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REVIEW

Affective neuroscience of self-generated thoughtKieran C.R. Fox,^{1,2,*} Jessica R. Andrews-Hanna,^{3,*} Caitlin Mills,² Matthew L. Dixon,^{2,4} Jelena Markovic,⁵ Evan Thompson,⁵ and Kalina Christoff^{2,6}

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Despite increasing scientific interest in self-generated thought—mental content largely independent of the immediate environment—there has yet to be any comprehensive synthesis of the subjective experience and neural correlates of affect in these forms of thinking. Here, we aim to develop an integrated affective neuroscience encompassing many forms of self-generated thought—normal and pathological, moderate and excessive, in waking and in sleep. In synthesizing existing literature on this topic, we reveal consistent findings pertaining to the prevalence, valence, and variability of emotion in self-generated thought, and highlight how these factors might interact with self-generated thought to influence general well-being. We integrate these psychological findings with recent neuroimaging research, bringing attention to the neural correlates of affect in self-generated thought. We show that affect in self-generated thought is prevalent, positively biased, highly variable (both within and across individuals), and consistently recruits many brain areas implicated in emotional processing, including the orbitofrontal cortex, amygdala, insula, and medial prefrontal cortex. Many factors modulate these typical psychological and neural patterns, however; emerging affective neuroscience of self-generated thought must endeavor to link brain function and subjective experience in both everyday self-generated thought as well as its dysfunctions in mental illness.

Keywords: self-generated thought; mind-wandering; stimulus-independent thought; task-unrelated thought; rumination

Introduction

Over the past few decades, an increasing amount of scientific attention has been focused on understanding self-generated thought—mental content that occurs largely independent of the external environment, forming a stream of thinking that can include memories, future plans, daydreams and fantasies, simulated social interactions, rumination, dreams, and more.^{1–8} This growing body of research has brought considerable progress in characterizing the first-person phenomenological content of self-generated thought (reviewed in Refs. 9–11). At the same time, there has been a dramatic increase in the number of functional neuroimaging and

electrophysiological studies aiming to elucidate the neural correlates of self-generated cognition. A general picture of the brain networks involved in self-generated thought is gradually emerging,^{4,5,8,12} and initial steps have been taken to correlate the specific sensory modality and emotional valence of self-generated mental content with specific patterns of brain activity.^{13–15}

Given that some two-thirds of self-generated thought is tinged with emotion of some kind,¹⁶ the role of *affect* in self-generated thought has been drawing increased attention in recent years.^{16–20} The affective properties and psychological consequences of self-generated thought have become the subject of an ongoing debate,¹⁸ with some researchers emphasizing its positive, constructive nature,^{21,22} and others casting it in a conspicuously negative light.^{16,17}

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As part of this debate, we have recently attempted to draw attention to the mildly positive average affect, but also the high variability, of emotional experiences in self-generated thought,¹⁹ as well as the diverse patterns of brain activity associated with it.⁴

The aim of the present review is to develop an integrated affective neuroscience encompassing many forms of self-generated thought—normal and pathological, moderate and excessive, in waking and in sleep. In synthesizing existing literature on this topic, we reveal consistent findings pertaining to the prevalence, valence, and variability of emotion in self-generated thought, and highlight how these factors might interact with self-generated thought to influence general well-being. We integrate these psychological findings with recent neuroimaging research, bringing attention to the neural correlates of the diverse forms of affect in self-generated thought. Furthermore, we illustrate the many ways in which various forms of self-generated thought can become negatively or positively biased, whether through innate predispositions, neuropsychiatric conditions, or deliberate training. Our central aims are to (1) provide an integrative review of existing research in order to promote cross-talk among psychological, neuroimaging, and clinical researchers; (2) elucidate mechanisms that could help to improve well-being in psychiatric and neurodegenerative dysfunctions of self-generated thought; and (3) integrate empirical work that can lay the foundation for an affective neuroscience of self-generated thought.

A note on terminology

A brief discussion of terminology at the outset will help clarify what we mean by “self-generated thought.” In line with our previous work in this area, we use this as an umbrella term to refer broadly to cognition, imagery, and emotions that are largely independent of the external environment and sensory stimuli.^{6,8,23,24} Self-generated thought can be *spontaneous* (i.e., not controlled, directed, or initiated in a deliberate, top-down manner)^{1,5} or intentionally directed. Self-generated thought can also be *automatically* constrained by bottom-up factors such as perceptual or affective salience⁵ or habitual patterns of thinking.²⁵ Self-generated thought therefore includes predominantly unconstrained forms of cognition like dreaming, mind-wandering, and creative thinking, but also automatically constrained cognition such

as rumination and obsessive thinking, or other habitual patterns of thought (Fig. 1).^{5,25}

In experimental contexts, self-generated thought has so far been primarily operationalized as thought that is task-unrelated (or “off-task”), stimulus-independent, or spontaneously arising,^{26–28} but the interrelations between these different dimensions of thought are complex and our scientific understanding of them continues to evolve. Off-task thought, for example, has until recently been assumed to be undirected, but recent research has shown that a considerable proportion (perhaps as much as one-third^{29–31}) of off-task thinking is at least *initiated* intentionally³² (the question of how much control is exerted over the subsequent stream of thought remains largely unexplored³¹). The term mind-wandering is also often employed, but its various definitions and operationalizations have not yet fully taken into account its relationship to the many dimensions of self-generated thought. For instance, most studies define mind-wandering simply as off-task thought,³³ but being off-task is only one of many possible dimensions of thought; results from detailed experience sampling show that whether or not thoughts are off-task does not correlate strongly with how *freely moving* they are³³ (i.e., to what degree they lack deliberate or automatic constraints; cf. Fig. 1). Although much of what we believe we know about mind-wandering has been gleaned from studies of off-task thought, just as much can be learned with task-free paradigms involving periods of unstructured “resting state” cognition.^{13,17,31}

We have recently advanced a framework that embraces various kinds of self-generated thought, from the fully spontaneous to the more intentionally directed and automatically constrained (Fig. 1).⁵ In this context, mind-wandering denotes a specific cognitive mode that falls in the middle of a state space, flanked on one side by more spontaneous and unconstrained forms of cognition (such as dreaming and psychosis), and on the other by more automatically and deliberately constrained forms of cognition (such as rumination or goal-directed thought, respectively. See Fig. 1). Throughout this review, we therefore discuss the results of each study in terms of what was experimentally measured, rather than necessarily employing the terminology used by the original authors. Our intended meaning of *self-generated thought* encompasses a cognitive state space that morphs gradually from

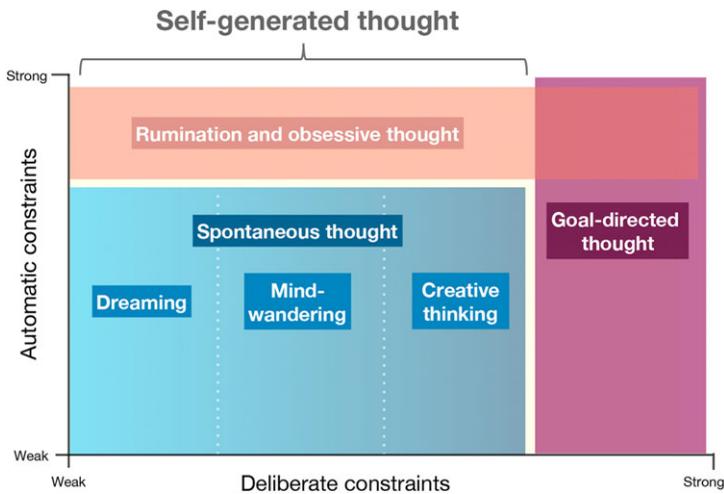


Figure 1. Conceptual space relating the concept of self-generated thought to deliberate and automatic constraints on cognition. Self-generated thought, by which we mean all those types of thought that are relatively independent of the external environment and immediate sensory inputs, spans a broad cognitive state space. Within this cognitive state space, both deliberate (intentional, top-down) and automatic (unconscious, bottom-up) constraints can influence the content of thought. “Spontaneous” thought is not only self-generated, but is also specifically characterized by relatively weak deliberate and automatic constraints. Rumination and obsessive thought are likewise self-generated and low in deliberate constraints, but are characterized by strong automatic constraints. Modified with permission from Ref. 5.

spontaneous to more constrained forms of thought, rather than drawing sharp boundaries within that space (Fig. 1).

It is also important to describe the way we use the term “affect” throughout this paper. Here, we use *affect* to broadly encompass features of emotions, moods, and other affective states. We acknowledge the ongoing debates about the conceptualization of emotions and ways of describing the underlying structure of affect,^{34–37} but our aim here is not to draw distinctions between different approaches or discuss any particular theories in detail. Rather, our goal is to synthesize the available literature that considers any aspect of emotion, affect, or mood as it relates to self-generated thought. It will become clear throughout this review, however, that the majority of studies to date have focused on just a single dimension of affect—valence—and that an important goal for future research will be to develop a more nuanced picture considering various other dimensions (e.g., level of arousal and diversity of emotions).

