Review article

Anticipatory feelings: Neural correlates and linguistic markers

Elka Stefanova[a,b,]*, Olga Dubljević[b], Cornelia Herbert[c], Beth Fairfield[d], Matthias L. Schroeter[e], Emily R. Stern[f,g], Sébastien Urben[h], Birgit Derntl[i], Christine Wiebking[c], Carina Brown[f,g], Anat Drach -Zahavy[j], Leonie Anne Kathrin Loeffler[k], Franziska Albrecht[e], Rocco Palumbo[l], Sydney Weber Boutros[m], Jacob Raber[m,n], Leroy Lowe[o]

[a] Faculty of Medicine, University of Belgrade, Serbia
[b] Neurology Clinic, Clinical Center of Serbia, Serbia
[c] Department of Applied Emotion and Motivation Psychology, Institute of Psychology and Education, Ulm University, Ulm, Germany
[d] Department of Psychological, Health and Territorial Sciences, University of Chieti, Chieti, Italy
[e] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig & Clinic for Cognitive Neurology, University Leipzig, Germany
[f] New York University School of Medicine, New York, NY, USA
[g] Nathan Kline Institute for Psychiatric Research, Orangeburg, NY, USA
[h] Division of Child and Adolescent Psychiatry, University Hospital of Lausanne, Lausanne, Switzerland
[i] Department of Psychiatry and Psychotherapy, Medical School, University of Tübingen, Tübingen, Germany
[j] The Faculty of Health and Welfare Sciences, University of Haifa, Haifa, Israel
[k] Department of Psychiatry, Psychotherapy and Psychosomatics, Medical Faculty, RWTH Aachen University, Aachen, Germany
[l] Department of Neurology, Boston University School of Medicine, Boston, MA, USA
[m] Department of Behavioral Neuroscience, Oregon Health & Science University, Portland, OR, USA
[n] Departments of Neurology and Radiation Medicine, Division of Neuroscience, ONPRC, Oregon Health & Science University, Portland, OR, USA
[o] Neuroqualia (NGO), Truro, Nova Scotia, Canada

ARTICLE INFO

ABSTRACT

This review introduces anticipatory feelings (AF) as a new construct related to the process of anticipation and prediction of future events. AF, defined as the state of awareness of physiological and neurocognitive changes that occur within an oganism in the form of a process of adapting to future events, are an important component of anticipation and expectancy. They encompass bodily-related interoceptive and affective components and are influenced by intrapersonal and dispositional factors, such as optimism, hope, pessimism, or worry. In the present review, we consider evidence from animal and human research, including neuroimaging studies, to characterize the brain structures and brain networks involved in AF. The majority of studies reviewed revealed three brain regions involved in future oriented feelings: 1) the insula; 2) the ventromedial prefrontal cortex (vmPFC); and 3) the amygdala. Moreover, these brain regions were confirmed by a meta-analysis, using a platform for large-scale, automated synthesis of fMRI data. Finally, by adopting a neurolinguistic and a big data approach, we illustrate how AF are expressed in language.

1. Introduction

The construct of "anticipation" has become the subject of increasing scientific interest in the last decade. This is mainly *because* anticipatory processes play a key role in many areas of research related to how humans and animals anticipate future actions as a function of affective and behavioral self-regulation. Anticipatory processes are involved in the regulation of simple organismic processes and in the regulation of complex behaviors, including decision-making, strategy formation and/ or regulation of affect and emotions.

Anticipatory feelings (AF) are defined as feelings related to anticipation; more precisely, as a state of awareness of physiological and neurocognitive changes that occur within an organism during a specific process of adapting to future events.

1.1. Overview

In absence of an established definition of AF in the literature, we

* Corresponding author at: Faculty of Medicine, University of Belgrade, Neurology Clinic, CCS, Dr Subotića 6, Belgrade, Serbia.
E-mail addresses: elka.stefanova@med.bg.ac.rs, steela21@gmail.com (E. Stefanova).

begin this review by providing a working definition of AF. We proceed by introducing influential neuroscientific theories and concepts related to AF, such as anticipation and expectancy, and by discussing neuroimaging findings with respect to the brain structures and networks assumed to play a crucial role in AF, in line with the working definition.

More specifically, in Section 1 we discuss how AF and emotional responses to events in both animal and human research are mediated by distinct neural systems, with special emphasis on fear and anxiety, as they are related to AF. In Section 2, the role of bodily-related stimulus processing in AF, including the role of bodily-related interoceptive processes and its neural correlates, is discussed. Section 3 focuses on neural mechanisms associated with dispositional factors underlying positive AF, including optimism and hope, as well as reward anticipation, as it includes activation in similar brain regions. Neural mechanisms associated with dispositional factors underlying negative AF, including pessimism and worry, are outlined in section 4. In section 5, we consider alterations of AF and their role as a potential risk factor for several mental disorders. The brain areas and brain networks relevant for AF that are identified in sections 1–4 and section 6 are validated by a meta-analysis using www.neurosynth.org, a platform for large-scale, automated synthesis of fMRI data including to date 507,891 activations from 14,371 studies. The results of this meta-analysis are included in section 5. Finally, in section 7 we present an initial, cursory review of feeling words that are articulated in the English language. Using a big data approach, we revealed a very nuanced list of AF constructs that have not yet been explored in neuroscience research.

The present review of AF is part of "The Human Affectome Project". The overarching goal of the Human Affectome Project is to summarize much of what is currently known about affective neuroscience while exploring the language that individuals use to convey feelings and emotions. In line with this goal, by adopting a neurolinguistic and a big data approach, we addressed the question of how language and AF might be related. Results from a big data approach analyzing words describing AF in English were reported. Word categories related to AF with respect to other words expressing other emotional and affective states (*e.g.*, physiological, social, the Self, anger etc.) were further discussed.

1.2. General concepts and theoretical considerations relevant to AF

1.2.1. A working definition of AF

Feelings are defined as the perception or awareness of events within the body, closely related to emotion (Augustyn et al., 2012). AF are related to anticipation, expectancy, planning and decision making but they are not equivalent to these concepts nor do AF include all emotions or all feelings. There is currently no unifying definition or theory available of AF. Therefore, this review includes a working definition to guide our understanding of AF. In particular, we consider AF as multifactorial constructs. More specifically, we consider:

1) expectancy and anticipation as key components of AF.
2) interoceptive signals and physiological signals as bodily cues of AF.
3) AF as arising in anticipation of behavioral choices that can have a positive or negative valence.
4) AF are influenced by individual differences, including personal beliefs, dispositional traits (*e.g.*, optimism, hope and pessimism, and worry) and can be regulated by emotion regulation strategies.
5) alterations in AF can be found in several mental disorders.
6) AF can be expressed in language and subjectively described by expressive-linguistic components.

Based on these criteria, as well as the definition of the concept „*feeling"*, we provide a working definition of AF:

AF are a state of awareness of physiological and neurocognitive changes that occur within an organism during a specific process of adapting to future events- anticipation, and their role may be to facilitate this process of *adapting to future events.*

1.2.2. Anticipation, expectancy, planning and the brain as a self-regulatory inference machine

From a neuroscientific perspective, AF are multicomponent (*e.g.*, subjective, physiological, affective) responses deriving from neural processes that are part of the core functions of the human brain. Indeed, the activity of all self-regulatory biological systems (like the human brain) seems to follow specific physical laws and probabilistic rules. These physical laws and probabilistic rules may be interpreted as to facilitate prediction and anticipation of an organism's current and future state. More interestingly, "global brain theories" (for an overview see (Friston, 2010) all hold the common assumption that the brain is "an inference machine". That is, the brain optimizes its processes by continuously updating stored representations with actual sensory input. In this manner, AF can be taken as the result of stimulus-driven, bottom-up and top-down controlled processing. Hence, anticipation, expectancy and resulting AF are main features of the brain, inherently bound to the functional organization of neural cell assemblies. In other words, the neural processes involved in anticipation and expectancy as well as those factors contributing to AF, are likely to be the result of interactions between bottom-up and top-down neural processes.

