solms, 2000). Nevertheless, it is very likely that a significant portion of the content of REM related dreams is related to and even a direct result of various components of REM physiology (Dement and Kleitman, 1957; Goodenough, 1991; Hobson, Pace-Schott, and Stickgold, 2000; Schonbar, 1961). For example, when ponto-geniculo-occipital (PGO) spikes occur during a REM episode one is more likely to get dream reports that contain rapid plot shifts and greater amounts of bizarre imagery. In addition, the limbic brain activation patterns that occur during REM very likely accounts for dreams containing emotionally charged social interactions (Maquet and Phillips, 1999; McNamara, McLaren, Smith, Brown and Stickgold., 2005). In short, it is not

unreasonable to treat dream reports that occur in temporal relation with REM episodes as part and parcel of REM physiology itself. To construct a theory of dream function it is reasonable to bring in an account of REM physiology.

Some progress has been made in our understanding of REM physiology including REM dream content by adopting evolutionary approaches to dream function. For example, the so-called “threat simulation theory” (Revonsuo, 2000) of dream function can claim some empirical support given that some studies of dream content are consistent with the theory. In addition, unlike classical Freudian or Jungian theory, threat simulation theory is consistent with a broad range of data from the evolutionary sciences and theory. No elaborate interpretation of dream content is needed to square the dream content data with the (evolutionary) theory. The data or at least some portion of the available data on dream content is nicely predicted by the threat simulation theory. Evolutionary approaches to dream function have the advantage of putting severe constraints on the scope of the theory proposed – namely that the theory be consistent with both the facts concerning dream phenomenology and the rest of the evolutionary sciences. It is not enough to speculate about what dreams might do for the organism – one must propose a function that is consistent with some part of evolutionary theory. If dreams are good for something, that something must be with reference to some part of evolutionary theory.

We situate our approach to understanding dream phenomenology and dream function within that part of evolutionary theory known as Costly Signaling Theory (CST; Bliege Bird and Smith, 2005; Bradbury and Vehrencamp, 1998; Grafen 1990; Johnstone 1997; Maynard-Smith and Harper, 2003; Zahavi, 1975; Zahavi and Zahavi 1997). CST is concerned primarily with understanding animal signaling behaviors. The basic idea is simple: for signals between two parties to be workable or believable by both parties they must be reliably unfake-able. Only signals that can’t be faked can be trusted to carry honest information. Un-fakeable signals are those signals that are metabolically, motorically, or behaviorally difficult to produce (costly). Their production costs or “costliness” is their certification of honesty. Costly signals are preferred by animals under conditions where the animals are capable of deception but require reliable and honest signaling between the parties (e.g., between the two sexes during mating season). . For a signal to classify as a handicap, the net benefits for displaying the signal (REM sleep intensity in our case) must be higher for a high-quality individual than a low-quality individual (or the costs of high REM intensity must be higher for low-quality individuals). Thus a low-quality signaler must be able to send a signal suggesting high quality; i.e. must be able to fake “high REM”. The signal must be costly to fake but not impossible to fake. The handicap principle asserts that low-quality signalers generally don’t send false signals because it simply does not pay; the net costs are too high.

Humans, of course, engage in a range of signaling behaviors, but can REM sleep and dreams plausibly be considered one of them? Human signaling behaviors include everything from speech and language exchanges to emotional displays, “body-language” (e.g. clothes, postures, tattoos etc) and other non-verbal behaviors. Our basic claim in this paper is that dreams associated with so-called rapid eye movement or REM sleep can function as signals. Dreams can also function to facilitate production of signals when they produce some daytime effect such as a memory or a mood (or both) or a behavior that communicates a message to an observer. A person, for example, who awakens from a disturbing dream may behave differently during the day from a person who awakens from, for example, an erotic dream or a bizarre dream and so on. Many dreams, even un-remembered dreams create background moods and behavioral dispositions that linger through much of the subsequent daytime period (Kramer, 1993). While it

is difficult to demonstrate that un-recalled dreams can influence daytime mood and behavior, we know that depriving a person of his or her REM/dream sleep can significantly alter daytime mood states—at least in some vulnerable individuals (for reviews see Bonnet, 2005; Dinges, Rogers and Baynard, 2005; Moorcroft, 2003; Vogel, 1999).

It is much easier to demonstrate that recalled dreams can influence daytime mood and behavior. We know from personal experience that this is the case. A bad dream can color one's mood throughout the day. Most people have had such experiences fairly frequently it seems. Kuiken and Sikora (1993) for example, found that 13% of 168 respondents to a questionnaire on dream recall reported that they, at least 12 times in the past year, had had dreams that significantly influenced their daytime mood; 25% of respondents indicated that they had had such dreams at least 4 times in the past year and 44% at least twice in the past year. Like any other mood state, these dream-related dispositional and mood states, we claim, can be “read” by observers as informational about the internal states and quality of the dreamer.

