

TOWARD A BIOLOGICAL UNDERSTANDING OF MORTALITY SALIENCE (AND OTHER THREAT COMPENSATION PROCESSES)

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Terror management theorists have proposed explanations of why death anxiety has a special status beyond other anxieties and furthermore argue that awareness of death elicits a defense mechanism that is qualitatively different from other sorts of threat-defense mechanisms. Our review suggests that the biological mechanisms through which thoughts of mortality motivate defensive behavior are not unique. Rather, we propose that an evolutionarily primitive, biologically based anxiety system underlies mortality salience (MS) effects. Death anxiety may well be a mainspring of human activity, yet we suggest that a fundamental set of biological responses to uncertainty—and the processes associated with them—lie at the root of MS defenses. Our proposed motivational account of mortality salience provides a biologically informed, mechanistic elucidation of threat-compensation processes that may be applied to a wide range of social psychological phenomena.

Based upon cultural anthropologist Ernest Becker's (1973) theory of Generative Death Anxiety, terror management theory (TMT; Greenberg, Pyszczynski, & Solomon, 1986) proposes that much of human behavior is unconsciously generated to deflect fear of inevitable death. TMT has been applied to a wide variety of domains and has a large following. Since its original conception in 1986, a new field of social psychology, *experimental existential social psychology*, has been established. Indeed, over 5,300 articles have been published citing the term *terror management* since the mid-80s and a widely disseminated, award-winning film, *Flight from Death* (Shen, 2006), has been produced.

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TMT has not been without its detractors, however. Some have argued that the putative mortality salience defense effect is driven by fundamental psychological needs not specific to death management, such as general needs for certainty, meaning, and control. TMT theorists have accorded special status to death anxiety, arguing that it is distinct from—and supersedes—all other anxieties (Greenberg & Arndt, 2011; Greenberg et al., 1986). Yet such theorists have not proposed any biological mechanism to account for what they suggest is its pervasive influence upon human behavior.

We review the research literature related to the biological basis of threat-defense responses in an effort to account for mortality salience effects. In doing so, we address the issue of whether awareness of death elicits a defense mechanism that is qualitatively different from other sorts of threat-defense process mechanisms. Based on this review, we suggest that the biological mechanisms through which thoughts of mortality motivate defensive behavior are not unique. Rather, a generalized, evolutionarily primitive, anxiety system may underlie mortality salience effects. This broad-based motivational account of defense against death anxiety provides a biologically informed, mechanistic elucidation of threat-compensation processes that may be applied to a wide range of social psychological phenomena.

MORTALITY SALIENCE DEFENSE: A SELECTIVE REVIEW OF THE PROPOSED MECHANICS

Proponents of TMT suggest that humans, unlike other animals, have the cognitive capabilities to conceive of their own mortality, which in turn instills in them an anxiety like no other (Greenberg & Arndt, 2011; Greenberg et al., 1986). As a result, they suggest that humans have developed a unique system of buffering this death anxiety. TMT posits a dual-process model in which (1) conscious thoughts of death are avoided by *proximal* defenses such as rational threat-focused attempts to suppress awareness or distract attention from death, and (2) unconscious thoughts of death are defended against with *distal* defenses such as bolstering conceptions of self and reality that provide a sense of symbolic immortality (Pyszczynski, Greenberg, & Solomon, 1999).

Distal defenses have been of particular interest to social psychologists. TMT theorists have proposed two fundamental defenses that alleviate existential terror: (1) a *cultural worldview*—a shared symbolic construction of reality that entails a set of standards for attaining a sense of personal value, and (2) self-esteem, which is facilitated by the belief that one is living up to the standards of value proscribed by a cultural worldview (Pyszczynski et al., 1999).

TMT advocates argue that research supports the existence of both of these processes. Reminding individuals of their mortality, a paradigm known as mortality salience (MS), leads them to exhibit an increased need to believe in their cultural worldview. Yet this effect is attenuated among individuals with stable, high self-esteem (Harmon-Jones, Simon, Greenberg, Pyszczynski, Solomon, & McGregor, 1997; Schmeichel, Gaillot, Filardo, McGregor, Gitter, & Baumeister, 2009).

The MS paradigm has been exemplified in a great number of studies in which experimenters remind participants of their mortality, administer a distractor task to ensure that the participants are not able to work through their death anxiety with rational *proximal* defenses, and then take note of increased need for faith in

their cultural worldview (see Burke, Martens, & Faucher, 2010 for meta-analytic review). The increased need for faith in the worldview is often associated with measures of *cultural worldview defense*, which is operationalized in terms of either more positive or more negative evaluation of people and ideas that respectively support or disconfirm their worldview.