Affect in the self-generated thought of healthy populations

A variety of research methods have been employed to investigate the affective qualities of self-

generated thought in healthy (i.e., nonclinical) populations. These include studies using experience-sampling methods in everyday life via smartphones,^{16,38} investigations in psychological laboratory settings,^{39,40} and more recently, functional neuroimaging investigations.^{13,15}

Across a dozen independent studies involving more than 5000 participants to date, investigations in disparate settings and across different task paradigms yield some consistent conclusions (summarized in Table 1 and Fig. 2). First, across all methodologies, self-generated forms of thought are rated as mildly pleasant, positive, and enjoyable, on average. In other words, self-generated thoughts, on average, display a mild positive affect bias. Proportionally, most self-generated thought is neutral or positive in valence, with a minority being negatively valenced.

Only a single study deviates somewhat from this trend.⁴¹ Consistent with the high proportion of neutral thought found in other studies,¹⁶ Banks and colleagues⁴¹ found that neutral off-task thoughts occurred significantly more frequently than valenced off-task thoughts in three datasets (but did not ask for ratings on a scale and are thus not included in Table 1 or Fig. 2). However, they also found significantly more negative versus

Table 1. Studies directly examining the affective content of various forms of self-generated thought

Study	N	Setting/method	Dimension measured	Summary of emotional valence findings ^a
Killingsworth and Gilbert ¹⁶	2250	Real-world/experience sampling via smartphones	Task-unrelated thought	Of all “mind-wandering” episodes, 42.5% were rated as “pleasant;” 31.0% as “neutral;” and 26.5% as “unpleasant” Participants were also asked: “How are you feeling right now?” and answered on a scale from (0 = very bad to 100 = very good) A weighted average was used to compute the average happiness rating from the numbers reported in the paper: estimated $M = 58$.
Stawarczyk <i>et al.</i> ⁴⁰	53	Laboratory/SART with thought probes	Stimulus-independent task-unrelated thought	On a scale of -3 (“very negative”) to $+3$ (“very positive”), the mean rating was 0.62 (1.25) and 0.19 (0.88), respectively, for the two experimental groups (i.e., mildly positive in both cases)
Song and Wang ³⁸	165	Real-world/experience sampling via smartphones	Task-unrelated thought	On a 1–5 scale (1 = “negative;” 3 = “neutral;” 5 = “positive”), mean rating was 3.32 (i.e., mildly positive) ^c
Andrews-Hanna <i>et al.</i> ⁴²	76	Laboratory/thought sampling paradigm	Recalled thoughts recently on their mind in daily life	On a 0–10 scale (0 = “very negative;” 5 = neutral; 10 = “very positive”), average rating of spontaneous thoughts was 5.9 (i.e., mildly positive)
Diaz <i>et al.</i> ¹⁵⁷	1367 813 ^b	Home setting, laboratory, and MRI scanner/retrospective survey about thoughts and feelings (ARSQ)	Task-free thinking period	Numerous questions asked on a 5-point (1–5) scale (1 = “completely disagree;” 5 = “completely agree”); most relevant questions: “I felt happy”: $M = 3.3$ (0.9) “I enjoyed the session”: $M = 3.0$ (1.1) “I had negative feelings”: $M = 1.80$ (1.0)
Poerio <i>et al.</i> ²⁰	24	Real world/experience sampling via smartphones	Task-unrelated thought	On a scale of 1 (happy) to 5 (sad), the mean rating was 2.58 (i.e., mildly positive) <i>during</i> task-unrelated thought, $M = 2.51$ before, and $M = 2.40$ after
^c Ruby <i>et al.</i> ¹⁰⁹	85	Laboratory/choice reaction time task/thought-sampling paradigm	Task-unrelated thought	On a 1–9 scale (1 = “not at all,” 9 = “completely”), average rating in response to the question “How positive were your thoughts?” was approximately 6 (estimated from their fig. 3A). Average rating in response to the question “How negative were your thoughts?” was approximately 3.4. Thoughts were significantly more positive than negative ($t(82) = 9.39$, $P < 0.001$).

Continued

Table 1. *Continued*

Study	N	Setting/method	Dimension measured	Summary of emotional valence findings ^a
Stawarczyk <i>et al.</i> ³⁹	67	Laboratory/SART with thought probes	Stimulus-independent task-unrelated thought	On a scale of -3 (“very negative”) to +3 (“very positive”), the mean rating for future-oriented spontaneous thoughts was 0.57 and for nonfuture-oriented thoughts, 0.46 (i.e., mildly positive in both cases)
Gorgolewski <i>et al.</i> ¹³	166	MRI scanner/retrospective survey about thoughts and feelings (NYC-Q)	Task-free thinking period	On a 1–9 scale from “completely did not describe my thoughts” to “completely did describe my thoughts”: “I thought about something that made me happy”: $M = 5.17$ (2.03) “I thought about something that made me cheerful”: $M = 5.19$ (3.05) “I thought about something that made me sad”: $M = 3.12$ (2.04)
Tusche <i>et al.</i> ¹⁵	30	MRI scanner/thought-sampling paradigm	Task-free thinking period	On a scale of -3 (negative valence) to +3 (positive valence), the mean rating was 0.77 (0.52) (mildly positive)
Wilson <i>et al.</i> ¹⁷	220	Mixed laboratory setting and home/retrospective survey about thoughts and feelings	Task-free thinking period	On a 1–9 scale of how “enjoyable” spontaneous thinking was (1 = “not at all enjoyable;” 5 = “somewhat enjoyable;” 9 = “extremely enjoyable”), the mean rating was 5.21 (i.e., “somewhat enjoyable”). On a similar 1–9 scale of how “entertaining” it was, the mean rating was 4.24 (i.e., “somewhat entertaining”)
Choi <i>et al.</i> ²³⁶	603	Real-world/experience sampling via smartphones	Task-unrelated thought	Participants were asked: “How are you feeling at the present moment?” and answered on a scale from (0 = very bad to 100 = very good) $M = 58.04$, $SD = 22.06$

^aStandard deviation values are given in brackets for each mean score, when these data were available in the original publications.

^bA subset of participants were used in Diaz and colleagues¹⁵⁷ data analyses after screening participants on five validation items of the ARSQ.

^cPrecise numerical values were not provided in this study, and were conservatively estimated from figure 3A in Ruby and colleagues.¹⁰⁹ ARSQ, Amsterdam Resting-State Questionnaire; MRI, magnetic resonance imaging; NYC-Q, New York Cognition Questionnaire; SART, sustained attention to response task.

positive off-task thoughts in one of their three studies (but no significant difference between them in their other two datasets). To our knowledge, this is the only published result that contradicts the positivity bias noted throughout the rest of the literature on affect and self-generated thought. However, it is important to note that the sample size was relatively small ($N = 53$), relatively few thought probes were administered ($N = 12$), and two other studies from the same article did not replicate this finding. These

divergent results⁴¹ therefore do not seem to provide a substantial counterpoint to the large and growing body of research suggesting the opposite trend (Table 1; Fig. 2).

A second broad conclusion to be drawn is that the “positive” averages reported in numerous studies are observed in the context of high intra and interindividual variability. Individuals’ average emotional experiences during self-generated thought differ widely from one another, with people falling along

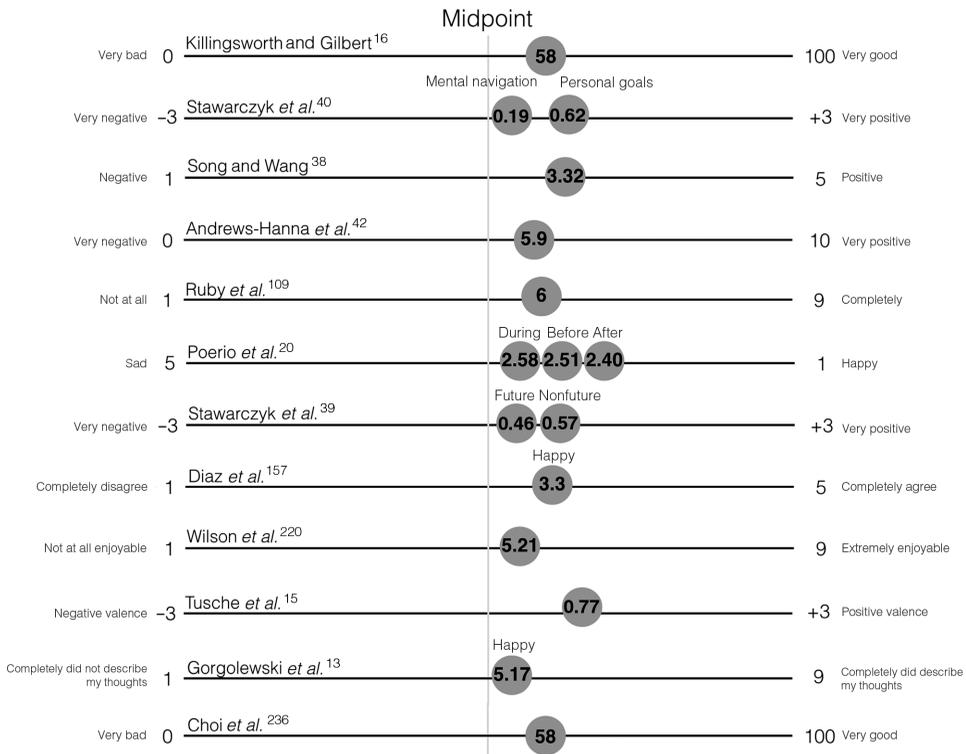


Figure 2. Summary of average affective valence in 12 studies of self-generated thought.