Dreams can also affect daytime mood and behavior by being shared with others. Given what we know concerning the centrality of group dream sharing in pre-modern tribal groups (Gregor, 1981; 2001; Schneider and Sharp, 1969; Tedlock, 1992), we can assume that dream sharing was a common practice in early human groups in the “environment of evolutionary adaptation” (EEA). Even today young adults recall one to two dreams per week with 37% of these reporting that they recall a dream “every night” or “very frequently” (Belicki, 1986; Goodenough, 1991; Strauch and Meir, 1996). In representative samples of the general population between 40 and 75% recall between one to five intense and “impactful” dreams per month (Borbeley, 1984; Kuiken and Sikora, 1993; Stepansky et al., 1998). Once recalled a dream is typically shared with another person (Stefanakis, 1995; Vann and Alperstein, 2000). Once shared it has the potential to go on influencing daytime mood and behavior.

Like many other costly signals, dreams are considered to be involuntary cognitive and emotional experiences and thus less fake-able. Sharing a dream with another gives the “other” a direct window into recent brain/mind REM activity and thus a direct window into the quality of the individual sharing the dream.

We contend that many of the signals produced by the dreaming brain can be and should be construed as “costly signals”—emotions or mental simulations that produce daytime behavioral dispositions that are costly to the dreamer. For example, often the dreamer will appear in the dream as handicapped in some way (i.e., no clothes, no ID, no money, is under attack, being chased etc.) The dreamer, during waking life, is then influenced by the carry-over effect of the unpleasant dream content. The informational and affective content of the dream creates a mental set in the dreamer that operates during the daytime to facilitate the signaling of a “handicapped” Self. The subtle signaling effect might be via display of the intense emotions or physical demeanor that had first appeared in the dream. In effect, the dreamer uses his or her dreams to adopt a self-handicapping strategy when dealing with significant others. The increased use of costly signals (the self-handicapping strategy) during the daytime then facilitates some vital communicative goal of the dreamer.

We realize that this theory is at this point purely speculative. We nevertheless contend that there is a great deal of evidence that supports its basic suppositions. In what follows, we summarize the main arguments for our CST approach to REM sleep and dreams and then provide some preliminary suggestions as to what CST theory would predict concerning dream content.

CST first emerged in the context of sexual selection theory (Zahavi, 1975) but it has more recently been used to address broader issues communication, coordination and cooperation between parties with partially differing genetic interests. Sexual selection theory suggests that some traits may have evolved because they signal fitness of the bearer. If, for example, the trait in question is facial symmetry, a feature apparently correlated with attractiveness ratings in humans, then sexual selection theory would predict that the trait “facial symmetry” would likely be correlated with some fitness-enhancing gene such as a disease-resistant gene. Potential mates will then favor reproductive partners who display facial symmetry, and thus the trait “facial symmetry” will increase in the population. Other traits such as large antlers might indicate the presence of parasite-resistance genes in a reindeer or an elk. Large antlers will, in effect, advertise presence of these “good genes.” This, in turn, creates selective pressures for displaying and enhancing such advertisements. Males without the parasite-resistant gene will not be able to display large antlers, as they will not be able to metabolically grow and maintain the antlers without paying a metabolic cost that in turn will make them more vulnerable to parasite infestation. Thus, large antlers, although costly to produce and thus an expensive handicap, will nevertheless constitute an honest signal of good genes, and thus, honest communication between potential mates will be possible. In short, costly signaling makes communication possible under adverse conditions – that is, conditions in which the parties have partially conflicting interests.

According to costly signaling theory, a signal is defined as a behavior, expression, or phenotype produced by one individual (the signaler) that aims to influence the behavior of a second individual (the receiver). Extensive modeling and empirical studies in CST (Bliege Bird and Smith, 2005; Bradbury and Vehrencamp, 1998; Grafen 1990; Johnstone 1995; Maynard-Smith and Harper, 2003; Zahavi, 1975; Zahavi and Zahavi 1997) have demonstrated that any trait at all can function as a costly signal as long as it a) can convey reliable information about inter-individual variation in the underlying quality being advertised and b) imposes a cost on the signaler that is linked to the quality being advertised. Under conditions of genetic conflict, the two parties in a communication game may be motivated to transmit nonveridical, deceptive information in order to obtain an advantage. If one individual can gain an advantage from another by concealing information or by sending misleading information, he or she will do so. In the short run, at least, using deception would sometimes seem to have advantages.