In line with this view of the brain as an inference machine, anticipation and expectation are considered crucial for human adaptation to the environment (Bubic et al., 2010). Drawing inferences from anticipations and expectancies allows individuals to flexibly adjust behavior in accordance with their intentions and future goals. Theoretically, individuals make choices based on estimates of how well a chosen behavior will lead to desired results. Thus, according to expectancy theory (*e.g.*, (Vroom, 1964)), individuals select behaviors depending on how different motivational elements involved in the decision process are processed. Thus, anticipation and expectations permit foreseeing future events which, in turn, allows individuals to organize behavior proactively and cope with the impact of those events.

AF are considered to occur prior to an event and the bodily changes accompanying AF are thought to act as markers that influence our choices during decision making (*e.g.*, (Bechara et al., 1997)). Accordingly, anticipatory processes underlying decisions of how to behave are determined by the outcome of previous behavior, by bodily responses and by the individual's ability to plan, *i.e.*, to mentally anticipate the correct way to carry-out a task or reach a specific goal. Planning involves a series of mental processes that allow an individual to select necessary actions, put the actions in the correct order, assign each task to the corresponding cognitive resource (attention, working memory), and establish a plan of action in order to reach the specific goal, and can be modulated by emotions and affective experiences, such as reward and punishment experiences (Table 1).

Consequently, decisions that produce behavior include processes that have been completed before making a choice (Kuhl and Fuhrmann, 1998). AF then are feelings that arise in anticipation of future events (Macleod, 2017) and that accompany action planning and goal orientation, without which an individual would be unable to persevere with or resume difficult goals. Therefore, there is widespread acceptance that AF arise during planning and decision making in humans and

Table 1
Examples of how anticipated interactions or outcomes can shape the emotional and behavioral state of people.

Anticipated Interaction/Outcome	Behavioral Adjustment
Confrontational	Upregulate negative emotions
Sick child	Upregulation of worry
Competition (anger helpful)	Upregulation of anger
Competition (anger harmful)	Downregulation of anger
Collaboration	Upregulation positive emotions
Helping others (at a cost)	Downregulation of compassion
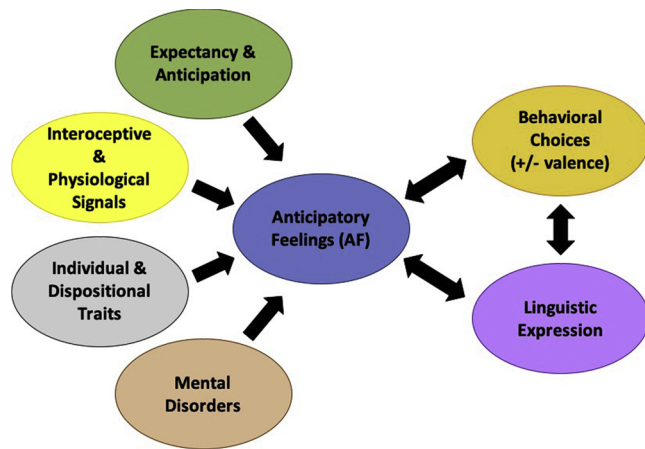
Fig. 1. The multifaceted components of AF (AFs). Expectancy and anticipation are key characteristics of AF. Additionally, interoceptive and physiological signals affect the sensation of AF and influence their presence. Building on that, individual traits and general disposition, partnered with emotional regulation strategies, will influence AF. Lastly, many mental disorders involve disruption to typical anticipatory regulation. All these lead to actions in response to behavioral choices, which could have either positive or negative valences, and linguistic expression, which, in turn, feed back into the AFs.

consequently modulate performance (Fairfield et al., 2015). In this manner, internal bodily visceral states, as well as personal beliefs, and dispositional traits such as optimism or pessimism, hope and worry (defined as the expectation of positive or negative outcomes) contribute to AF by altering decision making even without the explicit knowledge of an individual (Fig. 1).

1.3. Anticipation vs. AF: evidence from other species

The ability to anticipate events is a skill not only inherent in humans, but also in non-human animals (Blancas et al., 2014; Krupenye et al., 2016; Pezzulo and Castelfranchi, 2009; Riegler, 2001). Indeed, several other species also possess the ability to anticipate, although what exactly this implies is currently subject to debate. Accordingly, there is no clear definition of what anticipation is, or at least one that is universally accepted amongst researchers. For example, researchers who use a broad concept of anticipation, define anticipation as the process that allows the future to become part of "an action". According to this definition, most behaviors that are not a reaction to direct stimuli can be considered indicators of anticipation, since some believe almost all behavior is goal directed (van den Bos, 2017). Moreover, taking this definition to an extreme, many elementary cognitive processes in animals, such as visual attention and motor control, could be attributed to an anticipatory system. That is, a system that can predict the effect of its action, as opposed to a reactive system that produces behavior in response to the environment or an internal need (Pezzulo and Castelfranchi, 2009). It has even been proposed that all motor control is mediated by anticipatory prediction, since the execution of fine motor actions requires precise timing in the order of milliseconds

Other definitions of anticipation suggest that more complex cognitive abilities are required, such as awareness of past, present, and future on behalf of the subject (van den Bos, 2017), and anticipatory emotions and states are thought to be closely related to planning and decision making. Many animal species exhibit these abilities. For instance, corvids spontaneously show analogical reasoning, episodic-like memory, tool use, complex social interactions and insight into the mental state of conspecifics (Balakhonov and Rose, 2017). In fact, it has been reported that crows are able to produce a tool by bending a wire into a hook and then use it to reach food from a tube or a bucket, a feat that requires complex planning, timing and anticipatory abilities (Weir et al., 2002). This finding confirms that crows are also capable of compound tool

construction and tool innovation, skills that require anticipation (Bayern et al., 2018; Rutz et al., 2016; St Clair et al., 2018). Consequently, it seems that the ability to perceive the passing of time is the minimal requirement to deem an organism capable of anticipation and/or anticipatory states. However, this timing can occur at different levels. For example, the motor preparation for the prey-catching behavior of the jumping spider requires precise acute timing (Schomaker, 2004). On a larger scale, timing can be observed in circadian rhythms. In mammals circadian rhythms in behavior and physiology, such as daily nursing in rabbits, or sleeping schedules in some species, are coordinated by an internal clock, the suprachiasmatic nucleus in the hypothalamus (Klein et al., 1991; Moore, 2013). Mice and rats exhibit still other mechanisms (*e.g.*, learning and memory) proposed to be necessary in order to learn the scheduled time of a significant event (Antle and Silver, 2009) such as daily access to food (Balsam et al., 2009).

Riegler (Riegler, 2001) proposed three distinct types of anticipatory capabilities in different animal species: inborn, emotional, and cognitive. Inborn anticipation occurs as the result of phylogenetically acquired patterns (*e.g.*, hibernation, or migration in some species). Anticipation is emotional if it is driven by an instinct, such as hunger. While cognitive anticipation occurs when the animal is able to make predictions about the remote future and those predictions are not dependent on the current state. The emotional and cognitive capabilities proposed by Riegler (Riegler, 2001) should not necessarily be viewed as completely distinct processes; rather, these processes should be viewed as affined (Erk et al., 2006). Consistent with this definition, anticipation occurs in many different forms in the animal kingdom, since many living organisms have developed different mechanisms that allow them to make, at least implicitly, (large or small) estimates of future states of affairs in the environment.

