Neural evidence that the behavioral inhibition system is involved in existential threat processing

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ABSTRACT
According to threat-general perspectives, existentially threatening prospects such as the inevitability of mortality or uncontrollability represent motivational discrepancies that activate the behavioral inhibition system (BIS). The aim of the present paper is to test this claim using neuroimaging and neurophysiological methods. In Study 1, we used neuroimaging to show that both mortality- and uncontrollability-related stimuli elicit activation in the anterior cingulate cortex, which is a key BIS region in humans. Focusing on the idea that BIS activation is associated with increased attention, Study 2 used electroencephalography to demonstrate that both mortality- and uncontrollability-related stimuli enhanced the late positive potential, an indicator of motivated attention. Together, these studies provide support for the model’s prediction that existential threat activates the BIS.

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It is a well-known fact that all living things ultimately die. It is also well-known that the future is not entirely predictable and that people have only a limited amount of control over how it will unfold. Thinking about these and other givens of existence often creates what one might call existential anxiety, or angst (Greenberg, Koole, & Pyszczynski, 2004).

Psychological theories on existential anxiety disagree over whether concerns about the inevitability of mortality should have a special status beyond other existential concerns (Tritt, Inzlicht, & Harmon-Jones, 2012). Terror management theory (Greenberg et al., 1990; Rosenblatt et al., 1989) proposes that the threat of mortality is distinct from all other types of anxiety, and even supersedes them, possibly because unlike many other things, death is inevitable, or because it undermines all human needs, including control, growth, and affiliation (Greenberg & Arndt, 2012), instead of just one or a subset of these needs. Furthermore, the theory proposes that coping with the awareness of mortality relies on highly specialized psychological processes that are qualitatively different from others: Upon detection, death-related thoughts are usually suppressed automatically (a process termed “proximal defense”), and after suppression, these thoughts are unconscious, but in a state of high accessibility. While terror management theory views the problem of death as being distinct from other existential threats, the anxiety-to-approach model of existential threat and defense (Jonas et al., 2014), as well as other theoretical perspectives (McGregor, 2006; Proulx, Inzlicht, & Harmon-Jones, 2012; Tritt et al., 2012), argues that detecting and coping with a range of existential threats partly rely on the same set of psychological and biological mechanisms. In the following, we will collectively refer to these approaches as threat-general perspectives.

Threat-general perspectives share the assumption that an evolutionarily old behavioral inhibition system (BIS; Gray & McNaughton, 1982, 2000) is key for understanding responses to existential threat. The BIS is constantly comparing perceptual inputs with representations of goals and detects goal conflicts. Existential threats cause BIS activation because they highlight mismatches between current or anticipated circumstances and existential needs. When it detects conflicts between concurrently active goals, it leads to a cessation of the pursuit of currently active goals (hence the term “behavioral inhibition”) in order to permit the individual to gather information (i.e., the “attention” output of the BIS (Gray & McNaughton, 2000). Threat-general theories therefore predict that existential threat, regardless of whether it is related to mortality or not, should activate the BIS.

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How can this prediction be tested empirically? First, Gray and McNaughton clearly suggested where the BIS should be located in the brain. Based on pharmacological studies on rats, they (Gray & McNaughton, 1982) originally proposed that the BIS depends crucially on the septo-hippocampal system. Newer evidence from other (including human) lines of research suggests that additional regions in the frontal lobe such as the anterior cingulate cortex (ACC) are also important BIS substrates (Amodio, Master, Yee, & Taylor, 2008; Gray & McNaughton, 2000). Consistent with the idea that the ACC is essential to the BIS, neuroimaging evidence in humans has shown that the ACC is involved in the detection of errors, conflict, and surprise (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Egner, 2011; Oliveira, McDonald, & Goodman, 2007; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Shackman et al., 2011; Stevens, Hurley, & Taber, 2011). Moreover, there is direct evidence of the involvement of the ACC in threats such as cognitive dissonance (Kitayama, Chua, Tompson, & Han, 2013; van Veen, Krug, Schooler, & Carter, 2009) and mortality salience (Quirin et al., 2011). In Study 1, we used neuroimaging to demonstrate that existential threat activates the ACC. In Study 2, we focused on the “increased attention” output of the BIS, and tested whether existentially threatening stimuli attract more attention than similarly unpleasant, yet nonexistentional ones. Here, we relied on an event-related potential (ERP) component termed the “late positive potential” (LPP), an indicator of motivated attention (Bradley, 2009; Ferrari, Codispoti, Cardinale, & Bradley, 2008; Schupp et al., 2000; Schupp, Markus, Weike, & Hamm, 2003). Together, the two studies serve to test the hypothesis derived from threat-general theories that existential threat, regardless of whether it is related to mortality or not, will produce neural signatures characteristic of BIS activation.

Study 1

To test our prediction that existential threat activates the neural circuitry underlying the BIS (i.e., the ACC), we designed a functional magnetic resonance imaging (fMRI) experiment in which participants were presented with self-descriptive sentence items that fell into three categories: mortality (example item: Thinking about the finitude of life frightens me), uncontrollability (example item: I’m afraid of things I cannot control), and dental pain (example item: I’m scared of going to the dentist). Participants had to indicate whether the statements applied to them or not (Quirin et al., 2011). The dental pain category was intended to be a nonexistentional yet threatening condition against which the two existential conditions (i.e., mortality and uncontrollability) could be compared. We chose dental pain because it is the most commonly used control condition in terror management research (Burke, Martens, & Faucher, 2010). We predicted that activation in the ACC would be higher for both the mortality and uncontrollability conditions relative to the dental pain condition. In addition, we were curious as to whether activation would differ depending on whether participants agreed or disagreed with the statements. Responding affirmatively should reflect greater concern over the topic and hence stronger BIS activation, which should result in increased activation of the ACC.

Method

Participants

The sample consisted of 30 participants (20 females), with a mean age of 22.03 years (SD = 2.71) (range: 18–27). Five were left-handed and 25 were right-handed. All were students at the University of Salzburg. All participants gave written informed consent to participate in the study, which was ostensibly investigating emotional processing. Participants received course credits and a digital copy of their structural whole-head scan in return for participation. The study was approved by the ethics committee of the University of Salzburg. All participants could withdraw participation at any point, although no participant made use of this option.