But fundamentally, communication must require that signals be honest and reliable, at least on average. If they were not reliable, the intended receivers would evolve to ignore them. Costly signals appear to have evolved in order to guarantee the reliability and honesty of a communication system. Communication will be stable when the signaler and receiver pursue strategies that together comprise a signaling equilibrium such that neither party gains from unilateral defection to deception or change in strategy. To keep both signaler and receiver in the game, hard-to-fake signals must be utilized.

Hard to fake signals in the realm of human social interaction must at a minimum include the emotions (Frank, 1988) and REM sleep dreams specialize in the production of emotions (McNamara, 2004). When using the Hall/Van de Castle scoring rules for tabulation of dream content (Domhoff, 2003), emotions appear in virtually all dreams and negative emotions appear in about 80% of dreams for both men and women. The typical REM dream contains between two and three characters in addition to the dreamer, and these characters typically interact emotionally with the dreamer. The dreamer is typically striving to attain or to accomplish some goal, but is stymied in doing so by some other character or obstacle.

The other characters are typically depicted as attempting to interfere with the dreamer's attempts to achieve the dreamer's wishes or goal. Scenarios involving dreamer-involved successes occur in only about half of male dreams and 40% of female dreams, and misfortunes occur in at least one third of all dreams. The fact that two to four characters occur in an average dream suggests that dreams are social: that they depict social interactions. Social interactions do in fact frequently take place in dreams. For example, conversations between the dreamer and dream characters took place in two out of three dreams in the Strauch and Meier (1996) series. Interestingly, Strauch and Meier reported that they virtually never found a dream in which the dreamer was entirely alone. Instead, dreams typically involve the dreamer interacting with other persons or with other beings like animals. Dreams, in short, are often about emotional and social interactions. This singular fact is consistent with the idea that dreaming serves some function relation to social communication. Social communication in turn can be modeled using costly signaling theory.

The conditions for the evolutionary or game-theoretical stability of costly signaling in the realm of dreaming can be summarized as follows (for more technical analyses, see Gintis, Smith, and Bowles 2001; Grafen, 1990; Johnstone 1997): Individual differences or variation in REM/dreaming must be correlated with some value or quality (e.g. genetic quality) of the individual who uses REM dreaming to send signals to some observer. Or more precisely the cost or benefit (to the signaler) of dreaming must be quality dependent (i.e., the marginal cost or marginal benefit of dreaming is correlated with the signaler's quality).

There is good evidence for this condition of quality dependency with respect to REM sleep and dreaming. Depending on previous mental and physical health, individuals differ in their abilities to bear the cost associated with REM. This fact is seen clearly in effects of selective REM deprivation procedures. Some individuals experience little or no ill effects of REM deprivation while others suffer severe mood and cognitive changes including psychotic hallucinations (reviewed in Bonnet, 2005; Dinges et al, 2005; Eiser, 2005; Moorcroft, 2003). People too high or too low in the amount of REM sleep and dreaming they engage in tend to be at greater risk for ill-health (a proxy for genetic quality). For example, increased REM sleep durations (relative to the population norm) are significantly associated with increased risk for various medical conditions and for mortality (Brabbins et al., 1993; Dew et al., 2003; Kripke, 2003). The increased risk for these "co-morbidities" remains even after adjusting for age, gender, mental illness and "medical burden" or physical health status (Brabbins et al., 1993; Dew et al., 2003; Kripke, 2003).

Dew et al. (2003) were able to analyze measures of sleep architecture in relation to risk for mortality. They reported that three measures of sleep architecture best predicted mortality: 1) sleep latencies of greater than 30 minutes; 2) poor sleep efficiency and 3) an unusually high or low percentage of REM sleep. Sleep latencies of >30 minutes, and unusually high or low REM sleep durations, for example, more than doubled the risk of mortality in their cohort of initially healthy elders across an average of 13 years of follow-up. The authors noted that too much REM is often associated with disorders of mood such as depression that are independently associated with increased health and mortality risks. But it is likely that REM itself or at least excessive amounts of REM directly contribute to ill health (see below) for individuals unable to bear the costs of enhanced REM.

The fact that costs of REM sleep track with REM intensity (too much or too little) is entirely consistent with our theory. Although individuals who experience low REM intensity still experience costs associated with REM (after all we ARE arguing that REM is costly), the highest

costs should be borne by high quality individuals who can bear greater REM intensities. Thus, a host of carefully controlled experiments involving selective deprivation of REM sleep have demonstrated that effects of REM deprivation depend on the physical and mental health qualities of the individuals so deprived (reviewed in Bonnet, 2005; Dinges et al, 2005; Eiser, 2005; Moorcroft, 2003) with healthier individuals showing fewer signs of ill effect of the deprivation procedures. The fact that high REM intensity is associated with costs for some individuals demonstrates that it is an ideal trait for signaling purposes.