When assessing emotional and motivational states in experimental settings, it is difficult to reach clear conclusions without the risk of anthropomorphization. Most animal research on anticipatory behavior is based on food-anticipatory activity (Mistlberger, 1994), yet the related physiological and neural processes may yield measurable insight into underlying states of anticipation. Many studies of anticipatory states in animals concern the impact of daily food restriction in rodents (Caba and Gonzalez-Mariscal, 2009). Anticipatory activity starts about 1–3 hours before mealtime and is characterized by behavioral arousal, foraging, increased approach to a feeder, and the search for food (Blancas et al., 2014; Mistlberger, 1994). Other physiological and neural parameters are entrained by the periodic exposure to food (*e.g.*, a rise in body temperature) (Caba and Gonzalez-Mariscal, 2009; Mistlberger, 1994; Stephan, 2002). Behavioral activation can last for days after the cessation of the feeding protocol (Angeles-Castellanos et al., 2008). The procedure for inducing food-anticipatory activity in rodents by exposing them to a restricted food schedule is very similar to Pavlov's experiments with temporal conditioning. In these experiments, Pavlov fed his dogs in fixed intervals of time to show that an internal temporal cue can serve as a conditioned stimulus just as an external cue would. In his classical conditioning procedure, Pavlov repeatedly paired a conditioned stimulus (*e.g.*, sound of a bell) with an unconditioned stimulus (*e.g.*, presenting food). He found that in time, the animal exhibited the conditioned response (*e.g.*, salivation) when exposed to the conditioned stimulus alone. The associative neural mechanisms that underline classical conditioning and temporal conditioning are identical (Pavlov, 2010).

While some authors hypothesize that circadian clocks enable some animals to anticipate predictable daily opportunities to acquire food (Mistlberger, 1994, 2009) this does not appear to be the key mechanism underlying behavior of rodents exposed to restricted food schedules (Angeles-Castellanos et al., 2008; Blancas et al., 2014). In rodents, food-anticipatory activity is mediated by food-entrainable oscillators (FEO) independent of the intact or functional suprachiasmatic nucleus (SCN) (Mistlberger, 1994; Stephan, 2002) FEO can be understood as a network of interconnected brain structures that are independent of the

SCN and instead function as a self-sustained mechanism; they are entrained by integration of peripheral information provided by different humoral signals related to food intake (Carneiro and Araujo, 2012). Although several authors agree that FEO is responsible for food-anticipatory activity in rodents, there is still dispute on the exact locus of FEO.

Reward-related neural processes and goal-directed behavior are also considered in research on anticipation in animals. In monkeys, the ventral striatum was associated with reward expectation (Bowman et al., 1996; Schultz et al., 1992) in relation to dopaminergic projections from the midbrain (Schultz, 1998). Furthermore, this was shown to be more frequently linked to reward anticipation than loss of reward anticipation (Breiter et al., 2001; Dillon et al., 2008; Knutson et al., 2001a, 2003). In contrast, no difference was found in ventral striatal activation (Carter et al., 2009). It is possible that many of the brain regions associated with cognitive control and executive attention, such as dorsal striatum, prefrontal cortex, and anterior insula (Dosenbach et al., 2007; Smith et al., 2009; Vincent et al., 2008) are involved in both reward/gain and punishment/loss anticipation as they both would be expected to elicit an enhanced motivational state compared to neutral anticipation (Carter et al., 2009). A study by Hassani et al. (Hassani et al., 2001) further investigated the complex processes related to reward in the anterior striatum. They examined neural activity in monkeys while preforming a spatial-delayed-response task and found that a fraction of task-related neurons (e.g., spatial activations, compromising responses to instruction etc.) are activated by the anticipation of the upcoming reward. They also found that different levels of expected rewards influenced different behavior-related neuronal activity. Apparently, information about the expected reward is incorporated into the neuronal activity related to the behavioral reaction leading to the reward (Hassani et al., 2001).

1.3.1. Anxiety, fear learning and memory, spatial navigation, and their relation to AF

AF is also involved in anxiety and fear learning and memory, and forms of cognition such as object recognition and spatial navigation.

In tests assessing exploratory behavior and measures of anxiety, there is a balance or conflict scenario (approach-avoidance) between a drive to explore the novel environment on one hand and reducing time spent in more anxiety-provoking and potentially dangerous environments on the other hand. In the open field test, the center area is more anxiety provoking (Van Meer and Raber, 2005; Wilson et al., 1976). In the elevated plus maze (Laviola et al., 2003; Lister, 1987) and elevated zero (Kulkarni et al., 2007; Shephard et al., 1994), animals are driven by curiosity to explore the anxiety-provoking open areas of the maze. In the tests described above, the animal can select to enter or avoid the anxiety-provoking areas. While these tests are typically used in rodents, humanized versions of the elevated plus maze containing virtual reality and real-world elements have been developed as well to study anxiety-related behavior in humans (Biederman et al., 2017). In the acoustic startle test (Parham and Willott, 1988), animals are placed in a sound-attenuated box on a sensing platform; they receive acoustic stimuli consisting of white noise. These stimuli will startle the animal, resulting in a full-body flinch recorded by the sensing platform. When the stimuli are administered at equal and therefore predictable intervals, there could be AF (Webber et al., 2013). Acoustic startle tests are also being used in humans (Knudson and Melcher, 2016) and therefore involve AF as well. Place cells fire when an animal is in a given location in an environment; place cells with prospective activity prior to a choice point at which an animal chooses a path illustrates the close connection between AF and cognitive performance (Ainge et al., 2012; Grieves et al., 2016) (Fig. 2). In novel environments, the animals can vocalize that can be part of AF and affect AF in other animals too (Hollen and Radford, 2009; Wohr et al., 2008). Vocalization can also occur as part of conditioned fear (Kikusui et al., 2003). In addition to vocalizations, song learning in birds is also related to AF in both the singing bird and

the recipient listening bird (Alvarez-Buylla et al., 1988; Nottebohm et al., 1990).

Emotional learning and memory illustrate another example. For example, in the passive avoidance test, an animal is trained to refrain from entering a dark area they normally would prefer (Sanger and Joly, 1985). Thus, AF is important in the decision of the animal to enter the dark compartment the first time as well as during subsequent trials. AF is also involved in cognitive tests in which animals are trained to locate a platform beneath opaque water in the water maze (Morris, 1984) or when they are trained to locate an escape tunnel in the Barnes maze (McLay et al., 1999; Raber et al., 2004). As humanized tests of spatial learning and memory based on animal tests have been developed (Berteau-Pavy et al., 2007; Rizk-Jackson et al., 2006), AF would be pertinent to these human tests as well. Finally, AF is involved in associative learning and operant conditioning described in the previous section.

2. AF and bodily-related stimulus processing

As outlined in the Introduction, AF are feelings closely related to anticipation, decision making and action planning. However, which feelings (positive or negative) will be experienced in anticipation of an event is determined by situational and intrapersonal factors, as well as by bodily states (*e.g.*, interoceptive and somatic markers).

Theoretically, the somatic marker hypothesis (Damasio et al., 1991) as well as predictive coding theories and their extension to bodily and interoceptive processing (*e.g.*, (Seth, 2013) underscore the neural mechanisms and brain networks assumed to play a pivotal role in linking the processing and regulation of changes in the body with AF. The somatic marker hypothesis overcomes the traditional split between mind and body by proposing that bodily changes elicited by discrete emotional events are represented and stored in the brain as somatic markers. These somatic markers can then be activated in anticipation of a future event in order to guide future decisions based on past experiences (Damasio et al., 1991). Thus, according to the somatic marker hypothesis, interoceptive as well as proprioceptive bodily signal processing, together with its representation and integration in the brain, can be considered a fundamental component of AF.