Stimuli

We used four categories of stimulus items: death, uncontrollability, dental pain, and neutral. Some were taken from a previous fMRI study (Quirin et al., 2011). We complemented the original death-related and dental pain-related items with equal numbers of uncontrollability-related and neutral items. Example items: I am afraid of dying a painful death (death), I am afraid of going to the dentist (dental pain), I am afraid of not mastering important tasks in my life (uncontrollability), I sometimes find it hard to speak fluently and without errors (neutral). We pretested these experimental stimuli using online surveys to see whether the four stimulus categories differed in the intended way with regard to arousal, valence, and death-relatedness. A pretest on 10 participants (four males, six females; mean age = 22.80 years, SD = 2.04) served to determine whether and how the categories differed with respect to arousal (1 = not at all; 5 = very much). A separate pretest on 12 individuals (five females, seven males; mean age = 32.00
years, $SD = 13.45$) served to determine emotional valence (How emotional, positive or negative, do you find the statements? $-3 =$ very negative; $0 =$ neutral; $3 =$ very positive). A third pretest was conducted using 10 (five males, five females; mean age = 26.60 years, $SD = 10.50$) raters to see the extent to which the stimuli were related to mortality (How much does reading this statement make you think about death? $1 =$ not at all; $5 =$ very much). The reason for doing separate pretests was to reduce the duration of the surveys, in order to avoid a drop in participants’ motivation or concentration associated with very long surveys. Table 1 shows the mean ratings across participants for each of the three stimulus categories. Based on each item’s average rating, we manually selected 15 items per category for the final stimulus set. The goals of the manual selection were (1) to exclude items that everyone agreed or disagreed upon; (2) to ensure that the “threatening” death-related, dental pain–related, or uncontrollability–related items were moderately arousing and negative in valence; and (3) to ensure that the death-related and uncontrollability-related items were similar with regard to uncontrollability. The death, uncontrollability, and dental pain categories were designed to be moderately arousing and negative. The neutral condition was designed to be neutral in valence, and low in arousal. Supplemental Table 1 provides a complete list of the statements used in the experiment.

Next, we analyzed the items’ mean ratings obtained in the pretest using one-way ANOVAs and Bonferroni-corrected post hoc tests. Arousal was comparable across the four conditions, ranging from two to three on the five-point arousal scale. There was a main effect of sentence category, $F(2, 56) = 4.22$, $p = .009$, which was mostly due to neutral stimuli having higher arousal than the dental pain stimuli ($p = .005$). Death-related and uncontrollability items did not differ ($p = 1$). Also, dental pain did not differ from death ($p = .67$) or uncontrollability ($p = .58$). The mortality, uncontrollability, and dental pain conditions were slightly negative in valence, while the neutral condition was slightly positive in valence. Statistically, valence also differed between the four conditions, $F(3, 56) = 16.73$, $p < .001$. The neutral stimuli were judged as being more positive than the other stimulus conditions ($ps < .001$), but the death-related, uncontrollability, and dental pain statements did not differ ($ps > .64$). The stimuli also differed in the extent to which they were judged as being related to death, $F(3, 56) = 101.36, p < .001$. Death statements were rated as more death-related than uncontrollability ($p < .001$). Uncontrollability items were more death-related than neutral ($p = .009$) and dental pain items ($p = .003$), suggesting that although death was not mentioned explicitly, they elicited death-related associations. However, the mean difference between death and dental pain was four times higher (1.63) than the mean difference between uncontrollability and dental pain (0.39), suggesting that the mortality stimuli were related to mortality considerably more than the uncontrollability stimuli. Neutral and dental pain did not differ with regard to how much they were associated with the topic of death ($p = 1$).

To sum up, the neutral condition was rated relatively positive in valence and high in arousal compared to the death-related and uncontrollability-related items, but the dental pain condition fulfilled our requirements of having similar arousal and valence to the mortality and uncontrollability conditions. For this reason, we used only the dental pain condition as reference, and did not take the neutral condition into account.

**Task and procedure**

The stimulus sentences were presented visually on a screen at the headend of the scanner bore. Participants viewed them from inside the scanner using a mirror attached to the head coil. For stimulus presentation, we used the software Presentation (Presentation version 14.2, Neurobehavioral Systems Inc., Albany, CA, USA). Stimuli were presented in yellow letters on a uniformly black background. Each sentence was presented for 5 s, with an interstimulus interval (ISI) of 3 s. During the ISI, a fixation cross appeared on the screen. None of the participants reported any trouble reading the statements in time. The items were presented in a

| Condition        | Death       | Uncontrollability | Dental pain | Neutral    |
|------------------|-------------|-------------------|-------------|------------|
| Emotionality     | 2.45 (.49)  | 2.46 (.35)        | 2.15 (.36)  | 2.81 (.72) |
| Valence          | −0.50 (.66) | −0.74 (.45)       | −0.85 (.49) | 0.51 (.69) |
| Death-relatedness| 2.46 (.26)  | 1.22 (.50)        | .83 (.06)   | .86 (.15)  |

For the arousal and semantic relatedness ratings, we used a scale ranging from 1 (not at all) to 5 (very much). For the valence ratings, we used a scale ranging from −3 (very negative) to +3 (very positive).
pseudorandom fashion using four different stimulus sequences. The order of the sequences was counterbalanced across participants.

Upon entering the lab, participants were welcomed and informed about the experimental procedure and familiarized with the in-scanner task prior to scanning, which ostensibly investigated emotional processing. During scanning, participants were instructed to make binary decisions on whether each of the statements presented applied to themselves using a magnetic resonance imaging (MRI)-compatible response pad. Immediately before the presentation began, an instruction on the screen reminded them of their task (“Agree? Left button: yes, right button: no. Please answer quickly and intuitively”). After the sentence reading task, participants were given another in-scanner task, which involved visual presentation of photographs of people and personality adjectives. Participants were asked to indicate whether they believed that the adjective was descriptive of the person in the photograph. As this task does not present an opportunity to test the hypothesis put forward in the present paper, the data will not be reported here. After the second in-scanner task, a whole-head structural scan was acquired.