In addition to the satisfaction of formal criteria for application of CST, there is *prima facie* evidence that REM sleep dreams and physiology participate in some sort of signaling function for the individual. First, REM biology is associated with those paradigmatic human signaling displays—the emotions. The intense activation of the limbic and amygdalar regions (Maquet and Franck, 1997) in the absence of dorsal prefrontal inhibitory effects (Hobson, Stickgold, and Pace-Schott, 1998) during REM ensures intense emotionality during and after a REM episode. In short, the brain region that is responsible for emotional signaling during the waking period undergoes intense and repeated activation during REM. This fact is consistent with an emotional signaling function for REM.

Recently, a number of positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies of the sleeping brain have revealed that REM demonstrates very high metabolic activation levels in pontine, midbrain tegmentum, anterior cingulate, limbic, and amygdaloid sites, and deactivation of prefrontal areas, parietal cortex, and posterior cingulate (Braun et al., 1997; Hobson, Stickgold, and Pace-Schott, 1998; Maquet and Franck, 1997; Maquet et al., 1996; Nofzinger, Mintun, Wiseman, Kupfer, and Moore, 1997). The pattern of activation suggests a preference for sites linked with the production of intense emotions in humans – particularly negative emotions. For example, these imaging studies have consistently revealed exceptionally high activation levels in the amygdala during REM. The amygdala is known to specialize in mediation of fear and other aversive emotional states. When subjects are awakened from REM, they generally report a narrative involving the dreamer, with vivid visual detail, unpleasant emotions, and occasional bizarre and improbable events (Domhoff, 2003; Foulkes, 1962; Hobson and Pace-Schott, 2002; Nielsen, Kuiken, Hoffman, and Moffitt, 2001; Rechtschaffen, Verdonne, and Wheaton, 1963; Snyder, Karacan, Thorp, and Scott, 1968; Strauch and Meier, 1996).

We suggest that the emotions associated with a dream often persist throughout the day thereby exerting their effects on mood and behavior during waking life. But emotional signaling may not be enough given that the goal, by hypothesis, is to create reliably unfake-able and honest signals. Instead, some sort of handicap (e.g., the peacock's tail, the deer's massive antler's, the doe's stotting displays, the bird's apparently broken wing, etc.) may be necessary to convince the receiver of the sender's honesty.

REM biology, furthermore, is eminently capable of handicapping an individual—a frequent working definition of a “costly signal”. REM biology is demonstrably – even extravagantly – “costly”. This costly physiology makes sense if one assumes that its purpose is to handicap the individual. Although this claim sounds paradoxical much in biology is paradoxical. The aim is to produce enough of a handicap to convince the receiver that the sender is honest but too much of a handicap as that will only impair the individuals to function effectively. Thus, CST theory predicts that REM biology should to some extent have negative-even injurious effects on the health (but not the reproductive fitness) of the individual. There is in fact abundant

evidence that this is so. Consider the following well-documented characteristics of REM biology (reviewed in McNamara, 2004):

Although the cortex is activated in REM, arousal thresholds are often higher in REM than in the waking state (or in slow-wave sleep [SWS] for that matter). REM is also associated with autonomic nervous system instabilities (see below) that become more extreme as the average duration of a REM episode increases across the night.

These instabilities may be associated with the so-called pontine-geniculo-occipital (PGO) waves. PGO waves are generated in the pons and are propagated up through the lateral geniculate body (LGB) of the thalamus and then up to occipital and other cortical sites. Because the LGB and the occipital cortex are visual centers, it was originally thought that PGO waves could account for visual phenomena of dreams. It now appears that PGO waves are not confined to visual centers but may instead be quite prominent in the amygdala and in limbic and disparate cortical sites. PGO waves occur in bursts or spikes and thus are correlated with many phasic phenomena of REM, including increased emotions and bizarre elements in dreams.

Morrison and colleagues (Morrison, 1979; Morrison, Sanford, and Ross, 1999) have suggested that PGO waves are comparable to the well-known orienting reflex (OR) that occurs after startle, interest, or fear during waking. If PGO waves are associated with orienting, startle, and fear reactions, then organisms experiencing PGO waves during REM are likely undergoing regular and repeated startle reactions, orienting reflexes, and stress-inducing mobilizations to defend against hallucinatory threats each time they go into REM.