2.1. The role of bodily-related stimulus processing in AF - I: the somatic marker hypothesis and its neural correlates

Studies investigating AF in the context of planning and decision-making support a major role of the orbitofrontal cortices (OFC) and the medial prefrontal cortex in bodily-related stimulus processing (Kringelbach, 2005). Moreover, damage to the ventromedial prefrontal cortex (vmPFC), including the OFC, has been shown to impair the ability to predict the future consequences of one's actions (Rich et al., 2018; Schneider and Koenigs, 2017). Building on observations in patients with vmPFC damage, the somatic marker hypothesis (Damasio et al., 1991) posits a close interaction in the brain between the processing of bodily-related information, emotional states, decision-making and AF. In essence, the somatic marker hypothesis extends the James-Lange theory of emotion by stating that bodily changes and the perception of those changes are essential for the generation of emotions and the experience of emotions as feelings (James, 1890, 1894). Unlike James' theory, the somatic marker hypothesis specifically assumes that bodily changes are re-represented in the brain. Re-representation means that physiological changes and neural brain changes that develop in response to certain events are tied together and associated with specific emotional states. These "associations" between events, physiological changes in the body and feeling states are stored together as markers and are thought to influence planning and intuitive decision making through neural network activity including, amongst others, the OFC and the amygdala. This principle of re-representation in the brain, also called the as-if-body loop (*i.e.*, the possibility to simulate and imagine
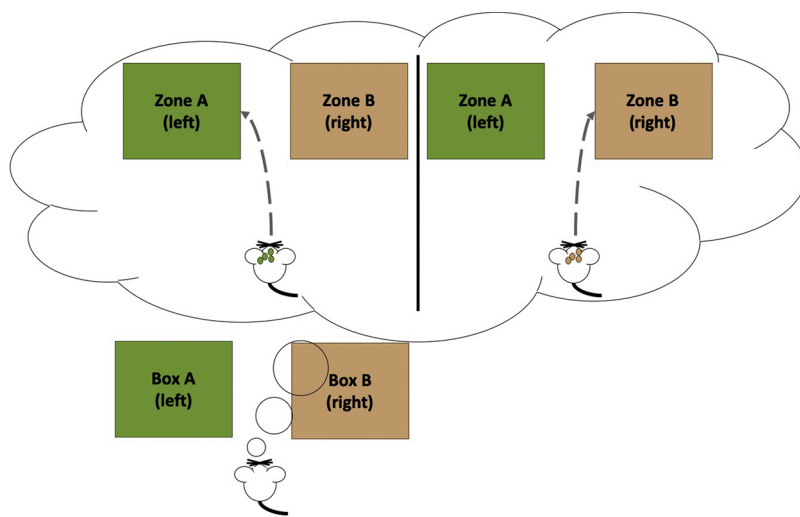
Fig. 2. An example of evidence that distinct sets of neurons will fire during the pre-behavioral stages of decision making in rodent models, for example prior to turning left or right, supporting AF. This has been shown prior to entering into a zone (or arm of a maze) either to the left or right (for a review, see (Eichenbaum, 2014)). A similar pattern would be expected for animals turning or entering a distinct zone in the behavioral test described above, including entering the dark compartment in the passive avoidance test or entering a open area in the elevated zero or plus maze.
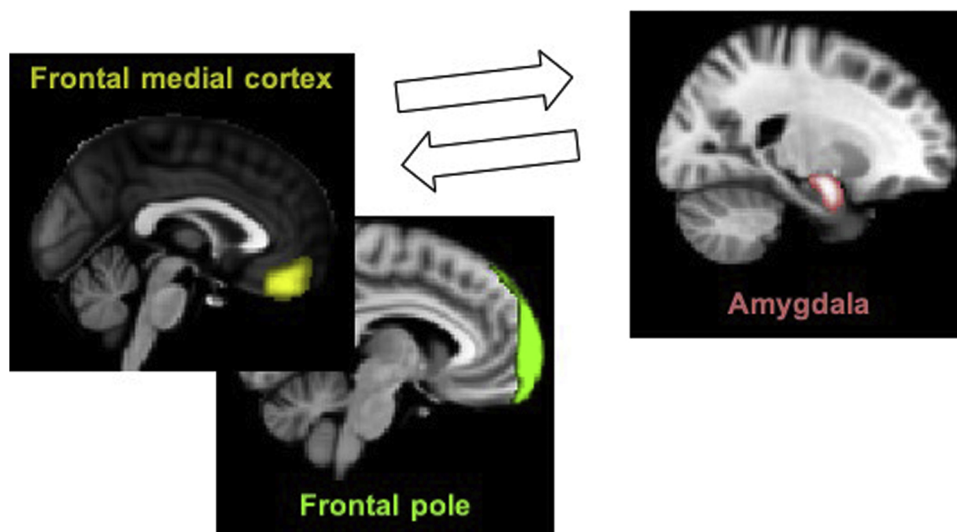
Fig. 3. The principle of **re-representation**: as-if-body loop between medial frontal cortical areas (green and yellow) and subcortical regions like the amygdala (pink). The anatomical areas are taken from the Harvard-Oxford Cortical/ Subcortical Structural Atlas and overlayed on a template in MNI space. The coordinates of the sagittal planes are: frontal medial cortex (yellow) x = 0, frontal pole (green) x = -6, amygdala (pink) x = 22.

behavior based on anticipated feelings without executing actions), has been considered the core of effective decision making. Ingrained body-related markers like anticipatory skin conductance response (Dawson et al., 2011), or "gut feelings" (Mayer, 2011), are thought to trigger positive behavioral effects: accelerating intuitive decision making, and facilitating beneficial planning to simulate embodied predictions of future events. Maladaptive decision making performance has been demonstrated in several mental disorders including addiction, which often go along with neuroanatomical and neurochemical abnormalities in corticolimbic brain circuits including the vmPFC and amygdala (Motzkin et al., 2015) (Fig. 3).

Additionally, another network has been proposed to play an eminent role. This network, the salience network (SN) (Menon, 2015), changes its activity whenever there is a switch from a resting, default mode to a task-related perceptual and emotional decision processing. The salience network comprises the insular and the anterior cingulate cortex and subcortical regions (amygdala, ventral tegmental area, thalamus) (e.g., (Menon, 2011; Menon and Uddin, 2010)(Fig. 4). Although the insular cortex is principally seen as a brain region involved in interoceptive awareness, emotional and empathic responses, it is also involved in a variety of processes necessary for predicting outcomes, anticipating gain and losses (Knutson and Greer, 2008; Knutson et al., 2007; Levin et al., 2012; Paulus and Stein, 2006), making decisions under uncertainty (Weller et al., 2007), and risk taking (Ishii et al., 2012, 2013).

Based on the anatomical and functional connections of the insula to the vmPFC/OFC, as well as the role of the posterior insula in internal (visceral) bodily signal processing and the role of its anterior part in the generation of subjective feelings states, it has been suggested that the insula constitutes an essential neural hub for integrating autonomic, affective and cognitive processing (Craig, 2009; Critchley, 2009; Namkung et al., 2017). The insula, then, can be considered a brain structure that connects bottom-up with top-down signal processing and external with internal signal processing. Accordingly, AF can be considered mutually connected (via the insular cortex and the salience network (SN) with the homeostatic state of the body as well as with emotional and motivational processes.

2.2. The role of bodily-related stimulus processing in AF - II: predictive coding and the homeostatic hypothesis

Akin to the somatic marker hypothesis, the homeostatic emotion hypothesis highlights the relevance of bodily-related stimulus processing in the generation and processing of AF. Specifically, homeostatic emotion hypothesis posits that key neuroanatomical substrates underlie interoception in humans and substantialize feelings from the body (in the insular cortex) together with homeostatic motivations that guide adaptive behaviors (in the cingulate cortex) (Strigo and Craig, 2016).