**Imaging parameters**

For MRI, we used a 3-T Siemens Tim Trio scanner together with a 32-channel head coil. For the functional runs, we used a T2*-weighted gradient-echo planar imaging sequence sensitive to blood-oxygen-level dependent contrast. Data were collected in two runs, each comprising 154 T2*-weighted whole-brain images (46 slices, slice thickness = 3 mm, field of view (FoV) = 210 mm, repetition time (TR) = 2900 ms, echo time (TE) = 30 ms, flip angle = 70°). Parallel imaging was used (GRAPPA level = 2). Six dummy scans were performed prior to each run and discarded prior to data analysis. A whole-head high-resolution structural scan was acquired using a T1-weighted MPRAGE sequence (FoV = 256 mm, slice thickness = 1.20 mm, TR = 2300 ms, flip angle = 9°), with a resolution of 1 × 1 × 1.2 mm. In addition, we acquired a gradient-echo field map (TR = 488 ms, TE 1 = 4.49 ms, TE 2 = 6.95 ms) for off-line geometric distortion correction of the functional images.

**Data preprocessing**

Preprocessing of the data was done with SPM8 (Wellcome Department of Cognitive Neurology, London, UK). First, head movements were estimated across the time course of the experiment. After unwarping and slice-timing with the middle slice as the reference slice, the functional images of each participant were co-registered to the corresponding structural image. The structural scan was then normalized to the ICBM 152 brain template (Montreal Neurological Institute (MNI), Montreal, QC, Canada). The resulting normalization parameters were applied to both the functional and structural scans. Functional images were resampled to 3-mm isotropic voxels and smoothed with a Gaussian kernel (8 mm full width at half maximum).

**Voxel-based statistical analysis**

For the voxel-based analysis, we used a two-stage mixed-effects model in SPM12 (Wellcome Department of Cognitive Neurology). At the first level, for each participant, each stimulus was modeled as a discrete event using separate regressors for the death-related, uncontrollability-related, and dental pain items. Neutral statements and statements that did not receive a response were modeled using regressors of no interest. The resulting model was convolved with a hemodynamic response function and its temporal derivative. Movement parameters obtained during head movement estimation (three for translation, three for rotation) were also included as covariates of no interest. The functional time series were high-pass filtered (128 s cutoff) and corrected for autocorrelation using an AR(1) model (Friston et al., 2002). At the second level, we first investigated areas of activation and deactivation that were common to all four stimulus categories relative to baseline (i.e., a combination of null events and the ISI). We investigated differences between the three conditions at the group level using a unifactorial ANOVA. Specifically, we chose a flexible factorial design with one-factor coding stimulus category (assuming dependencies between levels and equal variance among levels). Subsequently, we used t-contrasts to investigate between-condition activation differences.

To test our hypothesis that agreeing with the statements will lead to greater activation in the ACC than disagreeing, we created another first-level design for each participant in which we used two separate regressors per stimulus category to model statements that received “agree” and “disagree” responses. As in the previous first-level design, neutral statements and misses were modeled using regressors of no interest. Contrast images reflecting agree greater than disagree activation were analyzed at the second level using separate one-sample t-tests for mortality, uncontrollability, and dental pain items. One person had to be excluded due to a malfunction of the in-scanner
response device. No responses were recorded, which made it impossible to find out upon which statements they agreed or disagreed. In four participants, some contrast maps could not be created because they agreed or disagreed with all items from certain categories: Two participants disagreed with all dental pain statements; one disagreed with all uncontrollability statements; yet another participant agreed with all death-related statements. This made it impossible to generate agree greater than disagree activation maps for some conditions in these four participants.

Throughout all voxel-based analyses, our significance criterion was an initial voxel-wise threshold of \( p < .001 \) together with a cluster-level correction for multiple comparisons (false discovery rate, \( p < .05 \)). As suggested by Poldrack, Fletcher, Henson, Worsley, and Nichols (2008), we provided an image of the voxel mask used for the group-level statistical testing overlaid onto an average of the structural scans of all participants (see Supplementary Figure 1). Both images are available for online viewing and download in NIfTI format (voxel mask: http://neurovault.org/collections/JCYVUWUT/images/23341/, averaged structural: http://neurovault.org/collections/JCYVUWUT/images/23342/).

For the purpose of visualizing activation patterns in the ACC, we extracted data from a region of interest (ROI). This ROI was defined as follows. We performed a term-based meta-analysis of the term “dacc” in 102 studies using Neurosynth (neurosynth.org). We identified the activation peak in the forward inference map associated with the term (MNI \( x = 0, y = 16, z = 46 \)) and created a spherical ROI with a 6 mm radius at these coordinates (see Figure 3(b)).

**Results**

**Behavioral results**

We determined whether the in-scanner response times (RTs) differed between the three experimental conditions. Mean RTs were computed for each participant across all sentences of each category and subjected to a repeated-measures ANOVA with sentence category (death-related, uncontrollable, dental pain, neutral) as a single factor. RTs differed between sentence categories, \( F(2, 56) = 83.57, p < .001 \). Bonferroni-corrected post hoc tests indicated that participants responded significantly (\( p < .001 \)) faster to dental pain items (2729.92 ms, SD = 441.08 ms) than to mortality (\( M = 3079.20 \) ms, SD = 649.74 ms) and uncontrollability (\( M = 3365.85 \) ms, SD = 584.95 ms) items. Responses to uncontrollability items took significantly longer than responses to mortality and dental pain items (\( ps < .001 \)).

**fMRI results**

**Voxel-based results**

**Task-related activations and deactivations.** First, we determined which regions were activated (and deactivated) in conjunction with the mortality, uncontrollability, and dental pain categories versus baseline (which contained the null events and ISIs). We observed task-related activations in a network of bilateral occipital regions, including the occipital poles, inferior and superior occipital gyri, the fusiform gyri, and the calcarine cortices. Parietal regions (angular gyri, bilateral superior parietal lobules) participated, as did frontal regions (bilateral precentral gyrus, bilateral middle and superior frontal gyrus, both frontal opercula, bilateral anterior insula (AI)) and temporal regions (bilateral temporal pole and bilateral middle temporal gyrus). In addition, we found a cluster at the border between the bilateral anterior and middle cingulate, which also comprised the bilateral supplementary motor cortex. We will refer to this region as the dorsal ACC (dACC) for the remainder of this paper. We observed task-related deactivations in the bilateral precuneus, right posterior insula, bilateral supramarginal gyrus, bilateral superior and middle occipital gyrus, and bilateral anterior cingulate gyrus. Figure 1 provides a visual illustration of the task-related activations and deactivations.