For example, MS has been found to lead to more favorable evaluations of individuals who uphold culturally accepted moral standards (e.g., Florian & Mikulincer, 1997), but to less favorable evaluations of individuals who have transgressed against culturally accepted morals (e.g., Florian & Mikulincer, 1997). Following MS, participants have also been shown to judge less positively others who have criticized their culture (e.g., Greenberg, Simon, Pyszczynski, Solomon, & Chatel, 1992), or are dissimilar in some way from themselves (e.g., McGregor et al., 1998). MS moreover leads to more discomfort when perceiving behavior that is counter to cultural norms (Greenberg, Simon, Porteus, Pyszczynski, & Solomon, 1995). Consistent with the second type of distal MS defense strategy proposed by TMT, individuals with high, stable self-esteem show less anxiety in response to general anxiety threats (Greenberg, Solomon, et al., 1992) and less worldview defense in response to MS (Harmon-Jones et al., 1997; Schmeichel et al., 2009).¹

TMT theorists suggest that it is the accessibility of death-related thoughts rather than the direct emotional experience of fear or anxiety that drives the MS defenses (see Pyszczynski et al., 1999). In other words, TMT suggests that MS causes individuals to (nonconsciously) engage in defense mechanisms that allow them to avoid existential anxiety.

Before moving further with our discussion of the role of emotion in MS effects, it is important to define and discuss a few terms and issues concerning affective processes. We use the broad term "affect" to describe the moods/emotions that may be created by MS. This is to avoid the baggage associated with the terms mood and emotion.² Affective states are often regarded as involving subjective experience, changes in physiological arousal, and behavioral expressions. Decades ago, affective scientists realized that these responses do not intercorrelate highly (Lang, 1968). More recently, research has suggested that affective states can occur without conscious subjective experience (Winkielman & Berridge, 2004). The *experience* of anxiety, then, may refer to a state of physiological arousal that is not necessarily accompanied by self-reported anxiety/distress. Thus, the affective state evoked by MS may be unconscious or at least not verbalizable, but it may be measurable with physiological or behavioral assessments.

Some evidence suggests that this may be the case. MS inductions do not produce increases in self-reported negative affect, anxiety, or distress. In addition, self-reported affect is consistently found *not* to mediate the worldview defense in

1. TMT is a wide-ranging theory that addresses the many ways in which death- and self-awareness impact human culture, behavior, and attitudes. As such, TMT is not a single bounded theory but is a literature composed of numerous independent theories dealing with human mortality. Our review specifically and exclusively focuses upon elucidating the biological mechanism through which MS elicits cultural worldview defense. This is because this phenomenon has been the subject of comprehensive empirical and theoretical investigation.

2. Although psychological scientists who study affective processes often suggest that emotions and moods are distinct affective processes, Frijda (1986, p. 60) argued that the distinction between mood and emotion is "unsharp." This is exemplified, for instance, by the fact that moods, which are viewed as differing from emotions in that they are longer in duration and have a less definite cause, may sometimes be of long durations but be associated with known triggers (see Frijda, 1993).

response to MS (e.g., Arndt, Allen, & Greenberg, 2001; Pyszczynski et al., 1999). Indeed, some studies have found an inverse relationship between the amount of death-related distress expressed and the extent of worldview defense observed (e.g., Greenberg, Simon, Harmon-Jones, Solomon, Pyszczynski, & Lyon, 1995). In one of only a few examinations of physiological responses, however, Arndt and colleagues (2001) found that following a subliminally presented MS prime, individuals had greater muscle activity over their brows (corrugator muscle region). This is a psychophysiological correlate of increased negative affect, which suggests that mortality salience does induce physiologically experienced affect, though this did not mediate the effect of MS on cultural worldview defense.

Greenberg and colleagues (2003) provided evidence that they argue confirmed that it is the *potential for anxiety* and not the actual experience of anxiety that leads to cultural worldview defense following MS. Participants who believed that they had been given a memory enhancing drug exhibited cultural worldview defense following MS, whereas those who thought that they had taken an antianxiety drug did not. This finding suggests that the effects of MS are reduced (or even eliminated) when participants do not believe that they are capable of experiencing anxiety. According to the authors, this substantiates the notion that it is the *potential for anxiety* and not anxiety itself that leads participants to defend their cultural worldview in response to MS. It should be noted, however, that expecting to take an antianxiety drug might actually reduce experienced anxiety due to the well-known placebo effect. Placebos, which modify participant's expectations of their capacity to experience negative affect, have been found to alleviate symptoms of anxiety (e.g., see Clayton, Stewart, Fayyad, & Clary, 2006), depression (e.g., see Fournier et al., 2009), and pain (e.g., Benedetti & Amanzio, 1997). Recent functional neuroimaging research has suggested that placebo pills attenuate activation of neural processes associated with negative emotional responses to aversive visual stimuli (Petrovic et al., 2005). Accordingly, Greenberg and colleagues' (2003) findings may alternatively be interpreted as showing that the expectation of no anxiety created by labeling the pill influenced participants' *experienced* affective state, which in turn, influenced MS effects.