Mid-points of all scales are centered for comparison purposes. Anchors and scales were presented in the original studies as shown here, with the original labels reproduced. Mean ratings are indicated in solid gray circles with numeric values from the original datasets, except for Killingsworth and Gilbert,¹⁶ which was computed from their raw supplementary data.

a broad spectrum⁴² (i.e., variance associated with mean ratings tends to be high, for instance, a standard deviation of 1.25 on a 7-point scale⁴⁰). Moreover, any given individual’s thought valence (from positive through neutral to negative) can vary widely in the course of a single day⁴³ or even a brief (45 min) session of thought-sampling.³¹

There have also been a number of investigations of how affect relates to other qualities of self-generated thought. For instance, research has shown a relationship between negative mood and a retrospective temporal bias in mind-wandering,⁴⁴ whereas all else being equal there is normally a prospective temporal bias to mind-wandering.⁴⁵ Affect can also be related to the sensory modality of self-generated thought: for instance, negative affect correlates with increased narrative (verbal/auditory) thought, whereas positive affect correlates with thoughts that are more visual in nature.¹³

The ubiquity of emotion in self-generated thought (roughly two-thirds of all reports¹⁶) sug-

gests that it should regularly recruit brain areas and networks implicated in emotional processing. Recent functional connectivity-based parcelations of the human brain have delineated brain networks critically involved in emotion, most notably a “limbic” network that includes the medial orbitofrontal/ventromedial prefrontal cortex, temporopolar cortex (BA 38), ventral striatum, and aspects of the medial temporal lobe,^{46,47} and a “salience” network that includes the anterior insula, lateral orbitofrontal cortex (OFC), anterior and mid-cingulate cortex, amygdala, and hypothalamus.⁴⁸ The broad importance of these networks in emotion is corroborated by detailed reviews and fMRI meta-analyses of tasks evoking different types of emotional experience.^{49–56} A meta-analysis of functional neuroimaging studies recently conducted by our group found that elements of limbic, salience, and other networks (i.e., default and frontoparietal) that may interact during the construction of emotional experiences⁵⁷ were

consistently recruited by self-generated forms of thought.⁴ Meta-analytic methods also have important limitations, however, and so here we compile a list of affect-related brain areas and their recruitment in studies of various kinds of self-generated thought in waking and sleeping to give a sense of the frequency of activation of these areas in independent studies (Table 2 and Fig. 3). We use neuroimaging studies of rapid-eye-movement (REM) sleep as the best available (if admittedly limited) proxy for the psychological experience of dreaming, which we consider a form of self-generated thought; we have advanced detailed arguments for both of these decisions elsewhere.^{5,9,58,59}

An important point to note immediately is the apparently greater recruitment of affect-related areas in waking self-generated thought, especially more frequent recruitment of the insula, temporopolar cortex, and pregenual anterior cingulate cortex (pgACC) (Table 2 and Fig. 3). These apparent differences are misleading, however, for at least two reasons. First, there are far fewer neuroimaging studies of REM sleep conducted to date with readily comparable contrasts of interest,^{9,23} limiting the reported recruitment of affect-related regions. Second and more important, in all of the studies we explored, REM sleep was compared to waking rest as a baseline for consistency. Although self-generated thought during waking was not explicitly examined in any of these investigations, it is reasonable to assume that both pre and postsleep waking “rest” were accompanied by relatively high levels of self-generated thought of one kind or another. Given this analysis strategy, recruitment during REM sleep implies activations *greater than* activation during waking self-generated thought.⁹ The simplest interpretation, therefore, is that the amygdala, caudate nucleus, medial temporal lobe, and left OFC are *more* active during REM sleep than during waking self-generated thought, whereas activations in other areas are approximately equal in both states. Further subtleties must be accounted for, however—for instance, deactivations in REM sleep relative to waking rest.⁹ Pending a careful and detailed comparison of waking and sleeping self-generated thought, the above findings should be interpreted with caution.

The precise emotional (and/or other) functions of these various areas remain a matter of debate, but some tentative roles can be delineated. The lateral and medial OFC operate along-

side the amygdala and have long been associated with value-based appraisal and decision-making processes.^{60–63} The medial OFC may be especially relevant to *understanding* the affective qualities of self-generated thought, given that it plays a key role in assigning value to imagined scenes^{49,64} and autobiographical memories.⁶⁵ The rostromedial prefrontal cortex (RMPFC) is hypothesized to be preferentially involved in processing the self-relevance of self-generated thought and integrating a higher order emotional-evaluative response to this content.^{49,66–69} For example, self-generated thought often pertains to self-image and other people’s perceptions of the self, and the RMPFC appears to play a key role in assigning positive and negative value to the self.⁴⁹ While self-evaluations and RMPFC activation often display a positivity bias,⁷⁰ studies of rumination and maladaptive self-referential processing have also implicated the RMPFC.^{71–73}

The insula, on the other hand, is thought to be more involved in viscerosomatic sensations (cardiac, respiratory, etc.) and feeling states; such sensations might trigger, or be elicited by, mental content, including self-generated thoughts.^{27,74–78} A complementary role has been proposed for the insula in detecting and signaling affective salience.^{48,79,80} Existing work suggests that viscerosomatic information becomes progressively refined from the posterior to anterior insula, with the latter playing a key role in interoceptive awareness.^{53,78} Accordingly, the anterior insula may contribute to the extent to which thoughts trigger, or are triggered by, physiological arousal and other concrete bodily feelings. The pgACC is also involved in emotional feeling states, evidenced by activation patterns that correlate with the pleasantness and aversiveness of stimuli.^{81–83} However, its role appears to be specifically related to the process of attributing conceptual meaning to bodily sensations and interweaving feeling states with self-referential thinking.⁴⁹ For example, pgACC recruitment is associated with the capacity to label and understand feeling states.^{84–86}

Regions within the basal ganglia, including the caudate nucleus, putamen, and nucleus accumbens, are part of dopaminergic midbrain-striatal pathways that are involved in motivational drive and reinforcement learning.^{87–91} These regions are important for learning about the relationship between actions and reward/punishment via signaling prediction errors that represent discrepancies

Table 2. Neuroimaging studies of waking self-generated thought and REM sleep showing activations in affect-related brain regions

Brain region ^a	Waking self-generated thought ^b [Hemisphere]	REM sleep (~80% chance of dreaming) ^c [Hemisphere]
Amygdala	Mason <i>et al.</i> ²⁶ [R] Stawarczyk <i>et al.</i> ²³⁷ [L]	Maquet <i>et al.</i> ¹⁹⁹ [L + R] Nofzinger <i>et al.</i> ²³⁸ [L]
Caudate nucleus	Christoff <i>et al.</i> ²³⁹ [L] Stawarczyk <i>et al.</i> ²³⁷ [L]	Braun <i>et al.</i> ²⁴⁰ [L] Nofzinger <i>et al.</i> ²³⁸ [L] Finelli <i>et al.</i> ²⁴¹ [L] Fox <i>et al.</i> ⁹ [L]
Hypothalamus	Stawarczyk <i>et al.</i> ²³⁷ [R]	Nofzinger <i>et al.</i> ²³⁸ [R]
Insula	Christoff <i>et al.</i> ²⁴² [L] Mason <i>et al.</i> ²⁶ [L + R] Christoff <i>et al.</i> ²³⁹ [L + R] Dumontheil <i>et al.</i> ²⁴³ [R] Hasenkamp <i>et al.</i> ²⁴⁴ [L + R] Fox <i>et al.</i> ⁴ [L] Ellamil <i>et al.</i> ²⁷ [L + R]	Nofzinger <i>et al.</i> ²³⁸ [L + R]
Medial temporal lobe (excluding amygdala; including hippocampus, parahippocampus, and entorhinal cortex)	Binder <i>et al.</i> ²⁴⁵ [L] Christoff <i>et al.</i> ²⁴² [L + R] Mason <i>et al.</i> ²⁶ [L] Christoff <i>et al.</i> ²³⁹ [L] Wang <i>et al.</i> ²⁴⁸ [L] Stawarczyk <i>et al.</i> ²³⁷ [L] Hasenkamp <i>et al.</i> ²⁴⁴ [L + R] Kucyi <i>et al.</i> ²⁴⁹ [L + R] Fox <i>et al.</i> ⁴ [L] Ellamil <i>et al.</i> ²⁷ [L + R]	Braun <i>et al.</i> ²⁴⁰ [L] Nofzinger <i>et al.</i> ²³⁸ [L + R] Braun <i>et al.</i> ²⁴⁶ [R] Peigneux <i>et al.</i> ²⁴⁷ [R] Fox <i>et al.</i> ⁹ [L + R]
Orbitofrontal cortex	Binder <i>et al.</i> ²⁴⁵ [L] D'Argembeau <i>et al.</i> ²⁵⁰ [L + R] Spiers and Maguire ²⁵¹ [L] Dumontheil <i>et al.</i> ²⁴³ [R] Stawarczyk <i>et al.</i> ²³⁷ [L] Hasenkamp <i>et al.</i> ²⁴⁴ [L + R] Kucyi <i>et al.</i> ²⁴⁹ [L] Fox <i>et al.</i> ⁴ [L]	Nofzinger <i>et al.</i> ²³⁸ [L] Braun <i>et al.</i> ²⁴⁶ [L] Fox <i>et al.</i> ⁹ [L]
Pregenuan anterior cingulate cortex/ rostromedial prefrontal cortex	McGuire <i>et al.</i> ²⁵² [L] Mason <i>et al.</i> ²⁶ [R] Christoff <i>et al.</i> ²³⁹ [R] Fox <i>et al.</i> ⁴ [L + R]	Braun <i>et al.</i> ²⁴⁰ [R] Finelli <i>et al.</i> ²⁴¹ [L] Fox <i>et al.</i> ⁹ [L + R]
Temporopolar cortex	Christoff <i>et al.</i> ²⁴² [L + R] Spiers and Maguire ²⁵¹ [L] Christoff <i>et al.</i> ²³⁹ [L + R] Dumontheil <i>et al.</i> ²⁴³ [L + R] Fox <i>et al.</i> ⁴ [L] Ellamil <i>et al.</i> ²⁷ [L + R]	–
Ventral striatum	Mason <i>et al.</i> ¹⁸ [L + R]	Nofzinger <i>et al.</i> ²³⁸ [L + R]

^aA list of affect-related brain regions was compiled based on numerous in-depth reviews and meta-analyses (cited in the text).