**Between-condition differences.** To test our hypothesis that the ACC responds to both mortality and uncontrollability items more than to dental pain items, we conducted a conjunction analysis that contrasted the two existentially threatening conditions against the dental pain condition (i.e., mortality > dental pain > uncontrollability > dental pain). The conjunction analysis revealed activation in the dACC. This supports our prediction that both existential threats should activate this brain region. In addition, the bilateral supplementary motor cortex, left precentral gyrus, and bilateral cerebellar regions were also activated more strongly by existential than by nonexistential threat (see Table 2 and Figure 2(a)).

To see where mortality- and uncontrollability-related stimuli produced less activation than dental pain-related stimuli, we reversed the contrast of the previous conjunction analysis. This revealed clusters in bilateral precuneus and bilateral angular gyrus, which are central regions of the default mode network (Raichle et al.,
Figure 1. Task-related activations (yellow) and deactivations (blue) overlaid on an average high-resolution scan of the entire sample ($p < .05$, corrected for multiple comparisons using false discovery rate).
Figure 2. A figure summarizing the observed differences between existential (mortality and uncontrollability) and nonexistential (dental pain) threat. (a) Separately contrasting mortality- and uncontrollability-related sentences against dental pain sentences led to activation in the dorsal anterior cingulate cortex. The same was true when contrasting the two conditions against dental pain by means of a conjunction analysis. (b) Dental pain led to stronger activation in the precuneus and angular gyrus bilaterally when contrasted against mortality and uncontrollability sentences, also when tested in conjunction.
A cluster in the right inferior frontal gyrus was also more active for dental pain than for mortality and uncontrollability in conjunction (see Figure 2(b)).

When separately contrasting the two existential threats against dental pain, only uncontrollability, and not mortality, led to activation in a cluster comprising the right insula. Subthreshold activation was also present in the left insula (see Figure 3(a) and Table 2). In addition, uncontrollability led to more activation than mortality in the left calcarine cortex. However, this cluster was mostly within white matter, indicating that it likely represents a false-positive finding.

On the other hand, mortality led to more activation than uncontrollability in the bilateral superior frontal gyrus, posterior cingulate cortex, and bilateral angular gyrus (see Figure 3(a) and Table 2). Two of these regions, the posterior cingulate and bilateral angular gyrus clusters, are typically associated with the default mode network.

### Table 2. A list of regions that showed differential activation between the death-related, uncontrollability-related, dental pain-related, and neutral conditions. The anatomical labels were derived using the Neuromorphometrics atlas implemented in SPM12.

| Peak | Cluster | MNI | Cluster | MNI |
|------|---------|-----|---------|-----|
| Death > dental pain | L SFG | 4.89 | 271 | <.001 | 9 | 8 | 70 |
| | L precenral gyrus | 4.78 | 171 | .01 | 45 | –1 | 46 |
| | L + R cerebellum white matter | 4.67 | 353 | <.001 | 6 | –1 | 29 |
| | L + R caudate | 4.48 | 168 | <.001 | 9 | 20 | –2 |
| Dental pain > death | L + R precuneus | 5.25 | 213 | <.001 | 9 | –64 | 22 |
| | R inferior frontal gyrus | 5.14 | 58 | .022 | 45 | 41 | 7 |
| | L angular gyrus | 4.44 | 123 | <.001 | 51 | –73 | 28 |
| | R angular gyrus | 4.25 | 121 | <.001 | 57 | –52 | 22 |
| Uncontrollability > dental pain | L + R SMC | 7.07 | 966 | <.001 | 0 | 11 | 55 |
| | L + R cerebellar vermlobules VI-VII | 6.52 | 1078 | <.001 | 3 | –73 | 23 |
| | L anterior insula | 5.72 | 391 | <.001 | –30 | 23 | 1 |
| | R IFG | 5.20 | 238 | <.001 | 33 | 29 | –2 |
| | R occipital pole | 4.78 | 103 | .006 | 27 | –97 | 2 |
| | R precentral gyrus | 4.60 | 63 | .03 | 42 | 4 | 55 |
| | R SPL | 4.33 | 58 | .03 | 21 | –64 | 52 |
| | L thalamus proper | 4.04 | 114 | .004 | –24 | –28 | 22 |
| | L occipital fusiform gyrus | 3.91 | 62 | .03 | –18 | –94 | 11 |
| Dental pain > uncontrollability | L angular gyrus | 7.58 | 548 | <.001 | –42 | –73 | 37 |
| | R angular gyrus | 7.16 | 649 | <.001 | 42 | –67 | 40 |
| | L + R posterior cingulate gyrus | 6.65 | 722 | <.001 | 6 | –43 | 34 |
| | R middle temporal gyrus | 6.29 | 95 | <.001 | 60 | –40 | 11 |
| | R MFG | 5.63 | 145 | .002 | 33 | 11 | 52 |
| | R IFG | 5.33 | 46 | .005 | 45 | 41 | 7 |
| | L middle temporal gyrus | 4.93 | 44 | .05 | –57 | –43 | 11 |
| | R frontal pole | 4.25 | 70 | .01 | 18 | 62 | 7 |
| | L MFG | 4.19 | 81 | .01 | –18 | 26 | 37 |
| Death > uncontrollability | L + R posterior cingulate gyrus/precuneus | 5.40 | 181 | <.001 | 9 | –43 | 34 |
| | L angular gyrus | 4.13 | 75 | .016 | –39 | –76 | 28 |
| | R angular gyrus | 4.29 | 76 | .016 | 45 | –67 | 31 |
| | R SFG | 3.96 | 85 | .016 | –21 | 35 | 46 |
| Uncontrollability > death | L white matter | 4.97 | 65 | .14 | –24 | –64 | 7 |
| | R anterior insula | 4.55 | 77 | .04 | 42 | 17 | 4 |
| Conjunction: death and uncontrollability > dental pain | L precenral | 4.78 | 156 | <.001 | –45 | –1 | 46 |
| | L SMC | 4.84 | 232 | <.001 | 0 | 5 | 64 |
| | L + R cerebellar vermlobules VI-VII, VIII-X | 4.52 | 193 | <.001 | –3 | –64 | 32 |
| Conjunction: dental pain > death and uncontrollability | L + R precuneus | 5.07 | 189 | <.001 | –9 | –64 | 22 |
| | L angular gyrus | 4.44 | 249 | <.001 | –51 | –73 | 28 |
| | R angular gyrus | 4.25 | 93 | .006 | 57 | –52 | 22 |
| | R MFG/IFG | 5.14 | 51 | .036 | 45 | 41 | 7 |
| Dental pain: yes > no | L + R SMC/L SFG | 7.11 | 346 | <.001 | –3 | 5 | 55 |
| | L IFG/MFG/SFG/O anterior insula | 6.42 | 584 | <.001 | –57 | 20 | 22 |
| | L middle temporal gyrus | 5.19 | 69 | .015 | –48 | –37 | 11 |
| | L angular gyrus/SPL | 4.95 | 171 | <.001 | –36 | –64 | 40 |