Maquet and Phillips (1999) point out that REM-related amygdaloid activation may contribute to the profile of forebrain sites that are activated and deactivated during REM. Specifically, activated cortical areas receive amygdaloid projections, while deactivated sites do not. Maquet and Phillips also report significant positive interactions between amygdaloid blood flow and occurrence of REM in the temporal cortex.

The high activation levels of amygdaloid circuits during REM may carry negative health consequences for the organism because the central nucleus of the amygdala appears to be a regulatory center for neural circuits involved in fear, aggression, defense, the fight-or-flight response, and autonomic reactivity (LeDoux, 2000; Sah, Faber, Lopez de Armentia, and Power, 2003). The central nucleus is particularly important for mediation of fear responses. Fear-related responses are characterized by freezing, startle, release of stress hormones, rises in blood pressure and heart rate, respiratory distress, piloerection, and stereotypical threat displays. In humans, these autonomic responses are accompanied by a sense of dread, despair, anguish, anxiety, and intense distress. Activation of the central nucleus induces autonomic instabilities associated with these negative emotions. The medial portion of the central nucleus has substantial projections to the hypothalamus, bed nucleus of the stria terminalis, and several nuclei in the midbrain, pons, and medulla, associated with regulation of the autonomic nervous system (ANS). Projections to the brain stem are to three main areas: (1) the periaqueductal gray matter, which mediates startle, analgesia, vocalizations in response to threat, and cardiovascular changes; (2) the parabrachial nucleus, which is involved in pain transmission; and (3) the nucleus of the solitary tract, which contributes to regulation of the vagal system. Thus, the neuroanatomy of the amygdala allows it to regulate fight-or-flight responses, cardiac and respiratory functions, and other fundamental ANS responses. REM-induced phasic discharges occurring in the central nucleus may help to explain REM-related cardiac, respiratory, and autonomic instabilities.

Animal studies have, in fact, linked amygdaloid activation to phasic signs of REM. Electrical stimulation of the central nucleus of the amygdala increases PGO wave frequency

(Calvo, Badillo, Morales-Ramirez, and Palacios-Salas, 1987) and other signs of phasic REM. Carbachol injection within the same nucleus increases REM sleep duration and other REM indices (Calvo, Simon-Arceo, and Fernandez-Mas, 1996). Thus, activation of the amygdala during REM may be considered a phasic process of REM that is superimposed on a more tonic activation of the limbic forebrain in general during REM. Interestingly, measures of both REM and amygdaloid activation are enhanced in depression (Whalen, Shin, Somerville, McLean, and Kim, 2002).

Relative to the waking state, sympathetic activity rises during phasic portions of REM. As the duration of phasic REMs increases over the course of the night, so do the durations of sympathetic discharges giving rise to periodic REM-related sympathetic discharges or “storms.” These sympathetic discharges, in turn, may be linked to a host of negative cardiopulmonary changes that occur during phasic REM.

Cardiac output declines over the course of the night, reaching its lowest levels during the last REM period. During all REM periods, an acceleration of heart rate occurs at least 10 beats before EEG signs of phasic arousal, and then fluctuates dramatically during phasic REM. Systemic arterial blood pressure (BP), pulmonary BP, and intracranial arterial BP all exhibit increased variability relative to NREM and waking levels. There is marked vasodilation in all of the major vascular beds, including selected cerebral vascular systems. Because of the hemodynamic, ANS, and sympathetic alterations of REM, plaque rupture and coronary arterial spasm become more likely.

Both REM and NREM show reductions in ventilation (alveolar hypoventilation), but the REM-related reduction is severe (see review in Douglas, 2000). During phasic REM, respiration becomes irregular, with a waxing and waning of tidal volume that resembles Cheyne-Stokes breathing. The natural response to lowered O₂ levels is to increase inspiratory breathing, but this response (the hypoxic ventilatory response) is decreased by over 50% of normal capacity during REM. The REM-related hypoxemia and abnormal breathing patterns may cause life-threatening complications in vulnerable persons.

REM appears to involve a reversion to a poikilothermic state (Bach, Telliez, and Libert, 2002; Parmeggiani, 2000; Szymusiak, Alam, Steininger, and McGinty, 1998). Although brain temperature rises during REM, thermoregulatory responses such as sweating and panting do not occur in REM.

One of the most paradoxical features of REM is that phasic eye movements and muscle twitches occur upon a background of paralysis in the antigravity musculature, including the jaw, neck, and limbs. No-one has ever proposed a convincing functional explanation for this paralysis. Given that it makes the individual more vulnerable to predators it has to be considered a cost associated with production of REM.