^bDrawn from a list of whole-brain functional neuroimaging studies investigating some form of waking self-generated thought, as compiled in our group's recent meta-analysis.⁴

^cDrawn from a list of whole-brain functional neuroimaging studies investigating REM sleep, as compiled in our group's recent meta-analysis.⁹

L, left; R, right.

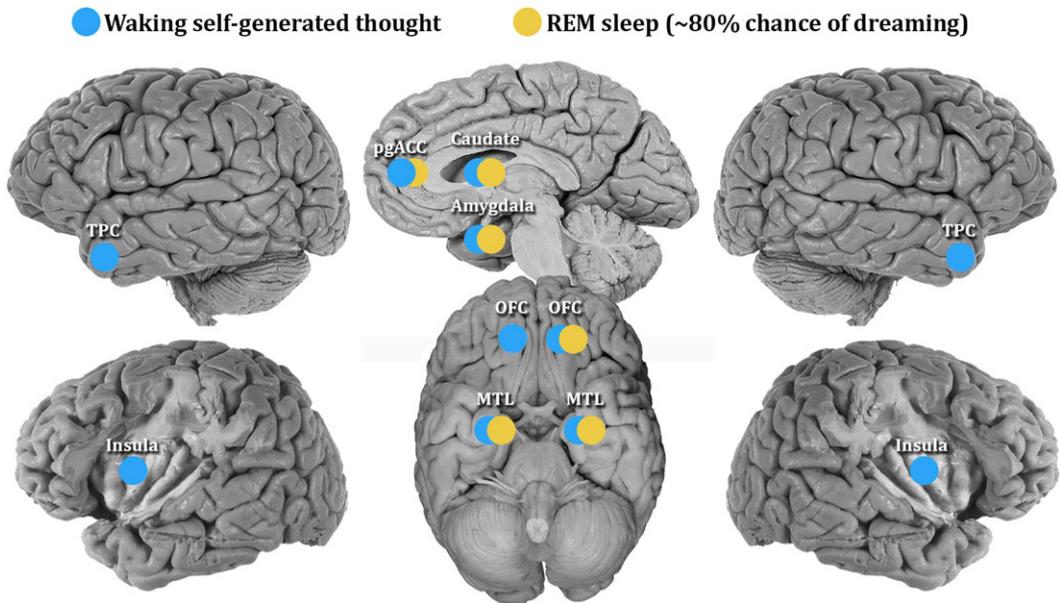


Figure 3. Affect-related brain regions recruited in waking self-generated thought and REM sleep. Affect-related brain regions recruited in waking self-generated thought (blue circles) or REM sleep (yellow circles), which is accompanied by self-generated thought and imagery (dreaming) ~80% of the time. Region labels are intended to be illustrative only and are not precise or based directly on coordinates. Figure based on data in Table 2: data are visualized where at least one general replication of a finding was observed (i.e., where two studies showed recruitment of the same broad region in the same hemisphere). The medial sagittal slice is shown only once to avoid redundancy as these regions generally showed bilateral recruitment (amygdala and pgACC); the exception is the caudate, which showed only left-lateralized recruitment. Note that the apparently greater recruitment of affect-related areas in waking self-generated thought is misleading because (1) there are far fewer neuroimaging studies of REM sleep and (2) REM sleep was compared to waking rest as a baseline, which implies high levels of self-generated thought. See text for further discussion. MTL, medial temporal lobe; OFC, orbitofrontal cortex; pgACC, pregenual anterior cingulate cortex; REM, rapid-eye-movement; TPC, temporopolar cortex.

between expected and experienced outcomes.^{92–94} This circuitry might bias the stream of thought toward a particular topic when a new thought is positive or negative.⁵ Other subcortical regions including the hypothalamus and periaqueductal gray directly contribute to the embodied aspect of emotion via the orchestration of patterned physiological responses (e.g., coordinated changes in heart rate, blood pressure, and hormone levels) to cope with emotionally significant events.^{95–97} Self-generated thought may therefore be especially likely to grab the reins of attention when subcortical regions are recruited and elicit changes in physiological arousal.

Finally, temporopolar cortex, although relatively poorly understood as a region, is hypothesized to act as a “paralimbic” area working closely with more canonical limbic areas.^{98,99} Temporopolar cortex shows dense anatomical interconnections to OFC, the insula, the amygdala, and other medial tempo-

ral lobe structures.^{98,100–102} A proposed role of this region is in binding visceral-affective assessments with highly processed perceptual information—that is, integrating affect with perception, presumably in the service of higher order decision making.⁹⁸ Recent work also suggests a causal role for temporopolar cortex in the initiation/creation of self-generated thought.^{8,24,103}

Two recent functional neuroimaging studies have more directly investigated neural correlates of affect in self-generated thought. A study by Tusche and colleagues¹⁵ used multivariate pattern analysis to investigate the emotional content of thoughts during unconstrained, task-free rest periods where participants simply stared at a fixation cross for 9 min in the MRI scanner and were occasionally interrupted by thought probes.¹⁵ The authors found that patterns of activity within the medial OFC predicted the valence (positive versus negative) of thoughts—not just during the initial session, but also at a follow-up

scanning session 1 week later.¹⁵ These findings support the notion (advanced above) that this region plays a role in assigning value to thoughts, including imagined events and memories.

Another relevant study collected detailed retrospective reports of self-generated cognition using a novel questionnaire and correlated these self-reported thought tendencies with intrinsic resting state brain activity in a large sample (N = 166) of participants.¹³ The authors reported that variation in low-frequency fluctuations in the dorsomedial prefrontal cortex and pgACC correlated negatively with the frequency of positively valenced thoughts, whereas positive associations were observed in medial occipital areas.¹³ The authors noted that their findings were congruent with meta-analyses showing consistent activation of visual cortices associated with positive affect.^{104,105} Moreover, they found a positive correlation between the fractional amplitude of low-frequency fluctuations in the cerebellum and the frequency of negatively valenced thought.¹³ The authors' observations of significant relationships with activity throughout default, visual, and subcortical regions corroborate a central hypothesis of this review, namely that the instantiation of affect in self-generated thought is likely to be a complex process involving distributed brain systems, warranting and requiring detailed investigation. In summary, the widespread recruitment of limbic and paralimbic brain regions in self-generated thought is consonant with the generally high levels of affect reported by nonclinical populations, but direct investigations specifically linking self-generated emotional thought to brain recruitment are still scarce, and much more work is needed along these lines. In particular, future work would benefit from testing targeted hypotheses about the roles played by different brain regions in the various affective qualities of self-generated thought.

Negatively biased self-generated thought: importance of state, trait, and clinical factors

The literature reviewed above (Table 1; Fig. 2) shows that the self-generated thought of healthy, nonclinical populations is characterized by a mild positivity bias on average. As noted above, however, these averages are accompanied by high variability both within and across individuals. Understanding the sources of such variability could shed important light on

the adaptive versus maladaptive roles of affect in self-generated thought and might elucidate interventions to improve well-being. Below, we review state- and trait-level factors (and associated neural underpinnings) that moderate the affective nature of task-unrelated and other forms of self-generated thought, beginning with factors biasing individuals toward negative thoughts.