Abbreviations: SFG = superior frontal gyrus, SMC = supplementary motor cortex, IFG = inferior frontal gyrus, SPL = superior parietal lobule, MFG = middle frontal gyrus, SFG = superior frontal gyrus, FO = frontal operculum.
Differences related to responding. Next, we tested our hypothesis of increased ACC activation when participants agreed with the statements, compared to when they disagreed. In the death and uncontrollability conditions, we found no reliable differences between yes and no responses. Agreeing with dental pain statements, however, led to greater activation in the dACC than disagreeing (see Figure 3(b)).

An ROI analysis confirmed that dACC only responded more to yes responses given to dental pain statements, but not to mortality or uncontrollability statements (see Figure 3(b)). Interestingly, dental pain statements that received affirmative responses elicited dACC activation levels that were comparable to those elicited by mortality and uncontrollability statements.

Discussion

The aim of Study 1 was to test whether existential threat activates the ACC, which has been argued to constitute a key region underlying the BIS in humans (Amodio et al., 2008; Gray & McNaughton, 2000). In line with our prediction, mortality- and uncontrollability-related stimuli activated the dorsal aspect of the ACC (dACC) more than dental pain-related stimuli.

Dental pain items that participants agreed on evoked ACC activation levels comparable to those elicited by death and uncontrollability items. This is not surprising since agreeing with dental pain items should reflect greater anxiety related to dental pain, resulting in more BIS activation. Surprisingly, this effect was absent with the mortality and uncontrollability items: Here, ACC activation was unrelated to whether people agreed or disagreed. One possible, albeit speculative explanation for this result is based on the idea that humans use suppression and denial to deal with existential concerns (Pyszczynski, Greenberg, & Solomon, 1999) more than they do with dental pain. As a consequence, self-reported existential anxiety might be a worse indicator of actual anxiety than self-reported dental anxiety because a lot of existential anxiety is suppressed and is therefore not accessible to self-report.

In line with previous findings (Han, Qin, & Ma, 2010; Klackl, Jonas, & Kronbichler, 2013b; Shi & Han, 2013),
the insula was not activated by mortality compared to dental pain items. Uncontrollability, however, led to reliable activation in the insula relative to dental pain and mortality. This latter effect was significant in the right insula and failed to reach significance in the left insula. Because the insula has been argued to be highly relevant to conscious awareness (Craig, 2002, 2009), insula hypoactivation to mortality-related stimuli has been interpreted as reflecting a transient decrease in awareness (Klackl et al., 2013b) or a “weakened sense of the sentient self” (Han et al., 2010, p. 3441).

A different, yet related, interpretation of the activation patterns observed in both the ACC and the insula is possible against the background of a network perspective that argues that cognitive functions result from interactions between distributed brain areas that operate in large-scale networks (Bressler & Menon, 2010). Together, the ACC and the insula form the so-called “salience network,” which is deemed responsible for orienting attention to important intra- or extrapersonal events (e.g., surprising, self-relevant, punishing, rewarding, or emotionally engaging stimuli). Once detected, the salience network is thought to implement top-down attention, stimulus selection, and access to resources needed for goal-directed behavior (Menon, 2015; Menon & Uddin, 2010). In this implementation phase, it then activates the central executive network (right dorsolateral prefrontal cortex and right posterior parietal cortex) and deactivates the default mode network (ventromedial prefrontal cortex, posterior cingulate cortex, medial temporal lobes, and the angular gyri). In the present study, both mortality-related and uncontrollability-related threat led to activation in the ACC, whereas only uncontrollability led to more insula activation than dental pain, indicating that the two existential threats recruited different aspects of the salience network to different extents. Although the two main cortical nodes of the network are sensitive to rewarding, punishing, self-relevant, emotionally engaging, and surprising stimuli (Menon, 2015), the AI seems to be more involved in detecting salient stimuli, whereas the ACC is more involved in selecting appropriate responses to salient stimuli (Menon & Uddin, 2010). Viewing these findings in light of the BIS concept, one could also assign “feeling” and “acting” functions to the AI and the ACC, while “feeling anxious,” an important subjective quality associated with BIS activation, might be represented in the AI, whereas behavioral inhibition itself (i.e., the cessation of goal-directed behavior) might depend on the ACC. Applying this reasoning to the present data, one could speculate that compared to dental pain, both types of existentially threatening stimuli activated the behavioral aspects of BIS, but only uncontrollability activated the “feeling anxious” component of the BIS. In line with the idea that the salience network exerts a muting effect on the default mode network, existentially threatening stimuli not only activated the salience network but also the default mode network more than dental pain stimuli.

Study 1 provided support for the idea that the BIS responds to existential threat by showing that stimuli related to existential threat activate the ACC, the primary BIS region in humans. In addition, the insula and parts of the default mode network responded differently to the two existential threats. In Study 2, our goal was to collect additional evidence for our proposal. This time, instead of gauging BIS by measuring activation in BIS-related brain regions, we decided to use a neurophysiological measure of attention to gauge the “increased attention” output of the BIS.