In sum, it seems that more evidence is needed to substantiate the notion, put forward by TMT, that it is the *potential for* and not the actual *experience of* anxiety that leads to cultural worldview defense following MS.³

THE PSYCHOLOGICAL MECHANISM OF MORTALITY SALIENCE DEFENSE: INTEGRATING ALTERNATIVE THEORIES

Several alternative explanations have been put forward in recent years to account for the MS phenomenon. Taken together, these imply that cultural worldview defense is elicited by a general mechanism for dealing with a wide array of psycho-

3. Indeed, the only supporting evidence for the notion that cultural worldview defense is not mediated by self-reported negative affect relies on a null effect. Because any number of factors can cause a null effect, the lack of mediation does not provide strong evidence. This is particularly problematic because the measures used to assess cultural worldview defense are influenced by variables besides MS (e.g., pre-existing attitudes), which may negate its sensitivity to detect significant relationships with mediating variables.

logical threats, associated with *experienced* rather than *potential for* anxiety per se, as has been hypothesized in the TMT literature. Misattribution of arousal, unconscious vigilance, cognitive dissonance, and uncertainty management, for instance, have all been suggested as psychological mechanisms, unrelated to death anxiety, which may underlie the MS effect.

Misattribution of Arousal (Dutton & Aron, 1974; Schachter & Singer, 1962)—which occurs when individuals are induced to feel arousal and then falsely attribute such arousal to an unrelated activity—has been argued to underlie the MS effect (e.g., Proulx & Heine, 2008). Participants may misattribute their aroused state in response to MS to their positive or negative reactions to in-groups and out-groups, respectively, causing the cultural worldview defense phenomena. This seems particularly plausible given that a distraction exercise is often administered following MS, which may distract participants from acknowledging the cause of their arousal (death anxiety).

In support of the notion that misattribution of arousal plays a role in MS defense, research indicates that when participants are given external cues upon which they can misattribute their feelings, the effects of MS disappear (Goldenberg, Arndt, Hart, & Routledge, 2008). If it is the case that MS defense effects are attributable to misattribution of arousal, then this might suggest that *experienced* anxiety stemming from any threat—rather than the *potential for* death anxiety, specifically—should lead to cultural worldview defense, provided that individuals do not correctly attribute their negative affect or arousal to the actual cause of the arousal. In support of this possibility, Proulx and Heine (2008) exposed participants to absurdist information that violated their expectations and found that this led to cultural worldview defense reactions. However, this effect only occurred when participants were not given an explanation of their arousal. This suggests, then, that the consequences of MS may be due to arousal that is not worked through, rather than death anxiety, specifically.

In a similar vein, Holbrook, Sousa, and Hahn-Holbrook (2011) have suggested that cultural worldview defense may be caused by *unconscious vigilance*—a state of arousal initiated by alarm cues processed below the threshold of consciousness that heighten the intensity of reactions to positive and negative affective stimuli. These researchers argue that MS-induced unconscious vigilance (rather than death anxiety, per se) leads to polarized perceptions of in-groups and out-groups. Support was found for this hypothesis in a series of four studies where MS led to biased judgments of sounds and images unrelated to cultural worldview, and where subliminal threats unrelated to death evoked cultural worldview defense (Holbrook et al., 2011).

The reduction of cognitive dissonance (Festinger, 1957) may provide yet another explanation of MS defense. Cognitive consistency is an essential component of any cultural worldview. Some theorists (e.g., Jonas, Greenberg, & Frey, 2003) have accordingly argued that a cultural worldview may alleviate cognitive dissonance, an aversive mental state that occurs when one's expectations have been violated (Festinger, 1957). MS may cause feelings of dissonance between an individual's behavior, which tends to serve long-term goals, and the realization that life could end at any instant. This dissonance may cause individuals to engage in worldview-consistent cognitions and behaviors as a means of reducing the dissonance. In other words, MS might arouse cognitive dissonance and worldview defense might act to relieve dissonance.

In sum, a number of theories suggest that more general psychological mechanisms than those articulated by TMT, associated with *experienced* rather than *potential* anxiety, may function to produce the MS/cultural worldview defense phenomenon. If this is the case, then psychological threats besides death anxiety should elicit cultural worldview defense. Although some studies have indicated that cultural worldview defense is elicited in response to death anxiety but not other anxiety-producing stimuli such as thoughts of physical pain, worries about life after college, or failing an exam (e.g., Greenberg, Pyszczynski, Solomon, Simon, & Breus, 1994; Greenberg, Simon, Harmon-Jones, et al., 1995), these stimuli may not be sufficiently troublesome and at the right level of unconsciousness to provide a good comparison for the effects of MS. It may be that a stimulus needs to be sufficiently anxiety provoking and at the right level of unconsciousness in order to incite a state of unconscious vigilance/arousal that motivates defensive reactions. Much research into the effects of affective states on other perceptions and judgments has revealed that consciousness of the source of the affective state and/or the affective state itself can eliminate the direct effect of the affective state on the perception/judgment (Berkowitz, 2000).