A phylogenetically novel ascending pathway which terminates partly in the mid/posterior insular cortex in primates was first proposed
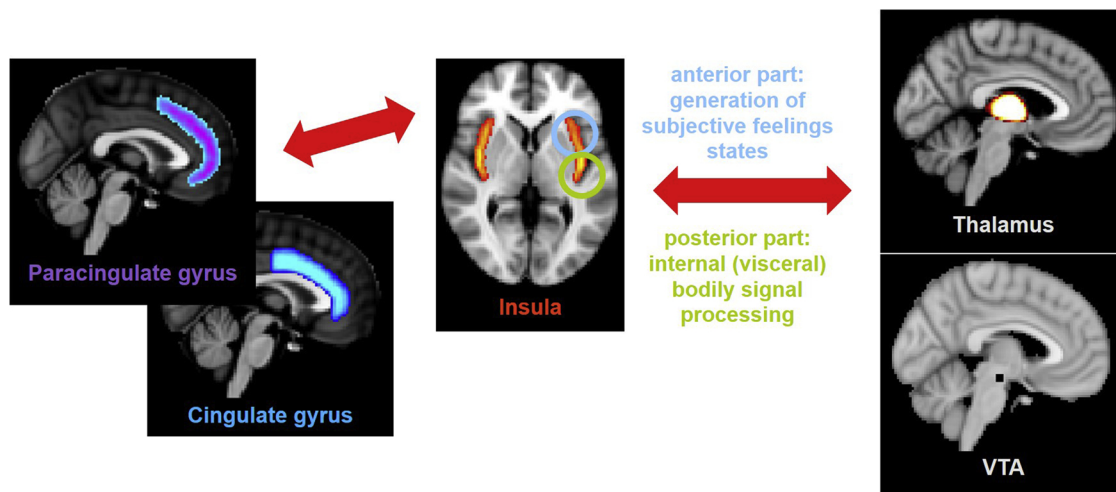
Fig. 4. The **salience network** comprises the insula, the anterior cingulate cortex (blue) and subcortical regions such as the amygdala, the ventral tegmental area (VTA, black) and thalamus (bright area). The insula is seen as the neural hub for integrating autonomic, affective and cognitive processing. The anterior part of the insula (circled in light blue) is assumed to be involved in the generation of states of subjective feelings, whilst the posterior part (circled in green) is assumed to be involved in internal (visceral) bodily signal processing.
The anatomical areas are taken from the Harvard-Oxford Cortical/Subcortical Structural Atlas and overlaid on a template in MNI space. The coordinates of the separate planes are: paracingulate gyrus (purple) x = 0, cingulate gyrus (blue) x = 0, insula (orange) z = 2, thalamus (bright) x = -4. As the VTA is not included in the Harvard-Oxford Cortical/Subcortical Structural Atlas, its location was rebuild based on Peterson et al. (2017) (Peterson et al. (2017): The effects of age, from young to middle adulthood, and gender on resting state functional connectivity of the dopaminergic midbrain. Front Hum Neurosci 11:1–14).

by Craig (Craig et al., 2000). Since then, the insular cortex has been considered the brain's homeostatic afferent side of the autonomic nervous system (Craig, 2002). In the human brain, those neural signals are processed in the (posterior) insula and concurrently in the anterior cingulate cortex. There is evidence that information processed in the posterior insular cortex is represented and integrated in anterior parts of the insula. In support of this, anterior insular activity has been found to be correlated with affective feelings (Craig, 2002, 2009; Craig et al., 2000), whereas posterior insular activity seems to be associated with discrete bodily, somatosensory and visceral sensations such as thirst (Meier et al., 2018), hunger (Wright et al., 2016), and taste (Schier et al., 2016).

An increasing number of functional neuroimaging studies investigating neural activity in the interoceptive cortex (the posterior insula) by manipulating subjects' physiological responses or directing subjective awareness to certain bodily sensations, have found that both consciously perceived feelings of interoception and unconsciously processed physiological cues may serve as substrate to constitute anticipatory (affective) feelings (Critchley et al., 2004) and influence planning and planning linked behavior. Hence, to promote homeostatic information during affective planning, feeling states are generated on the basis of past experiences and on the basis of predictions about the physiological state and condition of the body; a process argued to have anticipatory (bottom-up) and regulatory (top-down) properties. It is assumed that the human brain anticipates and predicts the impact of (potentially harmful) physiological stimuli from the internal and external environment and subsequently generates appropriate behavioral (planning) and physiological responses in order to adapt and accommodate changes that are anticipated. Related to AF, this also emphasizes the importance of physiological cues to guide human decision making and behavior. Anatomical and functional evidence from brain imaging studies supports the combination of two major neural brain networks: the so-called default mode network and the salience network (SN; see Fig. 4), including the insula as interoceptive cortex to preserve homeostasis during affective planning and during risky and uncertain decision making.

2.3. Neural networks related to AF and bodily-related stimulus processing: the special role of the insular cortex and medial prefrontal brain regions

Currently, the question is whether homeostatic regulation of bodily-related signal processing, including (dys)-functional neural activity in the networks outlined above, modulates the ability to appropriately anticipate bodily needs. Studies using different neuroimaging approaches, including cytoarchitectonic mapping (Kurth et al., 2010), diffusion imaging-based tractography (Cerliani et al., 2012), neurochemical (Wiebking et al., 2014) and task-related functional magnetic resonance imaging (fMRI) (Critchley et al., 2004) have underlined the complex role of the insula in affective, interoceptive and regulatory behavioral mechanisms. Consequently, the potential involvement of insula dysfunction in the generation of dysfunctional AF has been investigated in both mental and somatic disorders. Investigating healthy individuals without prior history of psychiatric diseases revealed that task-related insula (and amygdala) activity increases during the anticipation of aversive events (Carlson et al., 2011). Activity changes in the right anterior insula predict the subjective experience of anxious anticipation during aversive anticipation, whereas activity changes in the left insula and left amygdala correlate with trait anxiety (Carlson et al., 2011). Thus, activity changes in the insula and the amygdala are related to anxiety (Critchley et al., 2004), to subjective feelings of anxious anticipation (Baur et al., 2013) and aversive anticipation (Meyer et al., 2018) in healthy individuals. Changes in insula-amygdala function have also been replicated in groups of patients suffering from clinical anxiety (Grupe and Nitschke, 2013) and depression (Paulus and Stein, 2010). This lends support to the view of anticipatory prediction processing as a general principle of the brain and highlights the role of the insular cortex (anterior insula) as a converging zone for impairments in affective regulation and the perception of internal body states.

2.4. AF, bodily-related stimulus processing and language: Is there a link?

Current neuroscientific research on AF outlined above suggests that on a neural level, most processes associated with AF are related to activity changes in brain areas that do not constitute typical language processing areas. Theoretically, language, emotion, and bodily processes have long been considered as independent processes. However,

embodiment theories have challenged this assumption and have suggested that even the most abstract cognitive processes and human abilities such as reasoning or language processing can be considered as embodied and grounded in internal models of perception and action (*e.g.*, for overviews see (Barsalou, 2008; Niedenthal et al., 2005)). Accordingly, the past decade of research has accumulated evidence challenging the view of language representations as being isolated from perception, actions or emotions. Several recent studies have shown that even reading single words or sentences with an emotional content (in the absence of additional sensory input) can be accompanied by physiological changes in the body (*e.g.*, changes in facial muscle activity, sympathetic arousal) and evoke neurophysiological changes in brain regions involved in motivational priming of approach-avoidance behavior, motor, sensorimotor and visual processing (for an overview see (Dreyer and Pulvermuller, 2018; Herbert et al., 2018; Kissler et al., 2006; Winkielman et al., 2015). Interestingly, the acoustically elicited startle reflex, typically elicited in animals (see section 1.2) and in humans in response to and during fearful anticipation (*e.g.*, (Sabatinelli et al., 2001) seems to be modulated by verbal foreground stimuli as well (Herbert and Kissler, 2010), particularly in anxious individuals (Miller and Patrick, 2000). Thus, the role of language in emotion and affective processing assumes a much stronger role in humans than has traditionally been considered. In particular, "transforming" subjective feelings into words may not only induce emotions and feeling states, but may also modulate emotion perception (Barrett et al., 2016; Herbert et al., 2013; Lindquist et al., 2015). Interestingly, reading words that refer to the reader's own emotions has been found to elicit changes in neural activity in the left and right insula, amygdala, and parts of the ventral medial prefrontal cortex (Herbert et al., 2011), all known to be critically involved in the awareness of body states (interoception), in self-referential processing of emotions and in feelings of emotional ownership (Northoff et al., 2006). The meta-analysis conducted within this review (see section 5) supports an overlap of activation in dedicated brain regions for language and affective feelings including the insula. Section 7 of this review presents the words in the English language that people use to express AF

3. Dispositional factors underlying positive AF

3.1. Positive anticipatory emotions

3.1.1. Optimism

The neurobiology of positive anticipatory emotions can be investigated by examining the relationship between brain function and structure with a trait or personality characteristic such as optimism. Optimism, defined as the expectation of positive outcomes, has been linked to psychological and physical well-being as well as higher life satisfaction (Hinz et al., 2018) and is believed to be very similar to the personality trait of hope (Bryan and Cvengros, 2004).