Study 2

In Study 2, our goal was to test whether existential stimuli lead to increased attention. To measure attention, we used an ERP component termed the LPP. Many studies have shown that the LPP reflects how much attention people pay to stimuli that are being processed (Bradley, 2009; Ferrari et al., 2008; Schupp et al., 2000, 2003). The LPP is considered to be part of orienting response (Sokolov, 1963, 1990, 2002), which is a nonconditioned, rudimentary decision to devote attention to salient or novel events. This phenomenon has been referred to as “motivated” or “natural selective” attention (Lang, Bradley, & Cuthbert, 1997), and stands in contrast to selective attention (i.e., the ability to focus on a certain object and filter out irrelevant information, regardless of whether that object is salient or novel). Gray and McNaughton (2000) proposed the increased attention output of BIS activation to serve information gathering and environmental scanning (i.e., when rats adopt “rearing” or “stretched attend” postures). In our experiments, however, participants’ attention is somewhat restricted to a computer screen, which, according to task requirements, they have to pay attention to at all times. Hence, attention is somewhat restricted to a specific location in time and space (i.e., the stimulus presentation). Under these circumstances, we assume that the increased attention output of the BIS will not lead to environmental scanning, but instead, the threat-eliciting stimuli themselves will receive the attention released by BIS activation.

While Study 1 used fMRI, Study 2 used electroencephalography (EEG), which puts different constraints on experimental design. Therefore, unlike in Study 2 (which used sentences as stimuli), we relied on single-word presentations because words are better suited than sentences for generating ERPs. As in Study
we presented participants with mortality-related stimuli (words such as “grave”) and uncontrollability-related stimuli (words such as “powerless”) to induce existential threat. We compared these conditions against two nonexistent control conditions. One of them was “just negative”, and consisted of negative words unrelated to existential topics (such as “sad”). The second control condition consisted of neutral stimuli such as “effect” (see Supplementary Table 2 for a full list of the stimulus words).

Existing evidence from neuroscientific studies has shown that the LPP is greater in response to mortality reminders than negative and neutral stimulus words (Bluntschli, Maxfield, Grasso, & Kisley, 2015; Klackl, Jonas, & Kronbichler, 2013a). For example, the LPP produced by words such as “grave” or “coffin” is greater than that produced by words like “sad” or “accident”, indicating that orienting to mortality-related words is stronger than can be expected based on how arousing they actually are. The aims of Study 2 are to replicate these findings and to see whether the LPP enhancement generalizes to death-unrelated existential threat.

Method

Participants

Forty participants (28 females), with a mean age of 30.27 years (SD = 15.95), participated in the study. None reported any history of neurological disorders or previous head trauma. All participants gave written informed consent to participate in the study, which ostensibly investigated emotional processing. Participants received €20 for participating in the study. The study was approved by the ethics committee of the University of Salzburg. All participants could withdraw participation at any point, although no participant made use of this option.

Stimuli

The stimuli were lists of words in four categories: 29 neutral (e.g., depth, effect, need), 21 unpleasant (e.g., sorrow, failure, pain), 20 death-related (e.g., graveyard, kill, crypt), and 22 uncontrollability-related (e.g., powerless, paralyzed, victim). For the neutral word category, we selected words that had no clear positive or negative connotation. The unpleasant words were clearly negative in valence and high in arousal. Their semantic meaning, however, was not connected directly with existential topics. Some of the unpleasant words were loosely related to existential threat. For example, the word sadness might have induced death-related thought, but is not necessarily death-related. None of the unpleasant words were clearly or directly related to a specific existential threat (death, meaninglessness, isolation, identity, freedom; Koole, Greenberg, & Pyszczynski, 2006). Supplemental Table 2 provides a complete list of the original German stimulus words and their English translations. For the uncontrollability-related word category, we chose items that pointed to an external locus of control (e.g., victim, hostage). Importantly, the uncontrollability word category was designed to be unrelated to death. In contrast, the death-related words contained words that were directly and specifically related to death. To ensure that our selection was valid, we asked a group of 23 participants (20 females, mean age = 20.35 years, SD = 2.34) to rate the 92 stimulus words with regard to valence, arousal, imageability, death-relatedness, and uncontrollability-relatedness using a seven-point Likert scale for imageability, a six-step Likert scale for valence (with lower values indicating negative valence and higher values indicating positive valence), and five-step Likert scales for arousal, death-relatedness, and uncontrollability-relatedness. The pretest was administered online using EFS Survey 10.4 (Questback GmbH, Köln, Germany). Ratings for each individual word were calculated by averaging across participants (see Table 3 for a summary). The pretest sample was recruited independently of the sample of the actual experiment.

The word categories differed with respect to arousal, F(3, 88) = 6.44, p < .001. Bonferroni-corrected post hoc tests indicated that unpleasant, death-related, and uncontrollability-related words were all more arousing than neutral words (ps < .05). The nonneutral categories

Table 3. Means (SDs) of the subjective arousal, valence, and imageability ratings of the four stimulus categories, as well as their average perceived semantic relatedness to the topics death and uncontrollability. The rightmost column indicates whether and which of the categories differed.

| Condition                        | Neutral (NEU) | Unpleasant (UNP) | Death (DEA) | Uncontrollability (UNC) |
|----------------------------------|---------------|------------------|-------------|-------------------------|
| Arousal                           | 2.86 (0.76)   | 3.42 (0.64)      | 3.39 (0.82) | 3.26 (0.72)             |
| Valence                           | 3.67 (0.30)   | 1.95 (0.39)      | 1.84 (0.42) | 2.02 (0.36)             |
| Imageability                      | 4.79 (0.72)   | 4.70 (0.80)      | 5.38 (0.60) | 4.57 (0.76)             |
| Death-relatedness                 | 1.89 (0.46)   | 2.83 (0.67)      | 4.61 (0.26) | 2.59 (0.68)             |
| Uncontrollability-relatedness     | 2.32 (0.51)   | 2.91 (0.63)      | 2.58 (0.82) | 3.90 (0.56)             |

Statistical comparisons:

- (UNC, UNP, DEA) > (NEU)
- (UNC, UNP = DEA) < (NEU)
- DEA > (UNC, UNP, NEU)
- UNP > (NEU)
- UNC > (DEA, UNC, UNP, NEU)
- UNP > (NEU)
did not differ ($p = 1$). The word categories also differed in valence, $F(3, 88) = 78.27, p < .001$. Valence was significantly more negative for unpleasant, death-related, and loss-of-control-related words than for neutral words (all $p$s < .001). The nonneutral categories did not differ ($p = 1$). Mortality-relatedness differed between word categories, $F(3, 88) = 86.21, p < .001$. It was higher for death-related words than for all other categories ($p$s < .001), higher for unpleasant than for neutral words ($p < .001$), and higher for uncontrollability-related than for neutral words ($p < .001$). The word categories differed in uncontrollability-relatedness, $F(3, 88) = 23.17, p < .001$. As expected, uncontrollability-related words were rated as referring to uncontrollability more strongly than death-related, unpleasant, and neutral words ($p$s < .001). Unpleasant words were also rated as more uncontrollable than neutral words ($p = .023$). Imageability did not differ between word categories, $F(3, 88) = 2.22, p = .091$. Also, there were no significant differences between the word categories in the number of letters, $F(3, 88) = 1.39, p = .250$, or number of syllables, $F(3, 88) = 1.08, p = .361$.