Every REM period is associated with penile tumescence. These REM-related erections apparently even occur in infants. They persist throughout the lifespan but are not reliably associated with erotic desire. There is some evidence that REM-related sexual activation may also occur in women as uterine contractions and pelvic thrusting, appearing with REM onset, but too few studies have been done on this topic to draw any firm conclusions.

This brief review of major physiologic properties of REM, including REM-related PGO waves, activations of the amygdala, ANS storms, cardiovascular instabilities, respiratory impairment, thermoregulatory lapses, and so on, suggests that REM is risky for one's health. These risky properties of REM appear to be primarily phasic processes, occurring in tandem with PGO waves and amygdaloid activation.

Even the tonic properties of REM (limbic forebrain activation with prefrontal deactivation, muscle twitching and muscle atonia, penile erections, etc.), however, may increase vulnerability to predators while not providing any apparent benefit. There can be little doubt, then, that processes of REM are energetically costly. Given the apparently risky, injurious, costly, and paradoxical properties of REM, why would Nature produce such a system?

We believe that REM's risky traits are not mere side effects of some other functional process of REM, but are part and parcel of REM's primary biological function. REM exists to produce those risky or costly traits that, in turn, perform some service for the organism. We suggest that that function is the facilitation of the production of costly and handicapping signals in service to the communicative needs of the organism.

REM is designed to produce the kinds of costly traits like emotions that can be used in a social interaction and that are often experienced as a handicap by the individual. REM's stock in trade is production of emotional signals, as these are hard-to-fake costly signals (Fessler and Haley 2003; Frank, 1988). The individual uses these signals strategically in exactly the same way other animals use costly signals and handicaps: as signals in a communication game and as advertisements of one's genes as well as one's resources, willingness to cooperate, reliability, honesty, and so forth.

REM-related production of emotional states and costly signals would influence dream content and the display of emotional signals the person emits the next day, whether or not the person remembered any dream that morning, though of course recalling a dream ensures an effect of REM on daytime mood/behavior. Both the evidence from REM deprivation studies and REM/daytime effects studies support this claim. There is abundant evidence that REM influences daytime mood (Kramer, 1993), memory (Walker and Stickgold, 2006), and appetitive drives (Vogel, 1999). REM deprivation selectively disrupts mood, appetitive, and memory function (Bonnet, 2005; Moorcroft, 2003). Longitudinal and correlational studies also demonstrate links between REM and dream variables to daytime mood (Agargun et al., 1998; Agargun and Cartwright, 2003; Kramer, 1993; Mannix, 2006; Pesant and Zadra, 2006; Zadra and Donderi, 2000).

Pesant et al., (2006), for example, conducted a longitudinal study to determine effects of dream content on daytime mood and mental health variables. They found that measures of psychological well-being were consistently related to dream content variables over time. The greater the aggressive content in a dream the lower the overall well-being and the greater the daytime distress. Mannix (2006) examined relationships between dream recall frequency and a host of daytime mental health variables. She reported that many individuals report dreams that they claimed caused them to experience a negative emotion (anxious, scared, distressed, sad) or negative physical sensation (tense, drained, heart racing, tears) upon waking.

In perhaps the most convincing case of the effects of dream content on waking mood/behavior we have the clinical syndromes of post-traumatic stress disorder (PTSD) and suicidal ideation. REM and nightmare content indicators are significant predictors of suicidal ideation in depressed individuals (Agargun et al., 1998; Agargun and Cartwright, 2003). It is also fairly well established that specific content indicators (e.g. fearful or unpleasant emotional imagery) of REM-related mentation of persons with post-traumatic stress disorder (PTSD) predicts severity of PTSD (Germain and Nielsen, 2003). Indeed incorporation of trauma-related memories into dreams is one of the DSM-IV criteria for the disorder

Also as mentioned above one clear and unambiguous case of where a product of REM has an effect on daytime mood and behavior is when a person recalls and thinks about or shares a

dream (Vann and Alperstein, 2000). Here we are relatively certain that the influence on mood and behavior is coming from REM sleep (most but not all spontaneously recalled dreams are from late night early morning REM period; Goodenough, 1991; Schonbar, 1961; or at least no different in content from late REM period dreams, Domhoff, 2003). Even specific dream content variables (such as number of characters appearing in early morning dreams) have been shown to have significant links with daytime mood (Kramer, 1993).