While optimism and hope both involve positive future-oriented expectations and are often used synonymously in the literature, some researchers argue that they are dissociable constructs. Optimism is proposed to reflect a state of general positive expectancy (e.g., today will be a good day), whereas hope is associated with personal agency and self-initiated actions that are expected to result in specific positive outcomes (e.g., getting a good grade on a test) and are more closely related to wanting "states (Alarcon et al., 2013; Bruininks and Malle, 2005; Gallagher and Lopez, 2009).

Investigations of the neural basis of these constructs have indicated that the OFC, particularly its medial region (referred to as medial OFC or vmPFC), plays a key role in trait optimism and hope. In one study, the fractional amplitude of low-frequency fluctuations with resting-state fMRI, which measures the strength or power of low frequency (< 0.8 Hz) oscillations, trait hope was negatively correlated with power in the bilateral medial OFC during rest (Wang et al., 2017a). Trait optimism has been shown to be negatively correlated with resting-state

connectivity between the vmPFC/medial OFC and right inferior frontal gyrus (IFG) (Ran et al., 2017), and positively related to gray matter volume in the lateral and medial OFC (Dolcos et al., 2016) as well as the thalamus/pulvinar (Yang et al., 2013). In a task-based investigation where participants imagined future events, greater trait optimism was associated with increased activity in a region appearing to include the vmPFC, referred to in the article as rostral anterior cingulate (Sharot et al., 2007) when comparing positive with negative future event imagination. A critical component of trait optimism is believed to lie in a pervasive cognitive bias known as optimism bias. This is broadly defined as the tendency to overestimate the likelihood of positive events occurring (*e.g.*, living longer than average) and underestimate the likelihood of negative events occurring (*e.g.*, getting a divorce) (Kress and Aue, 2017; Sharot et al., 2007). The optimism bias can be found in the majority of people, i.e. in about 80 % - even in animals such as rats and birds - but it disappears in psychiatric diseases such as depression (Garrett et al., 2014; Sharot, 2011) or anxiety disorders (Blair et al., 2017). Remarkably, optimistic illusions seem to be only adaptive misbeliefs (McKay and Dennett, 2009). It is possible that optimism bias could be related to inaccuracies in affective forecasting, or the ability to predict how one will feel about a future event. Individuals have a tendency to overestimate the intensity and duration of both positive and negative future emotional reactions (Miloyan and Suddendorf, 2015; Wilson and Gilbert, 2005), and it is possible that overestimations regarding the anticipated happiness that would result from a positive future event could further contribute to optimism bias.

Optimism bias is driven by the motivation to adopt the most favorable or rewarding expectations and dismiss evidence that would lead to unfavorable expectations, thus creating asymmetrical belief patterns in an overly positive direction (Sharot et al., 2011). In line with this supposition, studies have confirmed that healthy individuals consider themselves significantly more likely to experience positive events than negative events (Blair et al., 2013; Sharot et al., 2007). In recent neuroimaging research, several paradigms have been utilized to elicit the optimism bias. In one of the earlier fMRI studies focusing on optimism, Sharot et al. (Sharot et al., 2007) directed participants to think of either a past or future autobiographical life events (*e.g.*, winning an award, the end of a romantic relationship), which were then classified into positive, negative, and neutral events. Although this study did not compute the optimism bias behaviorally, the neuroimaging contrast (comparing brain activation when imagining future positive events to that when imagining future negative events) may provide a neural index of the asymmetrical relationship between positive and negative event processing that is at the core of the optimism bias. Results showed greater activity in vmPFC, the amygdala, and increased functional connectivity between the two regions when imagining future positive events relative to future negative events. In an adapted version of this paradigm, Blair and colleagues (Blair et al., 2013) presented participants with both positive future events (*e.g.*, finding a cure for AIDS) and negative future events (*e.g.*, being sentenced to jail). The optimism bias was behaviorally quantified through ratings where participants indicated the probability of each event occurring across their lifetime compared to individuals of the same age and gender. There was a highly significant optimism bias such that participants rated themselves as more likely than others to have positive events and less likely than others to have negative events. Similar to the results from Sharot et al. (Sharot et al., 2007), increased activity in the vmPFC was associated with thinking about positive versus negative future events; however, activity in this region was not modulated by individual participants' optimism bias. Instead, greater optimism bias for positive events was associated with increased rACC activity in a region that did not overlap with the vmPFC (area found for the contrast of positive vs. negative event processing), whereas greater optimism bias for future negative events was associated with reduced anterior insula and dorsomedial prefrontal cortex (dmPFC) activity (Blair et al., 2013). The authors argue that these findings distinguish between a more general evaluation

signal in the vmPFC (distinguishing "good" from "bad") – a sensitivity that could no doubt contribute to trait optimism (Sharot et al., 2007) - and other regions including rACC, dmPFC, and insula, which are involved in generating an individual's specific optimism bias. Research from Sharot's lab provides further evidence that patients with major depression tend to update their beliefs in a more unbiased way (Garrett et al., 2014). In their study, depressed patients updated their hopes in both ways, positive and negative, while healthy controls showed an optimism bias tending to more integrate positive news. Importantly, mild depressed patients suffer from a lack in a positive bias than the occurrence of a negative bias - leading to a more realistic view. Activation in fMRI showed that the left IFG and bilateral superior frontal gyrus mediate positive information, while the right inferior parietal lobule and right IFG processed negative information about the future.

Finally, in order to examine the maintenance of an optimistic outlook even in the face of disconfirming evidence, a belief updating paradigm was implemented in two studies (Kuzmanovic et al., 2016; Sharot et al., 2011). In both studies, healthy individuals updated their beliefs less after receiving unfavorable information (*i.e.*, the base rate of the negative event is higher than the participant estimated) versus favorable information (*i.e.*, the base rate of the event is lower than the participant estimated). That is, they showed a strong optimism bias since they were more likely to update their estimates in an optimistic direction after receiving a base rate that was better (*i.e.*, lower) than they had originally estimated, but less likely to update their beliefs in a pessimistic direction after receiving a base rate that was worse (*i.e.*, higher) than they originally estimated (Kuzmanovic et al., 2016; Sharot et al., 2011). Greater estimation updating following the presentation of favorable information was associated with augmented activity in the vmPFC (Kuzmanovic et al., 2016), as well as dmPFC and right cerebellum (Sharot et al., 2011). Interestingly, greater vmPFC activity was also linked to smaller estimation updates following the presentation of unfavorable information an effect that was also found in occipital and temporal cortex, dmPFC, ventral striatum, and thalamus (Kuzmanovic et al., 2016). Moreover, the results of Sharot and colleagues (Sharot et al., 2011) suggest a specific role for right inferior frontal gyrus (IFG) in the ability to integrate undesirable information and update likelihood estimates for negative events. Additionally, individuals with higher trait optimism show reduced IFG responses to unfavorable information,

3.1.2. Hope

Contrary to the abundant literature for optimism, only one fMRI study investigated the neural correlates of hope as a trait and its impact on anxiety (Wang et al., 2017b). The authors examined the fractional amplitude of low-frequency fluctuations (fALFF) with resting-state fMRI, which measures the strength or power of low frequency (< 0.8 Hz) oscillations. Stronger trait hope as measured with the dispositional hope scale (DHS) was related to lower fALFF in the bilateral medial OFC. Such an association was also detected between trait hope and regional homogeneity, but only if the association was analyzed in this region. Mediation analyses revealed that the trait hope might be regarded as a mediator between bilateral medial OFC and anxiety.