**Experimental task and procedure**

The stimulus words were presented in yellow 32 pt Arial font surrounded by a gray box displayed on a uniformly black background throughout the experiment. We used a 17-inch LCD monitor with a resolution of 1024 × 768 pixels and 60 Hz refresh rate. The viewing distance was held constant at 80 cm. Each trial began with a fixation cross being shown in the center of the screen for 800, 1000, 1200, 1400, or 1600 ms. The word presentation duration was 1000 ms. At stimulus offset, a fixation cross appeared again for 900 ms. Next, an empty screen was displayed for 1500 ms. To reduce the amount of data loss due to eyeblink artifacts, participants were instructed to avoid blinking during fixation and word presentation intervals and to blink preferably during the empty screen periods. Participants were instructed to press the left mouse button whenever they saw the same word twice in succession. On average, participants correctly detected 16.53 of the 19 one-back target words ($SD = 2.43$) and exhibited .78 ($SD = 1.06$) false alarms (i.e., pressed the response button in the absence of a one-back target). The one-back target trials were distributed evenly across the four conditions. One-back target epochs and epochs containing false alarms were excluded from the analysis. We first presented all neutral words ($n = 29$) in a block, followed by all unpleasant words ($n = 21$). Half of the participants continued with death-related words ($n = 20$) in the third block and uncontrollability-related words ($n = 22$) in the fourth block. Within each block, each stimulus word was presented twice. The other half of the participants received the uncontrollability-related words in the third block and the death-related words in the fourth block. This was done to exclude the possibility that the death-related or uncontrollability-related word categories would influence the processing of other words. For example, making death salient by presenting death-related words might lead to an enhanced perception of death-relatedness of words from the remaining categories that are actually not related to death.

**EEG recording and analysis**

We used a BrainProducts BrainAmp MR amplifier at a sampling rate of 250 Hz. We mounted 32 AgCl electrodes according to the 10–20 system using an EasyCap (EASYCAP GmbH, Herrsching, Germany) electrode cap with an online reference on Fcz. AFz served as ground. Scalp electrode positions were Fp1, Fp2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, TP9, TP10, Fz, Cz, Pz, FC1, FC2, CP1, CP2, FC5, FC6, CP5, and CP6. In addition, we recorded signals from electrodes attached to both earlobes. A horizontal electrooculogram (EOG) was recorded using two electrodes placed next to the lateral canthi of both eyes. A vertical EOG was recorded using one electrode placed below the left eye. First, the data were re-referenced off-line to a computed average signal of the left and right earlobe electrodes. Then, data epochs were filtered with an infinite impulse response (IIR) filter (high-pass cutoff: 0.1 Hz, slope: 24 dB/Oct; low-pass cutoff: 30 Hz, slope: 24 dB/Oct). After that, epochs of 1200 ms were extracted from the continuous data. After ICA-based eye movement correction, epochs were rejected if the signal exceeded 100 or −100 µV or if any channel contained signal differences of more than 100 µV within 200 ms, or both. Grand average ERPs were computed for each word condition separately. Participants contributed to the grand average ERPs with a mean number of 55.95 ($SD = 6.69$) neutral epochs, 40.70 ($SD = 5.69$) unpleasant, 38.20 ($SD = 5.78$) death-related, and 41.45 ($SD = 6.91$) uncontrollability-related word epochs.

Visual inspection of the grand average ERPs revealed an LPP at parietal sites starting at approximately 350 ms and lasting until stimulus offset at 1000 ms. An occipital P1–N1 complex was apparent with the P1 peaking at 70–140 ms at occipital sites and the N1 peaking around 140–200 ms near O2. At temporoparietal sites, we observed an early posterior negativity (EPN) (Junghöfer, Bradley, Elbert, & Lang, 2001) that peaked between 200 and 250 ms. A negative-going frontocentral component was apparent at 250–360 ms. This
Results

The LPP differed as a function of word category, $F(3, 117) = 12.46, p < .001$. The average amplitudes were highest for uncontrollability-related ($M = 5.84 \mu V$, $SD = 2.99 \mu V$), followed by death-related ($M = 5.81 \mu V$, $SD = 3.89 \mu V$), unpleasant ($M = 4.80 \mu V$, $SD = 3.03 \mu V$), and neutral ($M = 4.18 \mu V$, $SD = 2.98 \mu V$) words. Bonferroni-corrected post hoc tests indicated that the LPP did not differ between unpleasant and neutral words ($p = .287$). The LPP elicited by death-related words was marginally greater than that elicited by unpleasant ($p = .059$) and neutral ($p = .001$) words. The LPP was also greater for uncontrollability-related than for unpleasant ($p = .005$) and for uncontrollability-related than for neutral ($p < .001$) words. However, death-related and uncontrollability-related words did not differ ($p = 1$; see Figure 4).