State affect and other contextual factors can bias self-generated thought toward negative content

Although an established body of research has shown that one's affective state, or mood, can bias attention to negative stimuli,^{79,106–108} relatively few studies have examined relationships between state affect and the affective content of self-generated thoughts. Of these studies, some have found that individuals who score higher on constructs related to depression and trait negative affect on questionnaires also rate their self-generated thoughts as more negative in valence.⁴² More promising within-subject evidence comes from longitudinal paradigms that assess state affect and thought content across multiple time-points in daily life. These studies suggest that negative affect occasions are associated with an increased likelihood of negative task-unrelated thought,^{16,38} and that task-unrelated thought is associated with lower positive affect than attending to the task at hand, regardless of its affective valence.¹⁶ Such findings invite the question: is negative mood a cause or a consequence of negative cognition? Poerio and colleagues²⁰ addressed this question using time-lag analyses across short intervals (15 min) and found that self-generated thoughts were only predictive of subsequent negative moods when the content of the self-generated thought was sad. Overall, there is little evidence for the assertion that task-unrelated thought is a causal factor in subsequent negative mood. Instead, the relationship is more nuanced and dependent on various factors, such as the content of the thoughts (e.g., sad content²⁰ or past/other-related content¹⁰⁹) and the depressive symptomology of the individual in question.¹¹⁰

Experimental induction paradigms represent another promising avenue to assess causal relationships between state affect and the affective content of self-generated thought. A typical mood induction paradigm assesses affect and self-generated thoughts before and after prompting participants

to recall emotional memories or attend to emotional stimuli such as sad movies or music.^{111,112} Interestingly, paradigms designed to induce a negative mood increase the overall frequency of self-generated thought during experimental tasks,^{113,114} especially past-oriented content.⁴⁴ Similarly, self-focused rumination induction paradigms, in which individuals are asked to meta-cognitively reflect on their feelings and the causes or consequences of such feelings,¹¹⁵ increase negative thought content in individuals with high dysphoria.^{115,116} Paradigms used to induce worry, such as reflecting on a personal concern involving the future,¹¹⁷ or requiring participants to give an upcoming speech to a panel of judges, have also been shown to increase the frequency of self-generated cognition,³⁹ particularly negatively valenced cognition.^{118–120} These mood- and worry-induction paradigms have physiological concomitants: in one recent study, for instance, individuals who rated their thoughts as more negative in valence while anticipating a speech exhibited greater cortisol levels both at baseline and after the stress period.¹²¹ In summary, these studies suggest that one's affective state—whether in the laboratory or in daily life—can both bias, and be biased by, the affective content of self-generated thoughts. While the relationship between affective state and the affective content of self-generated thoughts likely depends on interactions between default, salience, and limbic networks, regions of the default network might play an especially important role. The pgACC and RMPFC in particular contribute to affective valuation^{122,123} and self-referential thought,^{124–126} and might be key cortical sites at which emotional feelings become intertwined with self-generated thoughts.⁴⁹

Depression, anxiety, and trait rumination can bias individuals toward negative self-generated thought

Accompanying this within-subject variability in affective thought content is substantial variability across individuals. Below, we summarize the importance of clinical factors and trait-like dispositions as a major source of this interindividual variability.

Alterations in thought content are a defining characteristic of numerous mental health disorders,¹²⁷ and negative content biases are most appreciated in major depressive disorder (MDD)¹²⁸ and generalized anxiety disorder. Cognitive theories

of depression emphasize the importance of negative schemas¹²⁹ and attentional biases toward negative stimuli and the self.^{130–134} Clinically depressed and dysphoric individuals exhibit elevated levels of off-task thought^{135–138} and often engage in repetitive negative thinking.^{139,140}

Even among nonclinical samples, participants reporting higher depressive symptoms and/or trait neuroticism rate their self-generated thoughts as more negative^{17,42,141,142} and more personally significant.⁴² These findings dovetail well with the notion that subclinical depression moderates the relationship between task-unrelated thought and subsequent negative thoughts, presumably because the content is frequently negative. For instance, a recent study found that rate of task-unrelated thought positively predicted negative cognitions after a task, but only for individuals who scored higher on a depressive symptom scale (at least 1 SD above the mean).¹¹⁰

Depressive rumination, a style of self-focused thinking centering on the causes and consequences of one's depressed mood,¹⁴³ is common in MDD and exacerbates its symptoms (reviewed in Ref. 145). Repetitive negative thought is also a common feature of anxiety disorders, especially generalized anxiety disorder.¹²⁷ In such disorders, repetitive negative thoughts often manifest as severe worry over what the future might hold.^{145,146} Along these lines, recent theoretical work suggests that self-generated thought may serve as a direct precursor to cognitive vulnerabilities (e.g., hopelessness, lowered self-esteem, and heightened rumination) in individuals with mood disorders.¹⁴⁷ Specifically, this framework builds on empirical work^{31,148,149} to propose that self-generated thoughts frequently contain evaluations and simulations of one's personal goals, and that the individuals with mood disorders may experience negative affect when goal discrepancies inevitably arise. This negative affect then facilitates cognitive vulnerability, which can further aggravate depression or other mood disorders.¹⁴⁷

Despite the wealth of experimental evidence for negative affective biases in depression and anxiety, few studies have used moment-to-moment experience sampling to examine the affective nature of self-generated thoughts in these clinical populations in the laboratory or in daily life. Assessing self-generated thoughts *in the moment* is critical, particularly in mental health disorders such as MDD,

where retrospective reports of thought content might be distorted by mnemonic biases or impairments and alterations in meta-awareness.^{150,151} The rise of smartphone technology provides a promising platform to more accurately assess self-generated thought content in real-time and in the more ecologically valid setting of everyday life.¹⁵² Additionally, it will be important to examine the relationship between viscerosomatic sensations and self-generated thought. Viscerosomatic sensations are a central component of emotional experience and are robustly represented in the brain via spinothalamic and vagus nerve pathways.^{153,153–155} Novel insights into the relationship between affective states and self-generated thought patterns in health and disease might therefore be gleaned by giving greater consideration to the bi-directional feedback loops between brain and body—especially given that thoughts about the body make up a considerable portion of self-generated thought content.^{27,156,157}

This psychological research on negatively biased self-generated thought has been paralleled by some preliminary investigations into its associated neural underpinnings. Both MDD and anxiety disorders are associated with alterations in large-scale brain systems important for internally oriented thought, attention, and emotion. For instance, when processing negative stimuli in the context of experimental tasks, depressed individuals exhibit greater activity in a network of regions associated with emotional salience—including the insula, dorsal anterior cingulate cortex, and amygdala—and lower activity in dorsolateral prefrontal and striatal regions important for emotion regulation and motivation.¹⁵⁸ Similarly, individuals with anxiety commonly exhibit hyperactivity of the salience network during anxiety-provoking tasks.^{159–161} During external attentional tasks involving nonemotional stimuli, both depressed individuals and nondepressed individuals who ruminate fail to fully deactivate key default network regions.^{162,163} This pattern of hyperactivity is accompanied by increases in resting-state functional connectivity among key default network regions; reduced connectivity between the medial prefrontal cortex and the nucleus accumbens and amygdala; and biased coupling of frontoparietal control systems with the default network and away from the dorsal attention network.^{133,164,165} Together, these results support a neurocognitive model in which depression is

characterized by heightened salience processing (especially in relation to negative information), and biased attention toward internal thoughts and away from the external environment.^{110,133,134,162}

Despite the growing number of studies examining functional alterations during cognitive tasks or the “resting state” in MDD and anxiety (Fig. 4), studies directly linking thought content to patterns of brain activity are scarce. One relevant study suggested that while patterns of default network and global functional connectivity indeed differed between depressed and nondepressed individuals at rest, such differences were enhanced following a rumination induction procedure in which individuals were asked to recall negative autobiographical memories.¹⁶⁶ Although some patterns of connectivity were also linked to individual differences in mood, the authors did not directly assess thought content during the rest epochs. Another study showed that depressed individuals scoring higher on a questionnaire assessing maladaptive forms of trait rumination exhibited greater default network “dominance” during rest periods, but thought characteristics during the scanning session were not assessed.¹⁶⁷ Of relevance to anxiety disorders, healthy individuals reporting greater prescan anxiety exhibit greater functional connectivity within the salience network during a period of awake rest.⁴⁸ In summary, preliminary neuroimaging analyses from state- and trait-level factors suggest that biases toward negative thought content are linked to heightened activity in emotional salience regions in response to negative stimuli, and heightened activity and connectivity in default network regions important for self-related processing and rumination.^{128,147}

Positively biased self-generated thought

Just as patients with MDD appear to have an overall negativity bias affecting their self-generated thought content compared to nonclinical populations, it is possible that certain populations might have positively biased self-generated thought. This possibility has been investigated in self-reported “excessive” daydreamers who report elevated levels of highly rewarding self-generated thought,^{18,168,169} as well with respect to the present-centered, nonjudgmental quality of awareness known as “mindfulness” cultivated in various meditation traditions.^{170,171}