Indeed, other studies that have compared the effects of MS to threats to other salient psychological needs have suggested that cultural worldview defense may not be specific to death anxiety. Threats to psychological needs such as certainty (e.g., McGregor, Zanna, Holmes, & Spencer, 2001; van den Bos, 2001), meaning (Proulx & Heine, 2008; Proulx, Heine, & Vohs, 2010; Randles, Proulx, & Heine, 2011; Simons & Rensink, 2005), affiliation/attachment security (Baumeister & Leary, 1995; Hart, Shaver, & Goldenberg, 2005), faith in the social system (e.g., Jost & Banaji, 1994; Lerner, 1980), and personal control (Kay, Gaucher, Napier, Callan, & Laurin, 2008; Whitson & Galinsky, 2008)—like MS threats—have all been found to evoke cultural worldview defense. Accordingly, some researchers have argued that a psychological need other than to buffer death anxiety may represent the prime mover of human behavior that underlie responses to MS (e.g., Hart et al., 2005; Hirsh, Mar, & Peterson, in press; McGregor, Zanna, Holmes, & Spencer, 2001; Proulx & Heine, 2008; Proulx et al., 2010; Randles et al., 2011; Simons & Rensink, 2005; van den Bos, 2001).

For instance, some theorists (e.g., Hirsh et al., in press; McGregor et al., 2001; van den Bos, 2001) suggest that uncertainty is the fundamental psychological need and motivator underlying MS effects. From this perspective, reminders of death conjure feelings of uncertainty, which in turn leads to cultural worldview defense. Most individuals act in accord with long-term goals rather than short-term impulses because they do not perceive death as immanent. Reminders of mortality often create feelings of uncertainty in regards to how to proceed in order to achieve goals and even about what those goals should be. According to uncertainty management theories, believing in the validity of culturally agreed upon norms (cultural worldview) is important not because it provides a sense of symbolic immortality, rather because it provides a sense of agreed upon rules, which, if they are respected, enable the individual to live in a predictable environment in which complexity and novelty are limited.

Proulx, Inzlicht, and Harmon-Jones (2012) have recently attempted to create an overarching theory that integrates findings from TMT, uncertainty management, cognitive dissonance, and other threat-compensation theories. The researchers

note that each threat-defense process involves: (1) an inconsistency that is detected between expectation and experience, (2) a state of aversive arousal, and (3) compensatory affirmation of some unrelated belief. Proulx and colleagues consequently coined the term "inconsistency compensation" to describe MS as well as uncertainty defense and other threat-compensation effects that have been noted in social psychology. According to this idea, expectancy violation (whether it occurs in response to MS or a novel perceptual stimulus) evokes a similar set of physiological (Croyle & Cooper, 1983; Mendes, Blascovich, Hunter, Lickel, & Jost, 2007) and neuroaffective (Hirsh & Inzlicht, 2008; Holroyd & Coles, 2002; Inzlicht & Al-Khindi, in press) responses, best characterized as aversive affect, which Proulx and colleagues propose is what motivates compensatory affirmation (in this case, cultural worldview defense).

In sum, psychological explanations of MS effects fall into two categories. The first stems from the TMT framework itself and suggests that mortality salience prompts the *potential for anxiety* that then elicits cultural worldview defense. The second category, exemplified by theories such as cognitive dissonance, inconsistency compensation, and uncertainty, complexity, and entropy management,⁴ suggest that MS prompts a form of *uncertainty* (a term used to describe the feeling of not knowing how to direct one's behavior to obtain goals and avoid threats) that is experienced as basic anxiety that then elicits cultural worldview defense. We address the validity of such an alternative explanation in the next section in which we review the biological mechanism through which MS defenses may occur.

MORTALITY SALIENCE DEFENSE: A BIOLOGICAL ANXIETY SYSTEM ACTIVATED BY PSYCHOLOGICAL UNCERTAINTY

If MS defense is attributable to a general psychological process, as we and others have hypothesized, then there must be a set of biological mechanisms that account for MS defense as well as uncertainty and other threat defense mechanisms. This biological process should not be a mechanism evolved specifically to buffer death anxiety. If death anxiety is special, however, then we should expect to find a qualitatively different biological mechanism for MS effects than for other threat defenses.

The notion of separate and distinct biological mechanisms of MS effects on the one hand and all other threat defenses on the other runs counter to prevailing views in neuroscience. The brain is thought to have evolved such that modern human brain functions are built upon older, more primitive brain functions (MacLean, 1990; Panksepp, 1998). In other words, the biological mechanisms underlying uniquely human behaviors are derived from evolutionarily old systems. For example, the uniquely human feeling of disgust in response to hearing about a morally reprehensible act stems from the same evolutionarily old, biological sys-

4. These models and theories each suggest that individuals are motivated to reduce uncertainty/inconsistency, which differentiates them from others that have proposed that individuals are motivated to *enhance* certainty/consistency (e.g., Festinger, 1957; Heider, 1958; Heine, Proulx, & Vohs, 2006; Osgood & Tannenbaum, 1955; Swann, 1983). We believe that there is more overall evidence for the former rather than the latter (see Beauvois & Joule, 1996).

tems that evolved to encourage animals to avoid contaminants such as spoiled food and disease (Chapman, Kim, Susskind, & Anderson, 2009).