Given the fact that upwards 80% of dreams contain negative emotions (Domhoff, 2003; Table 3.2, p.73), it may be that the bias over time is in creating emotional handicaps, but these in turn allow the person to advertise honesty in communicative interchanges, and so the long-term results are better social interactions for the individual and thus increased fitness. It may seem odd to us that the way Mother Nature defeats free riders and achieves cooperative interchanges among her creatures is to have them develop and display handicaps, after all negative emotionality is, on the face of it, not too attractive and many handicaps, like the paradigmatic peacock's tail, works precisely because it is attractive to peahens. So how can dreams serve a handicapping strategy if most of what they produce is content containing a lot of negative emotionality?

Negative emotions can be powerful signals when used as leverage in social interactions (e.g. eliciting sympathy/empathy from conspecifics (Hagen, 2003; Sally, 2000). Indeed signaling distress is a most effective way people and other animals elicit empathy, fellow-feeling and assistance from another is to signal distress via expressions of negative emotion (Preston and de Waal, 2002). The establishment of empathy with another is a reliable facilitator of social cooperation (Decety and Lamm, 2006) and signs of distress or negative emotion reliably elicit empathy from others through the crucial years of infancy right up to maturity (Preston and de Waal, 2002). It would be surprising if individuals neglected to use negative emotions to establish social ties and in some cases (when both parties express distress) even social solidarity.

If negative emotionality is such a powerful signaling device why don't people go around signaling distress all the time? They do! Most people experience distress frequently and have no qualms about expressing it openly. At least 30-50% of the population exhibit and report a chronic experience of negative emotionality (Watson and Clark, 1984; Kessler et al., 2005; Riolo, Nguyen, Greden, King, 2005). Negative emotionality treated as a trait evidences moderate to high levels of heritability (Bouchard, 2004). Evidently people who exhibit high negative emotionality are considered attractive enough to at least a portion of the general population as they marry, mates and produce offspring who inherit the disposition for negative emotionality.

Current evolutionary approaches to negative emotionality and game theory simulations of the evolution of cooperation in human groups predict that some portion of the population will exhibit high levels of negative emotionality as negative emotionality performs several different signaling and social functions including indicating the presence of cheats/free riders in the population, indicating withdrawal or voluntary abstention from social bargaining processes; indicating resilience against adversity (i.e. a character strength) and eliciting sympathy/empathy from conspecifics and thus enhancing social ties/alliances (Fehr and Gächter, 2002; Fessler and Haley, 2003; Hagen, 2003; Neese, 1998; Sally, 2000). It is not for us to solve the problem of the existence and widespread prevalence of negative emotionality. The available evidence however indicates that it IS widespread and it can function as a signal and be attractive to others.

While REM sleep via production of emotional states and dreams may be in a position to influence a person's waking mood state, it is not at all clear which REM period is most operative in that influence. There are between 3-5 REM periods per night in most healthy individuals. As

the night progresses, activation patterns become more intense and culminate the long dreams characteristic of the final REM period of the night. The early REM researchers, who were influenced by psychoanalytic theory, presented evidence that all REM episodes contribute to the emotional processing occurring during sleep but results of all this processing are summarized in the final REM episode of the night (French and Fromme, 1964; Trosman, Rechtschaffen, Offenkrantz, and Wolpert, 1960;).

Trosman, Rechtschaffen, Offenkrantz, and Wolpert, (1960) and French and Fromme, (1964) suggested that dreams at the beginning of the night would announce an emotional wish or emotional conflict that dreams later in the night would pick up and work with in an attempt to contain or resolve the emotional conflict. These investigators presented several case studies involving collection of dreams across the night that seemed to support the claim. For example, Offenkrantz and Rechtschaffen (1963) studied the sequential sleep patterns and dreams of a patient in psychotherapy for 15 consecutive nights. They noted that scenes from childhood memories never occurred early in the night but did occur on 8 of the 15 nights in dreams late in the night, after 4:30 a.m. They also noted that all the dreams of a night tended to be concerned with the same emotional conflict or a small number of such conflicts. They also claimed that they found evidence that the organization of a particular dream depended on the results of the dream work of the preceding dream, such that dream wishes required less and less disguise as the night progressed.