Together, research examining hope and optimism identified several key brain regions including OFC/vmPFC, dmPFC, rACC, and IFG (Fig. 5). Although results differ between studies, the prominence of the vmPFC indicates that this region likely contributes to the neural mechanisms of optimism, possibly due to its role in self-referential processing and evaluation (Blair et al., 2013; Kuzmanovic et al., 2016). The involvement of IFG, anterior insula, and dmPFC, regions associated with cognitive control and executive attention (Dosenbach et al., 2007; Smith et al., 2009; Vincent et al., 2008), may reflect the integration of information about the future that forms positive or negative beliefs (Kress and Aue, 2017; Ran et al., 2017; Sharot et al., 2011).

3.1.3. Reward anticipation

In addition to investigating how trait levels of optimism correlate with brain functioning, fMRI tasks can be devised to experimentally elicit positive emotions in individuals, allowing researchers to average brain patterns associated with positive anticipation. Probably the most widely investigated process related to positive anticipation in the field of cognitive neuroscience is the anticipation of monetary reward, which measures positive anticipatory experiences that are qualitatively different from those related to optimism. Whereas studies of optimism tend to examine positive anticipatory emotion related to personal, highly self-relevant, and potentially remote future events, reward anticipation studies examine brief time periods between a cue designating a potential monetary (or other non-personal reward) and receiving that reward, which is usually just a few seconds (Bradley et al., 2017; Breiter et al., 2001; Carter et al., 2009; Dillon et al., 2008; Ernst et al., 2004; Kirsch et al., 2003; Knutson et al., 2001a, b; Knutson et al., 2003; Rademacher et al., 2010; Spreckelmeyer et al., 2009). In most studies investigating reward anticipation, individuals are presented with a cue indicating that they could potentially gain money on a given trial. After, they are required to make a response when a target stimulus appears on the screen in order to receive the rewarding outcome immediately thereafter (Bradley et al., 2017; Carter et al., 2009; Dillon et al., 2008; Kirsch et al., 2003; Knutson et al., 2001a, b; Knutson et al., 2003; Rademacher et al., 2010; Spreckelmeyer et al., 2009). Less frequently, participants are simply presented with cues indicating they will receive an upcoming reward or no-reward without requiring a response (Breiter et al., 2001; O'Doherty et al., 2002) or select between "gamble" options that either lead to no-reward or varying amounts of monetary reward (Ernst et al., 2004). In most of these studies, reward anticipation is isolated by comparing activation during the time interval between the cue and the outcome for reward trials with that for no-reward (or lesser reward) trials, in order to control for general effects of anticipatory attention.

In general, results from these studies indicate that reward anticipation activates a network of brain regions including dorsal striatum (putamen, caudate nucleus), ventral striatum (nucleus accumbens), thalamus, medial prefrontal areas including cingulate cortex, dmPFC, and supplementary motor area (SMA), and insula (Bradley et al., 2017; Carter et al., 2009; Dillon et al., 2008; Ernst et al., 2004; Kirsch et al., 2003; Knutson et al., 2001a, b; Knutson et al., 2003; Rademacher et al., 2010) (Fig. 5), areas involved in processing saliency (striatum, insula, medial frontal cortex) (Seeley et al., 2007; Zink et al., 2004) and task-set initiation and maintenance (Dosenbach et al., 2007) (insula and medial frontal cortex). Less commonly, a wider network of areas has been reported, including midbrain regions (ventral tegmental area and substania nigra), OFC, parietal and temporal cortex, precentral and postcentral gyri, cerebellum, and occipital cortex (Bradley et al., 2017; Breiter et al., 2001; Ernst et al., 2004; Kirsch et al., 2003; Rademacher et al., 2010). The difference in these findings may be related to methodological factors. Indeed some studies reporting a more limited scope of neural activity did not acquire whole-brain images (Carter et al., 2009; Knutson et al., 2001a, 2003). Those studies identifying a wider network of brain regions suggest that reward anticipation may involve the engagement of a host of regions involved in the extended reward system (dopaminergic midbrain neurons projects to the nucleus accumbens, (Swanson, 1982), executive function (parietal cortex), sensorimotor processing (precentral and postcentral gyri and cerebellum), and even visual regions (occipital cortex) (Smith et al., 2009) Vincent 2008), revealing a complex network that goes well beyond those areas typically linked to reward.

4. Dispositional factors underlying negative AF

4.1. Negative anticipatory emotions: pessimism and worry

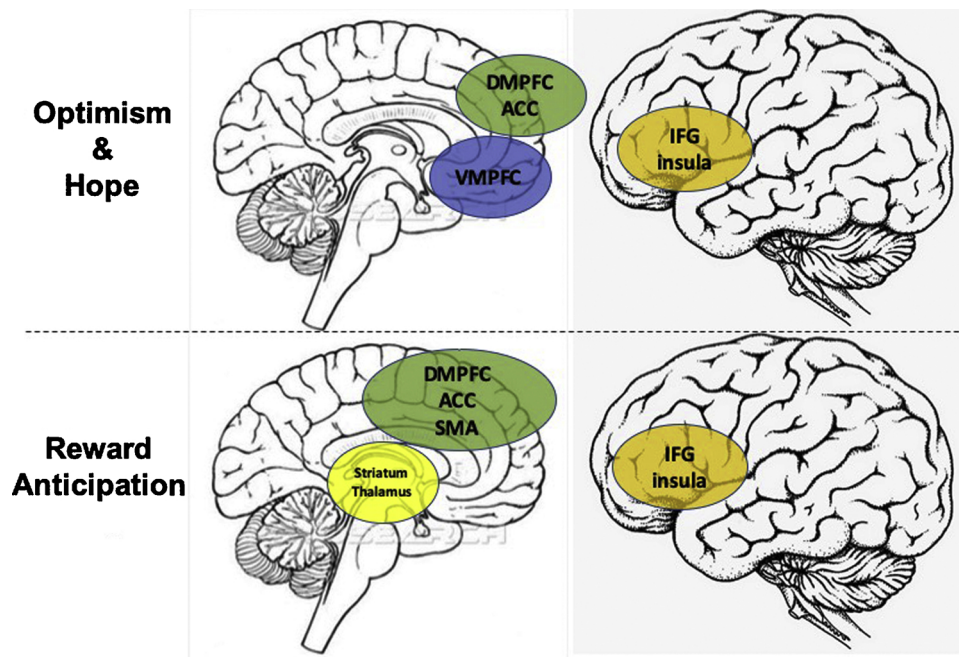The most commonly used psychological construct related to

Fig. 5. Brain regions involved in optimism and hope (top panel) and reward anticipation (bottom panel).

negative anticipation is dispositional pessimism, defined as a general tendency to expect negative outcomes (Norem, 2007). The term pessimism can also refer to a fixation on the "darker" aspects of a situation or event, to the acute expectation of a negative outcome, or to a lack of hope for the future (Carver and Scheier, 2014; Drozd et al., 2016). There are opposing views on whether optimism and pessimism should be approached as two independent constructs or as two poles of a single dimension. Authors who are inclined to the first approach argue that these distinct modes of thinking are best conceptualized, not rigidly and dichotomously but rather, as a continuum with many degrees of optimism and pessimism since a person can be optimistic with regard to a specific area of life (*e.g.*, expecting his/her marriage/relationship to succeed) but pessimistic concerning other aspects (*e.g.*, expecting financial difficulties ahead); people may also shift positions on the optimism-pessimism continuum as the timeline unfolds (Hecht, 2013). These two mental attitudes (optimism *vs.* pessimism) are linked with different processes of the brain. For example, converging evidence from psychology, physiology, psychiatry and neurology suggest that the two cerebral hemispheres are differentially involved in mediating the fundamental approach to life: pessimistic views are generally mediated by the right-hemisphere, whereas optimistic attitudes are mediated primarily by the left-hemisphere (Davidson and Sutton, 1995; Hecht, 2013; Kinsbourne, 1978). Specific cognitive aspects of pessimism are: a) selective attention and information processing (*e.g.*, focusing attention on the negative aspects of a situation or event), b) a lack of belief that one has power to influence relevant situations, events and relationships (locus of control), and c) a negative general schema one holds for interpreting personal events (negative attribution style).