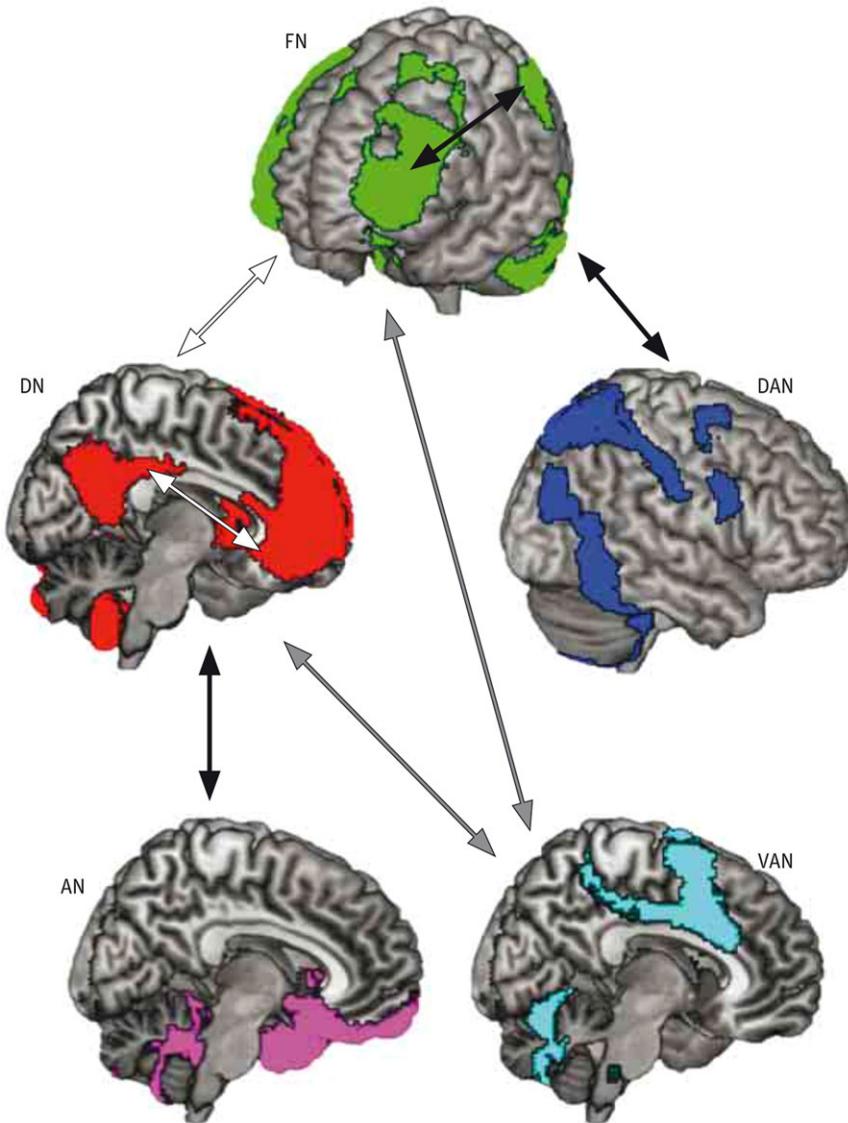


Figure 4. Large-scale brain network alterations in major depressive disorder. Individuals with MDD exhibit alterations in resting state functional connectivity within and between several large-scale brain networks, including the frontoparietal control network (FN), the default network (DN), the dorsal attention network (DAN), the affective network (AN), and the ventral attention network (VAN), or “salience network.” White arrows indicate hyperconnectivity in depressed versus nondepressed individuals, black arrows indicate hypoconnectivity, and gray arrows indicate generally altered connectivity. Note that depressed individuals exhibit greater connectivity within the DN and disproportionately greater connectivity between FN and DN versus FN and DAN, supporting a model of biased attention toward self-generated cognition. Figure reproduced, with permission, from Ref. 133.

Highly rewarding self-generated thought in “excessive” daydreamers

Several cases have been reported over the years of individuals who engage in immersive and highly rewarding daydreaming or fantasizing, but these reports have been mostly anecdotal. Lynn and Rhue,

for instance, discussed persons with “a deep and profound involvement in fantasy or imagination,”¹⁶⁹ and others have suggested that these “high fantasizers” may account for as much as 4% of the general population.¹⁶⁸ This daydreaming has been labeled “excessive” based on the observation that such

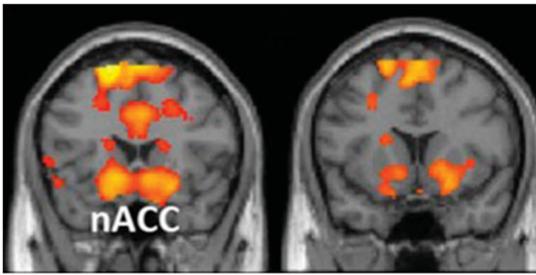


Figure 5. Brain activation associated with highly rewarding self-generated thought in an “excessive” daydreamer. Note the recruitment (among other areas) of the nucleus accumbens, an area critically implicated in reward processing. Reproduced, with permission, from Ref. 18.

persons “may devote as much as 50% of their waking time to daydreaming,” although it is not clear that this label is necessarily appropriate or endorsed by the persons experiencing highly rewarding and frequent daydreaming. In the case of one well-studied patient, “her main goal from childhood through the present has been to accommodate her ‘real world’ obligations in order to re-enter her compelling imaginary life” (Ref. 169, p. 291). The frequent daydreaming of these individuals differs from typical self-generated thought (which also occurs frequently) in that it is highly immersive as well as highly rewarding and enjoyable; negative feelings associated with this phenomenon have more to do with the social embarrassment or guilt associated with these excessive fantasies, as opposed to the content of the fantasies themselves.^{18,168}

To our knowledge, a single-subject case study reported by Mason and colleagues¹⁸ has been the only investigation of the phenomenon of “excessive” daydreaming with functional neuroimaging. Researchers compared brain activation during this individual’s fantasies to a condition where the subject was asked instead to concentrate intensively on a task, and found widespread activations associated with daydreaming (Fig. 5). Most striking were activations in the nucleus accumbens (Fig. 5), an area known to be critical to reward processing.^{172–175} The nucleus accumbens does not appear to be consistently recruited by mind-wandering in the general population,⁴ but given the small size of this brain structure and the limited number of neuroimaging studies investigating mind-wandering in real-time, future research could overturn this preliminary conclusion. Conversely, activation of the nucleus

accumbens might be specific to highly rewarding self-generated thought. Mason and colleagues¹⁸ further created a seed region of interest around their nucleus accumbens cluster and found that activity in the nucleus accumbens showed strong positive functional connectivity with many of the key areas implicated in mind-wandering and related forms of self-generated thought,⁴ including medial prefrontal cortex, posterior cingulate cortex, and the inferior parietal lobule bilaterally.¹⁸ Although highly tentative (being based on a single-subject case study), these findings suggest an interesting putative neural basis for highly rewarding self-generated thought, and could point the way for future investigations along these lines.

Relationships between meditation, mindfulness, and a positivity bias in self-generated thought

Several recent studies have examined relationships between mindfulness and the valence of self-generated thought, typically using mindfulness questionnaires. Note, however, that questionnaire-based assessments of mindfulness have been subjected to harsh and persuasive criticism;¹⁷⁶ for instance, the widely used Five Facet Mindfulness Questionnaire (FFMQ) correlates just as well with years of education as it does with meditation experience.^{177,178} These caveats should be kept in mind when considering the results described below.

Two recent studies^{42,179} correlated scores on the FFMQ, which purports to measure trait levels of mindfulness,¹⁸⁰ with the affective qualities of self-generated thoughts collected in a laboratory setting. Higher mindfulness scores significantly predicted more emotionally positive thought content in both cases.^{42,179} Consistent with this, others have found that dispositional mindfulness, as assessed by a similar questionnaire (the Mindful Attention Awareness Scale, or MAAS¹⁸¹), was negatively correlated with the frequency of negative thoughts.¹⁸² All of these results are consistent with related work showing that mindful individuals report heightened positive affect in general¹⁸¹ and suggest that meditation *training*, too, might lead to more positive thoughts overall. One recent study investigated the influence of training by measuring the effect of 9 weeks of compassion meditation training on the affective qualities of off-task thought.¹⁸³ They found that greater practice (i.e., more hours) of

compassion meditation predicted reduced off-task thoughts to both negative and neutral topics, and increased off-task thoughts to positive topics.¹⁸³

Based on the aforementioned results related to dispositional or “trait” mindfulness, there is good reason to expect that the neural correlates of emotional self-generated thought will differ in persons experienced in meditation practices. Unfortunately, to our knowledge, no study has directly examined changes in the affective content of self-generated thought in meditation practitioners with simultaneous functional neuroimaging. Nonetheless, many studies have examined the neural correlates of emotional processing across various styles of meditation,^{184,185} shedding some light on potential mechanisms. For instance, a recent neuroimaging study found that brief training in compassion meditation resulted in increased altruistic behavior; increased altruistic behavior was in turn associated with heightened functional connectivity between the dorsolateral prefrontal cortex and nucleus accumbens.¹⁸⁶ Further investigations along these lines could be helpful in elucidating the mechanisms whereby mindfulness and meditation might enhance mood.

Affect in self-generated cognition during sleep and dreaming

A related topic deserving of discussion is the affective qualities of self-generated thought during sleep, including dreaming and other sleep mentation.^{187,188} Elsewhere, we and others have argued at length that dreaming can be considered akin to waking self-generated thought, in that the two share many phenomenological and neurophysiological similarities.^{5,9,58,59,189} Dreaming can take place at any time throughout the night, but it is especially prevalent during REM sleep (~80% of the time) and tends to be sporadic across most non-REM sleep stages (~10–40% of the time).^{23,187,190} We therefore use REM sleep as the best available, although admittedly limited, proxy for the neural basis of dreaming (for further details, see Refs. 9,58, and 59). In the following sections, we discuss affect during sleep in healthy populations, as well as factors that can bias self-generated cognition in sleep and dreaming toward more negative or more positive content.

Affect in the dreams of healthy populations

Despite their many similarities, a critical difference is that dreaming appears to amplify many of the same qualities that distinguish waking self-generated thought from externally directed, deliberate thinking: for instance, dreaming is more spatiotemporally immersive, more richly visual, contains more imagined auditory content, tends to be more bizarre, and occurs in more temporally extended (i.e., longer) sequences than waking self-generated thought.^{9,58,191}

The affective qualities of dreaming in healthy populations appear to follow this trend, with dreams in general showing more emotion than waking self-generated thought.¹⁹² In one study, for instance, when participants rated the emotional qualities of their own dreams, they reported emotions in ~99% of them.¹⁹³ Independent judges detected less emotion, but still rated ~86.5% of reports as containing positive or negative emotion of some kind.^{192,193} Although in principle these values could represent exaggerated or chance findings, the results of many studies agree that *at least* 70–75% of dreams from REM sleep contain emotion.^{9,189,194–197} This is a somewhat higher rate than in waking self-generated thought, where affect appears to be present instead in roughly one-half³¹ to two-thirds¹⁶ of reports, but a more in-depth comparison of affect in waking self-generated thought and nighttime dreaming awaits future work.