In this context, we propose that it makes little sense for a specialized “death anxiety module” in the brain when a more general anxiety module would suffice. Given that MS defense entails detecting and reacting to threat, we suggest that it therefore must function, at least partially, through evolutionarily old threat-detection systems that developed in order to allow our nonhuman ancestors to avoid danger. Importantly, many (if not all) of these ancestors do not possess the cognitive capabilities to conceive of the inevitability of their own mortality, further implying a non-specialized biological mechanism.

We propose that the biological mechanism underlying MS effects is a brain-based anxiety system, the main instigator of which is psychological uncertainty. From an evolutionary perspective, resolving uncertainty is crucially important. When the significance of information in the environment is unknown, it is not clear to the individual what behavior will function optimally to fulfill one’s needs. The motive to avoid feeling uncertain (and so to avoid the unexpected) is accordingly a primitive and fundamental psychological requirement for humans, other primates, and indeed other mammals (Hirsh & Inzlicht, 2008).

Animals that do not have the cognitive capability to comprehend their own mortalities display a tendency to avoid uncertainty. Rats, for instance, prefer to consort with familiar than novel rats, presumably because their behaviors have already been deemed to be safe (Zajonc, 1968). In general, repeated exposure to a stimulus has been found in many species to increase liking (or decreased disliking) of the stimulus as the stimulus becomes more familiar (see Zajonc’s 1968 mere exposure hypothesis). This phenomenon has been demonstrated in nonhuman primates and 1-day old chicks, as well as in humans (Roberts, Marx, & Collier, 1958; Zajonc, Reimer, & Hausser, 1973). Furthermore, children below the age of 9–10 years, who are not yet cognitively capable of conceiving of death as universal, inevitable, and irreversible (see Nagy, 1948), exhibit behaviors that reflect uncertainty avoidance and ambiguity intolerance (see Furnham & Ribchester, 1995; Piaget, 1932). Children, monkeys, and rats, like adult humans, additionally engage in cognitive dissonance reducing behaviors (Egan, Santos, & Bloom, 2007; Lawrence & Festinger, 1962).

In sum, a biological mechanism specifically designed to buffer death anxiety does not seem plausible because physiological threat-detection systems are apparent in nonhuman animals, which are incapable of conceiving of their own death. A brain-based anxiety system, whose main instigator is psychological uncertainty, on the other hand, would seem to be a likely candidate for the biological underpinnings of MS—and other threat—defense phenomena. We suggest that the anxiety experienced by a human upon acknowledging his or her mortality stems from the same biological anxiety systems—and psychological reactions—that are roused when an animal is unsure about how to proceed to acquire rewards and to avoid threats. Because humans’ evolved cognitive processing capabilities allow them to think abstractly, the basic anxiety reaction may be generalized to a wider range of stimuli than uncertainty alone.

WHAT HAPPENS BIOLOGICALLY WHEN WE ENCOUNTER THE UNEXPECTED?

We have defined *psychological uncertainty* as an overarching term that captures the feeling of not knowing how to direct one's behavior to obtain goals and avoid threats. Self-regulatory systems constantly compare what we perceive to what we want (our goals) in an attempt to reduce mismatch (e.g., Gray, 1982, 1987; Gray & McNaughton, 2000; Luria, 1980; Sokolov, 1969; Vinogradova, 1961). What happens when individuals encounter information that makes them realize that they may be behaving in a way that will prevent them from getting what they want? Such expectancy violation or uncertainty threat activates a process known as the *orienting reflex* or *orienting response* (Sokolov, 2002; Vinogradova, 2001).⁵ The orienting reflex is an expression of the "septo-hippocampal comparator system" that compares neural signals stemming from representations of the environment with incoming sensory information (Brackbill, 1971; Vinogradova, 2001). If a mismatch is detected, tonic inhibition of the reticular formation by hippocampal CA3 neurons is released and a lower brain circuit including the amygdala is disinhibited, which activates circuitry in the right hemisphere (Tucker & Frederick, 1989) and subsequently inhibits the prefrontal left cortical hemisphere that is associated with approach motivation (see Harmon-Jones & Harmon-Jones, 2011). This causes a chain of reactions in which the heart rate rises (Fowles, 1980), cortisol floods the bloodstream (Gray, 1987), and noradrenaline and associated emotional arousal ensues as attention is quickly deployed upon the unexpected stimulus.

More generally, perceived mismatch between what one expects and the sensory information that one experiences produces activity in the Behavioral Inhibition System (BIS; Gray, 1982; Gray & McNaughton, 2000), which, according to Gray's model, forms the basis of a general anxiety network in the brain.⁶ This is evidenced, for instance, by the fact that the BIS is associated with a 7.7 Hz hippocampal theta response associated with behavioral indicators of anxiety such as inhibition of ongoing goal-directed behavior instigated by activity in the septal area. Moreover, septal lesions and pharmacologically reduced activity in the septal area have been found to attenuate behavioral inhibition. BIS activates circuitry in the right hemisphere (Tucker & Frederick, 1989), which inhibits the frontal and prefrontal systems of the left cortical hemisphere that are associated with approach motivation

5. Uncertainty may be experienced as a challenge rather than as a threat if an individual feels that s/he has the personal resources to cope with it (e.g., Blascovich & Mendes, 2000; Blascovich & Tomaka, 1996; Tomaka, Blascovich, Kelsey, & Leitten, 1993) and this is associated with a distinct set of cardiovascular responses (see Blascovich & Mendes, 2000; Blascovich & Tomaka, 1996, for reviews). However, expectancy violation has been found to lead to threat rather than challenge responses (Mendes et al., 2007) and we believe that MS should be responded to similarly.