In order to determine whether the order of the death and uncontrollability blocks had an effect on the LPP, we performed a 2 (condition: death, uncontrollability) $\times$ 2 (sequence: death first vs. uncontrollability first) ANOVA. As was expected based on the results of the previous ANOVA, the main effect of condition was not significant, $F(1, 38) = .05, p = .813$, indicating that death-related and uncontrollability words did not differ. The main effect of sequence was not significant, $F(1, 38) = 1.33, p = .256$, indicating that participants' average LPPs did not differ as a function of which of the two threats was presented first. However, an interaction was present, $F(1, 38) = 5.88, p = .02$: When the uncontrollability block preceded the death block, the LPP produced by uncontrollability words was marginally greater ($p = .07$). In contrast, when the death block preceded the uncontrollability block, the LPP produced by death words tended to be greater ($p = .12$). In other words, the LPP was always greater in the initial block, which is consistent with the finding that LPP amplitude can habituate slightly over time (Codispoti, Ferrari, & Bradley, 2007). Habitation might have artificially reduced the unpleasant greater than neutral, mortality greater than unpleasant, and the uncontrollability greater than unpleasant effects because the neutral blocks were always followed by the unpleasant and existential blocks. However, because the sequence of the death-related and uncontrollability blocks was randomized, habituation cannot account for LPP differences between death-related and uncontrollability conditions.

Discussion

The goal of this experiment was to test the central claim of threat-general theoretical approaches to existential threat and defense that experimental manipulations of various existential threats, including (but not limited to) mortality and uncontrollability, activate very similar psychological and biological mechanisms. Specifically, phasic activation of the BIS should be one of these processes involved in dealing with existential threat. Study 1 revealed that mortality and uncontrollability activate the ACC, which is thought to be a key region underlying the BIS. Study 2 indicated that relative to unpleasant words, both types of existentially threatening words also lead to comparable phasic increases in the amplitude of the LPP, an indicator of motivated attention.

Interestingly, while the LPP was significantly greater for existential than for both unpleasant and neutral stimuli, the LPP elicited by unpleasant words did not differ significantly from that elicited by the neutral words. This can be explained by the fact that most of the words of the neutral condition were neutral in valence, yet relatively high in arousal (e.g., venture, sharp, cliff). The LPP is sensitive to the arousal rather than the valence of stimuli (e.g., Bradley, 2009; Lang
et al., 1997), which might explain why the amplitude of the LPP was not greater for unpleasant than for neutral stimuli in this study. This, however, does not invalidate the key finding of the study that words related to both existential threats produced greater LPPs than nonexistential threats.

**General discussion**

In this paper, our goal was to test a prediction of the anxiety-to-approach model (Jonas et al., 2014) that existential threat causes BIS activation, regardless of whether that threat is related to mortality. In Study 1, we found that both mortality- and uncontrollability-related stimuli activated the ACC, the key brain region supporting the BIS in humans (Jonas et al., 2014; Tritt et al., 2012). In Study 2, we relied on measures of the amplitude of the LPP to gauge the increased attention output of the BIS (Gray & McNaughton, 2000). Uncontrollability- and death-related words produced increased LPPs relative to “just unpleasant” words, which did not entail any existential threat. This suggests
that both existential threats attracted more attention than nonexistential, yet unpleasant, stimuli. Together, these investigations provide neural evidence of BIS activation in response to existential threat, regardless of whether it is related to mortality or not.

On a cautionary note, the present results must be treated with some reservation for several reasons. First, the ACC is only one of many brain regions relevant for BIS, and BIS activation cannot be equated with ACC activation. Similar things can be said about the LPP, which is currently regarded as an indicator of motivated attention to both positive and negative stimuli and therefore reflects both defensive and appetitive kinds of attention; the former is more likely to be associated with the BIS than the latter. Another problem with the LPP is that although its amplitude was found to be consistently modulated by the motivational relevance of stimuli, it is more than likely that other factors apart from motivational relevance affect its amplitude. For these reasons, the present results should be regarded only as initial support for the hypothesis that existential stimuli activate the BIS.

**Threat-general and threat-specific processes**

The anxiety-to-approach model proposes that there are general mechanisms through which all threats produce their effects. Pyszczynski, Solomon, and Greenberg (2015) criticized this proposition, arguing that there is not enough evidence of similarity in the neurological correlates of various existential threats. The present results contribute evidence for threat-general processes (i.e., BIS activation). At the same time, however, they also highlight threat-specific processes that might rely on the insula. Although at present we can only speculate about the functional significance of the insula in the existential threat context, the findings of Study 1 advocate the existence of both threat-general and threat-specific processes. Importantly, although the anxiety-to-approach model emphasizes the importance of threat-general processes, it does not explicitly deny the existence or importance of threat-specific processes. Whether or not BIS activation also accounts for the effects that the threat and defense literature was mainly interested in (including, for example, cultural worldview defense and self-esteem striving) remains a matter for future research. It is possible that although existential threats do activate the BIS, other things apart from BIS activation might actually account for such defensive behavior. Recent evidence from our lab, however, indicates that BIS activation mediates the effects of mortality reminders on defensive behavior in individuals who habitually avoid unfamiliar and threatening stimuli (Agroskin, Jonas, Klackl, & Prentice, 2016).

**Two among many**

In our opinion, the most important limitation of this study is that death and uncontrollability are only two threats among a variety of existential threats that humans face. For example, based on the four givens of existence proposed by Yalom (1980), Koole et al. (2006) have argued that there are five core existential problems: First, meaninglessness, which arises from the problem of unpredictability and uncertainty. Second, people often have difficulty integrating their experiences into a sense of who they are (i.e., to form a stable identity). Third, subjective experience can never be truly shared with others, giving rise to feelings of isolation. Fourth, the freedom to choose, although usually preferred over external constraints, creates a burden of responsibility for one’s choices. Together with death, these existential givens form the “Big Five” existential concerns. Given that the present investigation only focused on two out of at least five distinguishable existential threats, one cannot conclude that all existential threats activate the BIS. Instead, our results merely demonstrate that, in principle, two different existential threats, mortality and uncontrollability, each of which is subject to a research literature of its own, activate the ACC, a key region associated with the BIS and increased attention, which is a central output of the BIS. It is unclear and a matter for future research whether this is also true for existential threats other than mortality and uncontrollability.

**Conclusion**

The results presented in this paper demonstrate that both mortality and uncontrollability activate the ACC more than nonexistential stimuli, which is the key BIS region in humans. In addition, electrophysiological data suggest that both threats enhance motivated attention. These effects cannot be accounted for by stimulus emotionality. The results advocate the idea put forward by threat-general theories of existential threat that both mortality-related and mortality-unrelated existential threat activates the BIS. Study 1 indicated that uncontrollability, but not mortality, is associated with insula activation, indicating that additional, threat-specific processes unrelated to the BIS might operate at the same time.

**Disclosure statement**

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