To our knowledge, no study has specifically examined the neural correlates of overall affect, or specific kinds of emotion, during sleep or dreaming. However, many studies have now examined general neural correlates of dreaming during REM sleep as well as other sleep stages, and this growing body of data has been integrated by some of us in both narrative reviews^{23,58} and a quantitative meta-analysis.⁹ These syntheses have allowed for a tentative delineation of the neural substrate of dreaming,⁹ which overlaps considerably with the neural correlates of waking self-generated thought.^{4,58}

Broadly speaking, the neural correlates of dreaming dovetail well with the phenomenological findings of widespread and diverse affect in dreams. In a meta-analysis of our brain imaging studies of the REM sleep stage (which has by far the highest chances of subjective dream content compared to other sleep stages^{187,190}), we found⁹ consistent activity differences in numerous brain regions with a

prominent role in emotional processing,^{50,198} such as the pgACC, the medial temporal lobe, the OFC, and the caudate nucleus. These results are consistent with the high frequency and sometimes high intensity of affect (both positively and negatively valenced) reported in normal dreaming.^{9,192} A critical caveat regarding these data, however, is that neuroimaging studies of REM and other sleep stages very rarely obtain dream reports upon awakening to confirm that participants were indeed dreaming. For instance, of the eight neuroimaging studies of REM sleep we recently reviewed,²³ only a single study directly confirmed dreaming with first-person reports.¹⁹⁹ Although the very high chances of dreaming during REM sleep mitigate this problem to some degree, in the absence of subjective reports, the idea that activations observed with neuroimaging during REM sleep reflect the neural correlates of dreaming itself ultimately remains an inference.

Further insights are provided by the investigation of nightmares and chronic nightmare-sufferers, as well as so-called “lucid” dreamers. Just as self-generated thought in waking can become biased toward negative content (for instance, in MDD) or positive content (for instance, in “excessive” daydreamers^{18,168} or those practicing mindfulness^{42,179,181,183}), so too can self-generated cognition in sleep become biased toward negative and frightening content in chronic nightmare-sufferers^{200,201} and ecstatic, joyful experiences in lucid dreaming.^{202–204}

Negatively biased affect in chronic nightmares and sleep paralysis

Despite the lack of research investigating neural correlates of specific affect in normal dreaming, there has been some preliminary research into the neural correlates of nightmares.²⁰¹ Broadly speaking, theoretical accounts have proposed that dysfunctional activity in the amygdala, medial prefrontal cortex, and medial temporal lobe (especially the hippocampus) is largely responsible for the generation and recurrence of nightmares.^{200,201} This model proposes that the medial temporal lobe binds fragmentary memory traces into a realistic visuospatial scene, which is provided with contextual information and affective cues by the amygdala; medial prefrontal cortical areas then give rise to an evaluation and subjective experience of the emotional qualities of this experience.²⁰¹

Some tentative support for this model comes from a positron emission tomography study of dreaming, which found that glucose metabolic rate in the medial prefrontal cortex during REM sleep strongly predicted levels of anxiety in dreams reported for this same period of sleep (dream reports were collected after awakening).²⁰⁵ Neurological patients with damage to these areas, including medial prefrontal cortex and medial temporal lobe, are also more likely to experience frequent recurring or nonrecurring nightmares²⁰⁶—consistent with a role for these areas in heightened negative affect during dreaming and nightmares.

Another sleep disorder resulting in frequent negative affect is sleep paralysis, in which individuals experience vivid, dream-like hallucinations accompanied by temporary paralysis during the sleep-wake transition. Sleep paralysis experiences are often severely negative, including feelings of threat, fear, and terror, and sometimes physical or sexual assault by imagined presences.^{207,208} Virtually nothing is known about the neural basis of these experiences, but existing evidence suggests that sleep paralysis takes place during, and might be a disorder of, REM sleep;²⁰⁹ additionally, its neurobiological mechanisms may overlap with those of chronic nightmares.²¹⁰

Heightened positive affect in lucid dreaming

Dreaming can also become characterized by a positivity bias. Anecdotal reports over the years have often mentioned experiences of bliss, joy, euphoria, and other highly rewarding experiences, which, although they can also occur in normal dreaming, appear to be much more common within the lucid dream state.^{202–204,211} Beyond more mundane pleasures such as the joy of flying²⁰⁴ or the euphoria of sexual encounters,²⁰² lucid dreamers have reported feelings of awe and love in the context of mystical experiences and encounters with what is perceived as the divine.²¹² Given some tentative evidence that lucid dreaming is a learnable skill that can be improved with practice,^{213–215} using lucid dreaming training to bias dream cognition toward highly rewarding and positive experiences is an intriguing possibility. Along these lines, lucid dreaming training has been pilot-tested as a means of reducing the frequency and severity of nightmares in chronic nightmare sufferers, with some limited success.²¹⁶ Similarly, the cultivation of dream

lucidity has been anecdotally reported as an effective treatment for severe sleep paralysis.²⁰⁷ Chronic nightmares (≥ 1 /week) and occasional sleep paralysis are much more common than generally appreciated: affecting an estimated 4%²¹⁷ and 7.6%²¹⁸ of the population, respectively, together they represent a serious source of personal distress for millions of people and a considerable public health burden. Any practice that holds promise for ameliorating these conditions warrants further investigation.²¹⁸

As with negatively biased self-generated thought in sleep, very little is known about the neural basis of lucid dreaming generally, or dreamt positive affect specifically. A single-subject case study of lucid dreaming with fMRI recently reported widespread brain activation in lucid versus nonlucid REM sleep,²¹⁹ but the differential activations were mostly observed in visual and executive regions, and their relevance (if any) to positively biased affect is impossible to discern at this point.

Outstanding issues and future directions

Here, we briefly consider several outstanding issues and future directions for research into the affective neuroscience of self-generated thought: first, the ongoing controversy^{17,19,220} over whether self-generated forms of thought are, overall, aversive; second, the developing field of study investigating changes in the frequency,^{221,222} content,^{223,224} and affect^{224,225} of self-generated thought over the lifespan; and finally, the increasing need to disentangle different *types* of self-generated thought, and the different *dimensions* of these types of thought, using carefully chosen terminology and questions for participants.^{5,33}

Is self-generated thought aversive?

Two high-profile studies have both concluded that self-generated thought is characterized predominantly by unpleasantness and unhappiness,^{16,17} despite the fact that their empirical results demonstrate a positivity bias—in line with every other study to date (Table 1 and Fig. 2). Such counterintuitive conclusions from prominent studies in this still-developing field warrant explanation; we therefore discuss the basis for these surprising claims here.

Both studies examined instances of self-generated thought, as well as enjoyment or happiness ratings, during common daily activities (such as using

the computer, listening to music, working, playing sports, and so on), and both found that, on average, ratings were somewhat higher for daily activities than for thoughts unrelated to the current activity.^{16,17} Both studies follow the same logic, arguing that the relatively higher happiness or enjoyment ratings for external activities demonstrate that “a wandering mind is an unhappy mind”¹⁶ or that people “did not enjoy spending 6–15 min in a room by themselves with nothing to do but think.”¹⁷

“Just thinking” might not be blissful, and it seems only natural that external activities should be somewhat more enjoyable, on average. But it is a *non sequitur* to conclude that the higher relative enjoyment of a given activity proves the aversiveness or unpleasantness of another.¹⁹ This argument is analogous to claiming that people find eating chocolate “aversive” and “not very enjoyable” simply because they consistently rate sexual activity as more enjoyable. Such a conclusion is clearly unwarranted—yet, both Killingsworth and Gilbert¹⁶ and Wilson and colleagues¹⁷ follow the same logic and draw the same conclusions.¹⁹ Yet, the relatively higher enjoyment of a particular activity (or class thereof) tells us nothing about the intrinsic enjoyment of some other activity.¹⁹ The most parsimonious path is to let self-report ratings of affect in self-generated thought stand on their own—and in that case, both of these studies agree with other work in showing widely variable, but on average mildly positive, affect in self-generated thought (Table 1 and Fig. 2).

Affect in self-generated thought across the lifespan

Several studies have now shown that patterns of self-generated thought are altered in the elderly,²²⁶ but relatively few investigations have been conducted to date and lifespan findings therefore need to be interpreted with caution. The best-replicated finding is that overall rates of self-generated thought are significantly reduced over the lifespan,^{221,222,227–229} but alterations in affect are much less well explored. Research conducted by Giambra suggests that the frequency of both positive *and* negative affect in self-generated thought is reduced over the lifespan, suggesting an overall reduction of affect,²²⁵ although other analyses have suggested that positive affect is more markedly reduced.²²⁴ These tentative findings are surprising given that elderly participants in fact tend toward a positivity

bias in numerous domains, including attention and autobiographical memory—the well-replicated “positivity effect.”^{230,231} Moreover, this positivity effect appears to be strongest in studies where cognition is least constrained by task demands.²³¹ Theoretical models of the positivity effect²³⁰ would therefore predict that the self-generated thought of the elderly should be predominantly positive, but to our knowledge this has not yet been experimentally assessed. A major goal for the affective neuroscience of self-generated thought will be to explore these lifespan effects and their neural basis.