6. Anxiety is distinguished from fear, which is associated with a fight/flight system (FFS), and results when one is exposed to non-uncertain threats such as pain, for instance. MS may be conceived as mapping onto the BIS rather than the FFS because although we are certainly going to die, it is unknown when and in what circumstances this will happen. This suggests that death-anxiety might better map onto the BIS than FFS.

(see Harmon-Jones & Harmon-Jones, 2008). BIS is the biological system that we suspect is most responsible for MS effects.

The anterior cingulate cortex (ACC) is thought to be a cortical extension of the BIS because it shares features with Gray's subcortical network. For instance, ACC activity has been directly linked to the orienting response in humans (e.g., Williams et al., 2000), and may be implicated in the electrical activity of hippocampal theta activity and associated anxiety and noradrenaline (e.g., see Hirsh et al., in press). The ACC is thought to play an especially important role in error monitoring and the detection of—and reaction to—*mismatch*. Indeed, it has been referred to as a “cortical alarm bell” which alerts a need for attention to be deployed to an unexpected event or error (Gray & McNaughton, 2000; Inzlicht & Tullett, 2010). Indeed, individual differences in BIS relate to greater ACC responses to errors (Amodio, Master, Yee, & Taylor, 2008). The ACC seems to be involved in detecting and resolving higher-order inconsistencies that occur, for instance, at the level of beliefs and actions such as cognitive dissonance (van Veen, Krug, Schooler, & Carter, 2009), as well as inconsistencies in lower-order response conflict such as occur while completing a Stroop task (Gehring, Goss, Coles, & Meyer, 1993). Taken together, it seems that the ACC plays a pivotal role in monitoring the potential for inconsistency, and in receiving “prediction errors” that cause attention to be drawn to unexpected information (Holroyd & Coles, 2002).

The “adaptive gain” framework (Aston-Jones & Cohen, 2005) provides an integrative model of locus coeruleus-noradrenaline (LC-NA) function that yields additional insight into the biological processes associated with encountering unexpected information. According to this model, there are two distinct modes of the LC-NA system operation: phasic and tonic. When the ACC and PFC signal that the current goal-pursuit strategy may not provide reward, such as occurs for instance during MS, then the LC-NA system shifts into an uncomfortable tonic mode in which (unrelated to any specific goal-related stimuli) there is increased baseline firing rates of noradrenaline. On the other hand, when the behavioral goal-pursuit plan is proceeding smoothly, the LC-NA system will operate in the more comfortable phasic mode in which noradrenaline is released in short bursts in response to goal-relevant information, which may help to cause attention to focus on this information. When in the tonic mode, however, such as in response to MS or another uncertainty threat, individuals will be motivated to attain a new and more rewarding course of action, framework, or goal, so as to switch back into a phasic state of being. Cultural worldview defenses may provide an opportunity to affirm goals that switch the participant back into the more comfortable phasic mode.

In summary, we suggest that priming participants to ponder their own mortality creates feelings of uncertainty about their goals and to their future. Such feelings of uncertainty signal an orientating response associated with BIS activation and associated release of noradrenaline, cortisol, and other stress hormones, and shifts into the tonic phase of LC-NA activation. In support of this notion, a recent electroencephalographic (EEG) study found that participants exhibited greater relative right frontal activity, a neurophysiological index of withdrawal motivation/BIS activity (Nash, Inzlicht, & McGregor, in press) during MS threat (Kosloff, Greenberg, Martens, & Allen, 2011). Moreover, a study by Quirin and colleagues (2011) found activation in the right amygdala, left rostral ACC, and right caudate nucleus after participants were primed to think about their own mortality (compared to

dental pain). The activations of these brain regions similarly implicate activity in a general anxiety module, most likely BIS. In the next section, we address what we believe is the biological mechanism through which this MS-induced BIS state leads participants to engage in cultural worldview defense mechanisms.

RESOLVING UNCERTAINTY: REACTIVE APPROACH MOTIVATION

We propose that individuals restore psychological homeostasis following MS-induced BIS/anxiety by engaging the dorsolateral prefrontal cortex (PFC) and associated left-hemisphere approach-motivational processes. The PFC is thought to be responsible for reducing dissonance in reaction to ACC-detected conflicts (see Harmon-Jones, Amodio, & Harmon-Jones, 2009), and thus may be involved in resolving MS effects as well.