A costly signaling approach to dream expression is broadly consistent with both the formal properties of dreams and with dream content. It predicts that dream recall will vary as a function of communicative need. Those individuals most in need will recall more dreams. One way to gauge “communicative need” is to look at people who want to enter into a romantic or sexual relationship. We (McNamara, Anderson, Clark, Zborowski, and Duffy, 2001) investigated differential recall rates as a function of “attachment status.” Attachment in this context denotes romantic emotional attachment to a significant other. Current attachment theory suggests that people generally fall into one of four attachment-related categories: (1) they are in a relationship and happy with the relationship (they are securely attached to their partner); (2) they are not in a relationship but want to be and are preoccupied with that goal; (3) they may or may not want to be in a relationship or may even be in a relationship but they are dismissive about the importance of the relationship to them; and (4) they are not in a relationship and do not want to be (avoidant). Now if dreaming somehow facilitates one’s communicative goals and in particular facilitates pursuit of emotional attachment strategies, then dream recall should be relatively lower in the groups of people who are satisfied with their current status (secure, dismissive, and avoidant) and relatively higher among the group of persons who want to change their status (the preoccupied group), and that is exactly what we found. Roughly 80% of preoccupied persons and about 35 to 40% of persons in the other three groups recalled at least one dream for purposes of the study. In general, the non-securely attached persons were much more likely to recall their dreams than securely attached persons. These results suggest that dream recall is strategic: it serves a person’s communicative and emotional goals.

Typical dreams involve unpleasant emotions and scenes that place the dreamer in a victim role or under some handicap (naked, disoriented, without identification, unable to move, etc.). All of these properties of dreams, while obviously consistent with the costly signaling approach advocated here, are also somewhat consistent with Revonsuo’s theory of dreaming as threat simulation. The two theories however suggest opposite functions for dreams: one to improve responding when under threat, and the other to handicap a person or to produce biased

emotional responding when awake. To some extent, the two approaches predict opposite effects of dreams when an awake person faces a threat: according to threat simulation theory, that person would react a little faster if he had just experienced a dream wherein the dreamer was attacked or a victim of aggression, and so on. According to costly signaling theory, the person would be handicapped if he had just experienced such a dream. Whatever beneficial effects such a dream might confer on a person (in terms of reaction times, etc., in response to a real attack), they would potentially be canceled out by the real purpose of the dream: to produce a handicapped self or a biased set of emotional signals during the waking state.

Another way to test the CST approach to dreams is to longitudinally examine the dreams and waking behaviors of people as they unfold over time. If certain dreams function to facilitate a self-handicapping strategy in persons facing vital communicative demands (e.g., a sexual courtship, ongoing scholastic or college-related demands, or a new business partnership perhaps), then we should see handicapping themes come and go in these people's dreams as a function of changing communicative challenges/demands. CST would also predict that memorable dreams for people facing unusual communicative demands would be those dreams that best facilitate the handicapping strategy (i.e. Unpleasant dreams that place the dreamer in a handicapped situation).

A third way to test the CST approach is to collect a sampling of dreams that could plausibly be ascribed to REM sleep states and then to compare these dreams to dreams collected from the NREM state. CST (as explicated above) is primarily concerned with REM sleep not NREM sleep. As mentioned above dreams collected from late in the night are more likely to come from REM than NREM and conversely dreams collected from early in the night are more likely to come from NREM than REM (as NREM predominates in the early part of the night and REM and the later part).

Our predictions would be as follows: relative to early NREM dreams, late REM dreams would 1) contain greater numbers of handicapping themes and 2) greater numbers of memories involving handicapping themes. There is some evidence that this is indeed the case. Offenkrantz and Rechtschaffen (1963) studied sequential NREM-REM dreams within a single night in three subjects who had previously demonstrated good dream recall from NREM sleep. They restricted themselves to noting only obvious connections between dreams in sequence rather than analyzing "latent" content or asking for the dreamer's associations to his or her dreams. They found repeated instances of dream elements recurring throughout the dream sequence but in more and more bizarre and threatening situations. For example, the image of a street corner appeared in the first NREM dream of the night. It later appeared as the place where the dreamer met a girl but felt unable to respond to the girl. Other repeating elements noted in dream sequences of other subjects included: riding a bicycle, looking at a photograph, attending an outing, picnic, or camping trip, taking exams, sensing a sunny day, and so on. These elements, settings, or themes recurred throughout dream sequences and often framed unpleasant emotional encounters in later dream images.

It is important to point out that self-handicapping themes cannot be reduced to scenarios involving threats to the dreamer as postulated by Revonsuo's threat simulation theory of dreams. It is hard to claim, for example, that the inability of the dreamer to produce an ID card is a threat to the dreamer (though it does of course handicap the dream ego). To our knowledge Revonsuo and colleagues themselves do not score situations involving social shame, etc. as threat simulation scenarios. Thus we believe we have identified a potential lead here in characterizing the special content that is associated with REM dreams: namely the tendency of REM dreams to

depict the dreamer as experiencing some sort of handicap or diminishment of the ego as described above. We have furthermore provided a theoretical explanation of this effect in the form of costly signaling theory. The CST approach to REM sleep and dreams may be promising and certainly will need to be rigorously tested in future studies.

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