Terminological clarity and explorations of the relationships between different dimensions of self-generated thought

At the outset of this review, we noted that many terms for self-generated thought are used relatively interchangeably or with minimal definition. Terminological fluidity is understandable, perhaps even inevitable, at the dawn of any new field of study,¹ but further progress depends on an increasingly judicious and transparent use of terms. Moreover, some *prima facie* paradoxical qualities of self-generated thought, such as the high frequency with which it is deliberately initiated³² and intentionally directed,³¹ have been underappreciated, and their consequences therefore ignored in most studies to date. We have recently advanced a theoretical framework that seeks to capture many of these qualities in a unified cognitive state space,⁵ and recent research has sought to address such issues with careful use of terms and detailed explorations of how different dimensions of self-generated thought are interrelated. For instance, Mills and colleagues³³ used a smartphone application to sample participants' thoughts in everyday life and investigated the extent to which thoughts that were task-unrelated and perceptually decoupled were also freely moving (i.e., the movement of the stream of thought was relatively free from deliberate or automatic constraints; “freely moving” is a key quality of mind-wandering in our theoretical model⁵). Neither perceptual decoupling nor task-unrelatedness correlated well with free movement in the stream of thought. This finding suggests that freedom of movement is a largely orthogonal dimension of thought—one not captured well by the two most common concepts in use today in the study of self-generated thought (perceptual decoupling and task-unrelatedness).³³

Other work has distinguished carefully between task-unrelated thought that is intentionally versus unintentionally initiated and how such qualities might relate to clinical conditions.³² Research has found that self-reported rates of unintentionally initiated task-unrelated thought correlate with both attention-deficit/hyperactivity disorder²³² and obsessive-compulsive disorder²³³ symptomatology. Research investigating not just how thought is initiated, but also whether or not it is intentionally guided over time, has also yielded intriguing findings. Recent work³¹ found that participants who reported more intentionally directed (versus spontaneously arising) stimulus-independent thoughts also reported significantly more thoughts related to their goals and personal concerns, as well as more positive affect in their thought content.

These examples are hardly exhaustive, but should suffice to show that the *terminology* employed by experimenters can influence how participants understand the experiment and classify their mental content,^{5,33} moreover, the *questions* experimenters pose will constrain the probable, and even possible, interpretations of their data. Careful consideration of these issues in future research will be crucial to understanding how various types of self-generated thought differ, how their different dimensions are interrelated, and how various types and dimensions of self-generated thought relate to everyday behavior and clinical conditions. Although differences in the subjective qualities of self-generated thought appear to have important cognitive and behavioral corollaries, subtle psychological differences might not necessarily be accompanied by observable differences in brain activity. For instance, a recent study found that the neural correlates of positive and negative thoughts during a task-free “rest” period differed little from brain activations associated with a task involving positive and negative self-referential attributions (e.g., “I am generous” or “I am moody”).¹⁵ Moving forward, the complexity and multidimensionality of self-generated thought can be captured more fully through careful theoretical and experimental work that acknowledges the multifaceted nature of this until recently largely neglected side of human thought.

Conclusions

Six broad conclusions can confidently be drawn from the preceding review. First, affect is ubiquitous

during self-generated thought. Emotional content is present in roughly 50–67%^{16,31} of waking self-generated thought (Table 1 and Fig. 2), and nighttime dreaming shows an even greater tendency toward emotional content, estimated to be present in roughly 75–95% of dream reports.^{9,189,194–197}

Second, self-generated thought is characterized by a great diversity of emotional content—perhaps as wide as the affective spectrum for externally oriented, deliberate forms of thought. Affect during self-generated thought can be pleasant, unpleasant, awe-inspiring, agonizing, and everything in between—whether we are awake and mind-wandering¹⁹ or asleep and dreaming.^{9,192} Whereas most work to date has focused on the affective *valence* of self-generated thought, future work could extend this line of enquiry beyond valence to investigate the *arousal* dimension of affect. It would also be helpful for future work to examine specific appraisal dimensions,^{49,234} as well as the frequency of occurrence of discrete emotions (e.g., sadness, fear, happiness, and more rare affective states) during self-generated thought. Further investigation of comparatively rare, but highly personally meaningful, emotions like awe and bliss would also be welcome.

Third, virtually every empirical study to date (with one exception⁴¹) shows a mild but nonetheless notable bias toward positive or pleasant affect, on average, in the self-generated thought of the general population (Table 1 and Fig. 2). This finding appears to be very robust, holding true across a wide variety of countries, cultures, research contexts, questionnaires, and thought-sampling methods.

Fourth, the average affective qualities of self-generated thought are influenced by a variety of factors, including innate predispositions,^{18,169,179,182} clinical conditions,^{139,200,201} and deliberate mental training.^{183,202,204,212} On the one hand, self-generated thought can become negatively biased in clinical conditions such as MDD¹³⁹ or chronic recurring nightmares.^{200,201} On the other hand, natural predispositions can also bias people toward *positively* valenced forms of self-generated thought: people who score high on trait (or “dispositional”) mindfulness, as well as “excessive” day-dreamers, both appear to have more rewarding and pleasant self-generated thought than the general population.^{18,169,179,182} Such positivity biases do not

appear to be restricted merely to trait characteristics beyond one’s control: deliberate training in meditation practices might also weight self-generated thought toward more pleasant topics,¹⁸³ and the cultivation of so-called “lucid” dreams appears to result in many rewarding and highly enjoyable dream experiences^{202,204,212}—and may even be a means of reducing the frequency and severity of negative dream content.²¹⁶

Fifth, the terminology employed in these investigations is of potentially immense significance, but until recently has been relatively imprecise and inadequate for capturing the complexity and multidimensionality of self-generated thought. Commonly used terms, such as task-unrelated thought and stimulus-independent thought, do not necessarily capture qualities of thought (like its freedom of movement)³³ that could prove crucial for a precise operationalization of otherwise nebulous terms like “mind-wandering.”⁵ Moreover, dimensions of self-generated thought that were mostly ignored until recently, such as intentionality,³² have turned out to be predictive of clinical symptomatology,^{232,233} as well as important thought content dimensions such as goal-relatedness and affective valence.³¹ As the field moves forward, careful definition of terms, exploration of both orthogonality and dependence among various dimensions of thought, and an appreciation that questions *not* asked could ultimately prove to be of paramount importance will all be critical.

Sixth, findings from functional neuroimaging investigations—although often tentative—appear to corroborate and support the first-person reports of a high prevalence and wide variability of affect in self-generated thought. Many regions critical to emotional processing are reliably recruited during normal self-generated thought (Table 2 and Fig. 3), and moreover, these areas show altered activity and functional connectivity commensurate with altered subjective experiences of self-generated thought affect—be they negative or positive.^{18,166,205,235}

It is clear that affect is one of the principal and most prevalent qualities of self-generated thought; the major task ahead is to further explore the full spectrum of affect in various normal and dysfunctional forms of self-generated thought and link these findings with underlying neural mechanisms. A better grasp of this poorly understood form of cognition and its mysterious functions will require a deep

appreciation of its relationship to human emotions in all their complexity and variety.

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Competing interests

The authors declare no competing interests.

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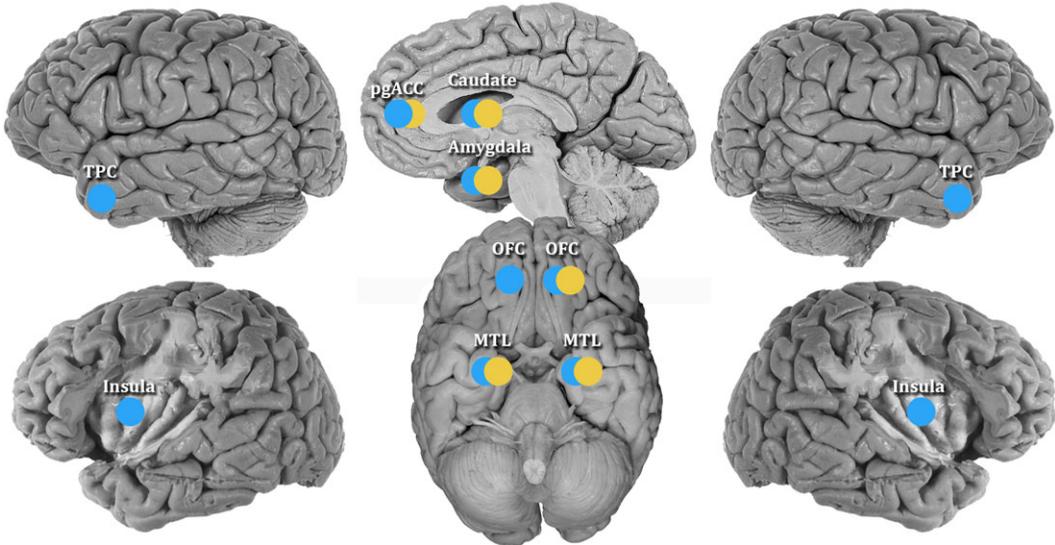
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Graphical Abstract & Image

● Waking self-generated thought

● REM sleep (~80% chance of dreaming)



Despite increasing scientific interest in self-generated thought – mental content largely independent of the immediate environment – there has yet to be any comprehensive synthesis of the subjective experience and neural correlates of affect in these forms of thinking. This review aims to develop an integrated affective neuroscience encompassing many forms of self-generated thought – normal and pathological, moderate and excessive, in waking and in sleep.