Much research has suggested that the left-frontal region of the brain is involved in approach-motivational processes (movement toward goals) and the right-frontal region is involved in withdrawal or inhibitory motivation (movement away from stimuli). This is exemplified by the finding that damage to the left frontal lobe causes depressive symptoms, which are associated with a lack of approach-motivational tendencies (Robinson & Downhill, 1995). Electroencephalographic (EEG) activity additionally suggests that greater left-frontal cortical activity is associated with state and trait approach motivation (Harmon-Jones, 2003, 2004; Harmon-Jones, Gable, & Peterson, 2010), with source localization of these EEG signals implicating the left dorsolateral PFC (Pizzagalli, Sherwood, Henriques, & Davidson, 2005). Finally, fMRI studies have noted greater left-sided PFC activity during retrieval of approach-related action words (e.g., Bunge, 2004). Such approach-motivated states are thought to reduce distress associated with the detection of inconsistency either by *accommodating* inconsistent experiences and thus facilitating effective action (Harmon-Jones et al., 2009) or by *affirming* consistent but unrelated commitments, alleviating feelings of uncertainty (McGregor, Nash, Mann, & Phills, 2010; see Proulx et al., 2012). Recent theories such as reactive approach motivation (McGregor, 2006) and the action-based model of cognitive dissonance (see Harmon-Jones, 2004; Harmon-Jones et al., 2009) suggest that aversive-motivated states cause individuals to engage in thoughts and actions that will shift them into an approach-motivated state so as to relieve the aversive distress and allow for unconflicted action. MS may cause cultural worldview defense because affirming one's worldview provides a means of shifting into an approach-oriented motivational state, which is associated with a psychologically comfortable, phasic state of LC-NA activation (Aston-Jones & Cohen, 2005). In support of this notion, cognitive dissonance has been found to evoke greater relative left compared to right prefrontal activity (Harmon-Jones, Gerdjikov, & Harmon-Jones, 2008; Harmon-Jones, Harmon-Jones, Fearn, Sigelman, & Johnson, 2008; Harmon-Jones, Harmon-Jones, Serra, & Gable, 2011). Similarly, uncertainty primes lead to shifts toward the type of left prefrontal cortical activity that is associated with approach motivation (McGregor, Nash, & Inzlicht, 2009). Such findings suggest that approach-motivated states are engaged following the detection of inconsistency, such as, for example, the realization that life could end at any moment.

The prediction of increased left frontal activity following MS is inconsistent with the findings of Kosloff et al. (2011) mentioned above. However, we believe that this is because the initial reaction to MS is an increase in right frontal activity (associated with BIS/anxiety), which is quickly followed by a switch to increased left frontal activity as the organism seeks to resolve the conflict/uncertainty. This notion is consistent with research by Amodio, Devine, and Harmon-Jones (2007), which found that a guilt induction led to right frontal activity, which was promptly followed by left frontal activity when participants were given an opportunity to engage in guilt reduction.⁷

In short, we propose that the biological underpinnings of MS defense entails a two-part system: (1) a system for detecting unexpected information (associated with an orienting response and associated BIS-related stress-inducing hormones and ACC activity), and (2) a DLPFC system whereby individuals restore psychological homeostasis by engaging in an approach-motivated affirmation of beliefs such as those exemplified by cultural worldview defenses.

WHY DOESN'T MS INDUCE NEGATIVE AFFECT?

We propose that the biological mechanism underlying MS effects is based on a basic and evolutionarily old anxiety system, most likely BIS. TMT theorists, in contrast, argue that MS creates the *potential* for anxiety rather than *experienced* anxiety. They make this argument because research mostly, but not always (see Arndt et al., 2001), finds that MS does not evoke negative affect. How do we reconcile our suggestion for a common underlying anxiety mechanism with repeated, albeit inconsistent, failures to identify aversive affect as the core mechanism?

We suggest that people might not be aware of how MS makes them feel because activity in BIS might be quickly and automatically defended against by self-regulatory motivational systems. In other words, the thought of death may automatically prime an avoidance motivational state, which immediately cues individuals to engage in approach-motivated thoughts and behaviors (such as cultural worldview defense), restoring a comfortable psychological state. The self-report assessments that have most commonly been employed in TMT research (e.g., Arndt et al., 2001; Greenberg, Simon, Porteus et al., 1995; Pyszczynski et al., 1999) may not be sensitive enough—or more specifically, fast enough—to detect changes in affect following MS threat. Interestingly, when researchers have turned to psychophysiological and neuroaffective assessments of mortality salience effects, negative affect is more likely to be spotted (Arndt et al., 2001; Quirin et al., 2011), and when participants are given external cues upon which they can misattribute their feel-

7. According to revised versions of Gray's reinforcement sensitivity theory (e.g., Gray & McNaughton, 2000), BIS conflict may be resolved by approach or avoidance. Although dissonance work so far has suggested that the inconsistency is resolved by increasing approach, the research paradigms used may encourage this in part because individuals have already made a commitment in a particular direction. It is possible that—at least some—individuals resolve the ACC-detected conflict instigated by MS through avoidance, that is, withdrawal from goals. In support of this notion, depressed individuals, who are known to be characteristically prone to avoidance rather than approach, are less likely to engage in cultural worldview defense following MS (Simon, Arndt, Greenberg, Pyszczynski, & Solomon, 1998). Such individuals may remain anxious in response to MS because they fail to engage the left frontal hemisphere activity.

ings, the effects of MS disappear (Goldenberg et al., 2008). Together, these types of studies support the notion of MS activating basic biological systems that are associated with aversive emotional states.

Some studies have found an inverse relationship between self-reported death distress and cultural worldview defense (e.g., Greenberg, Simon, Harmon-Jones et al., 1995). Although speculative, we wonder if this might be because to the extent that cultural worldview defense engages approach-motivated states, it should also alleviate avoidance-motivated negative affect (Nash, Inzlicht, & McGregor, in press). In this context, individuals who experience the most negative affect in response to MS should be the ones who fail to engage in approach-motivated defense (i.e., affirming their cultural worldview), and conversely, individuals who most quickly and effectively engage approach-motivated defenses should report less affective distress following MS.

In short, the biological basis of the phenomenon known as *potential anxiety* may be better thought of as BIS activity, which is automatically defended against by engaging in approach-motivated thoughts and behaviors, so that the individual never becomes consciously aware of that BIS activity. In other words, it might be best to retire the notion of *potential anxiety* and instead focus on the more biologically and evolutionarily plausible notion of general anxiety.

EVALUATING THE VALIDITY OF THE MORTALITY SALIENCE HYPOTHESIS IN LIGHT OF ITS BIOLOGICAL MECHANISM

Terror management theorists have proposed metaphysical explanations of why death anxiety has a special status above and beyond all other anxieties and furthermore argue that awareness of death elicits a defense mechanism that is qualitatively different from other sorts of threat-defense process mechanisms. Our review suggests that the biological mechanism through which thoughts of mortality motivate defensive behavior is not unique. Rather, we suggest that an evolutionarily primitive brain-based anxiety system activated by psychological uncertainty instigates the effects of mortality salience as well as other types of psychological threats.

The need to avoid acknowledging the ephemeral nature of our existence may be a most salient psychological threat, which—even though it is instigated by a biological mechanism evolved to deal with psychological uncertainty—is more potent and defended against more vehemently than uncertainty or other kinds of psychologically threatening information. Humankind's evolved cognitive capabilities create a desire for meaning that may sometimes override powerful primitive psychological needs for certainty stemming from evolutionarily basic threat-detection systems. Martyrs, for example, have overcome their deeply rooted desire to stay alive in order to serve some greater cause that will allow them to achieve symbolic immortality. Despite the extremeness of the motive to buffer death anxiety, however, we suggest that it cannot present a qualitatively different sort of threat than other psychological threats such as uncertainty. Rather than being different in terms of quality, we suspect that these motives simply differ in terms of quantity.

CONCLUSION: A REVISED UNDERSTANDING OF MS AND OTHER TYPES OF THREAT DEFENSE INFORMED BY SOCIAL AFFECTIVE NEUROSCIENCE

TMT has played an invaluable role in illuminating the pervasive effects of mortality salience on human behaviors and some of the deeply rooted psychological functions served by significant aspects of our culture such as religion (e.g., Inzlicht, McGregor, Hirsh, & Nash, 2009; Inzlicht, Tullett, & Good, 2011; Norenzayan & Shariff, 2008), in-group bias/out-group prejudice (e.g., see Greenberg et al., 1990), and the objectification of women (e.g., Goldenberg, Heflick, Vaes, Motyl, & Greenberg, 2009; Goldenberg, Pyszczynski, Greenberg, & Solomon, 2000). Relatively recent developments in the field of social neuroscience, however, are enabling re-evaluation—and refinement of theories such as TMT. Various advances in the field of social affective neuroscience point toward a generalized, rather than a distinctive, arousal system at the root of mortality salience effects. We suspect that such refined understanding of the mechanism of MS defense will continue to generate insight into—and enable a better understanding of—the nonconscious underpinnings of important human behaviors and the psychological functions served by our culture.

Our broad-based motivational account of MS provides a biologically informed, mechanistic elucidation of threat-compensation processes that may be applied to a wide range of social psychological phenomenon. Threats to individuals' sense of meaning, attachment security, certainty, faith in the social system, self-esteem, and personal control, as well as symbolic immortality, may each initiate defensive reactions through the same set of psychological/biological mechanisms (Proulx et al., 2012). That is, psychological threat induces an orienting response and associated BIS-related stress, which subsequently initiates affirmation of beliefs that engage the approach-motivated DLPFC system, and restore psychological homeostasis. By considering various threat compensation phenomena as manifestations of a unified motivational process, research attention will become more cohesively focused upon the fundamentals of defensive behaviors (Proulx et al., 2012).

In Ernest Becker's (1973) seminal work, *The Denial of Death*, he writes: "The fear of death haunts humans . . . It is a mainspring of human activity" (p. ix). Our review does not contradict this idea but it does complicate and clarify it by proposing that the biological mechanisms underlying MS defense are a general form of anxiety, no different from other anxieties. Death, in other words, is not so special.

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