Worry is a broader construct closely associated with pessimism, a complex cognitive phenomenon that is thought to incorporate different emotional and cognitive components, including a tendency to exhibit elevated subjective probabilities of negative events. The study by McLeod et al. (MacLeod et al., 1991) suggests that chronic worriers tend to use pessimistic subjective probabilities when thinking about future outcomes. Furthermore, they suggest that the underlying reasoning process can be described as an increased accessibility to explanations for why a negative event would occur, combined with a reduced accessibility to explanations for why it would not. Moreover, a later study confirmed that worriers are not only preoccupied with

future unpleasant outcomes but show a greater degree of belief in the likelihood of those outcomes (MacLeod, 1994). Although the concepts of worry and pessimism might seem similar, a correlational study by Sjoberg (Sjöberg, 1998) confirmed that they are in fact two different constructs. Results showed that pessimism, worry and risk perception consist of different emotional and cognitive components, although all are related to negative perception of future events and often interpretation of present events.

4.2. Neural correlates of pessimism and worry

Neuroimaging studies have shown that activity in the amygdala, prefrontal cortex, insula and ACC increase during the anticipation of threats, negative events and stimuli; fMRI studies have shown activity in the medial thalamus, right inferior and left posterior insula, right IFG and nucleus ruber in subjects with a pessimistic outlook that had high depression and neuroticism scores when expecting stimuli of an "unknown" valence (Herwig et al., 2007)(Fig. 6). Medial thalamic regions receive inputs from viscera-sensitive and pain mediating brain stem areas (Vogt, 2005), the insula is involved in discriminating negative and positive emotions and in anticipation of negative events (e.g., receiving an electroshock; (Chua et al., 1999) as well as in the amygdala, *i.e.*, valence detection (Sander et al., 2007). The IFG and vmPFC are associated with emotion processing and regulation (Morawetz et al., 2017) when anticipating a negative event (Ueda et al., 2003). These findings support the hypothesis that pessimists process unknown future events, as one would a potentially dangerous or negative future event.

Another important question is whether the brain regions associated with anticipating rewards are also activated when anticipating potentially negative outcomes or losses. Studies that have compared reward and punishment/loss anticipation have found overlap among involved brain regions including OFC (Carter et al., 2009; O'Doherty et al., 2002); but see Kim who found medial OFC for anticipation of reward only), lateral prefrontal cortex and temporal cortex (Breiter et al., 2001), dorsal striatum (Carter et al., 2009; Knutson et al., 2001a, 2003), anterior insula, and thalamus (Carter et al., 2009; Knutson et al., 2003), but see Kim (Kim et al., 2011) who found anterior insula increases for anticipation of loss only), medial PFC (Carter et al., 2009; Dillon et al., 2008; Knutson et al., 2003) and occipital cortex (Breiter et al., 2001;
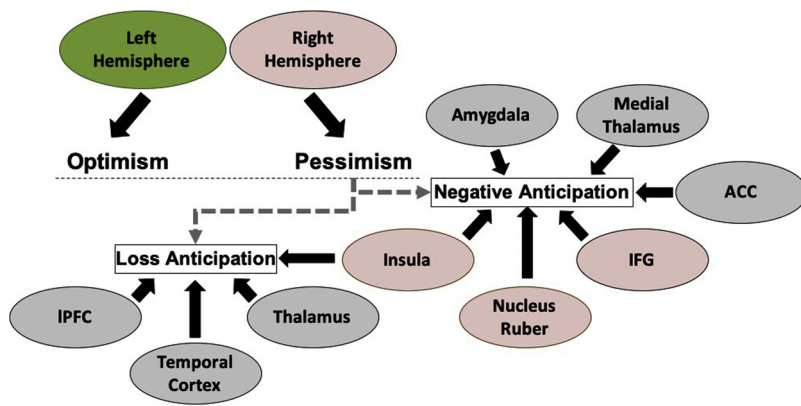
Fig. 6. Brain regions associated with negative anticipatory emotions. The right hemisphere has been shown to contribute more to general pessimistic anticipation, whereas the left hemisphere has been shown to be more associated with optimistic expectations. Under this category, negative anticipation (such as for negative events) is associated with activation of the right insula, right nucleus ruber, right IFG, as well as the amygdala, thalamus and ACC. When looking at anticipation of punishment or loss, the right anterior insula is also activated, in addition to the lateral PFC, temporal cortex, and thalamus.

Carter et al., 2009).

5. The neural correlates of AF and associated mental functions with quantitative and conjunction meta-analyses

We identified the neural networks of mental processes relevant for AF discussed in the review by calculating meta-analyses across imaging studies from the literature with the neurosynth database (http://www.neurosynth.org; (Yarkoni et al., 2011)). Results are illustrated in Table 2 and Fig. 7, left upper part. Overlapping networks include the nucleus accumbens, caudate nucleus, putamen, globus pallidus, thalamus, amygdala, midbrain, orbitofrontal cortex, (anterior) insula, frontomedian cortex, (anterior) cingulate cortex, subcallosal area and frontolateral cortex. Moreover, we conducted a conjunction analysis across the neural networks of all investigated mental functions to extract brain regions that reached significance with the chosen threshold (FDR corrected) criterion of 0.01 for more than one function (Fig. 7, right upper part). This conjunction analysis confirmed the nucleus accumbens, caudate nucleus, putamen, globus pallidus, thalamus, amygdala, midbrain, orbitofrontal cortex, anterior insula, frontomedian cortex, anterior cingulate cortex and subcallosal area as the most consistent hubs in this neural network.

Finally, we added a conjunction analysis with the aforementioned mental functions and language. As illustrated in Fig. 7 (right lower part), the conjunction analysis identified the same neural core network with a more pronounced cluster in the left anterior insula and two new clusters, one in the left posterior frontomedian cortex and the other in the left frontolateral cortex, i.e., mainly around the inferior frontal junction area but extending to the inferior frontal gyrus. These brain regions might be hypothesized as being relevant for interaction between the aforementioned functions and language. Note that comparing the language network with the networks for each of the other mental functions separately revealed, beside others, an overlap of language

with anticipation, emotion, decision and planning in the left anterior insula, with decision and planning in the left frontolateral and frontomedian cortex, and with emotion in the left orbitofrontal cortex.

Meta-analytic results for anxiety and fear are presented in Fig. 8. Obviously, these terms are contained conceptually in the term emotion, and, correspondingly, were associated with a similar neural network, i.e. the amygdala, (anterior) insula, globus pallidus, anterior frontomedian cortex, anterior cingulate cortex, and subcallosal area. The network for fear also included the midbrain, midcingulate and orbitofrontal cortex.

Although a quantitative meta-analysis as done here within the neurosynth database yields a potentially excellent platform for generating and validating hypotheses in cognitive neuroscience, its present value is limited due to the rather broad terms / concepts contained in this database with valid data, i.e. containing a sufficient number of studies, and due to the automatic and rather uncontrolled structure of neurosynth. Note also that the term AF itself is not contained in the neurosynth database, requiring other related terms to be used as a substitute. Accordingly, results require replication in other better controlled meta-analytic approaches containing more focused terms.

6. AF: valence, neural correlates, and related mental disorders

Alterations in AF may function as a potential risk factor for several mental disorders including schizophrenia, borderline personality disorder, depression, anxiety disorders as well as addiction.

Indeed, in children, low control-related beliefs might be related to the development of feelings of helplessness (low perceived control) and thus to depression (Abramson et al., 1989). Likewise, beliefs about the inability to control the environment might lead to frustration which in turn could lead to aggressive behaviors and subsequently externalizing psychopathologies (Garber and Hollon, 1991). In line with this, control-related beliefs have been found to be associated to both internalizing

Table 2
Neural networks related to mental functions as revealed by the neurosynth database.

	Anticipation	Prediction	Reward	Emotion	Decision	Planning
Nucleus accumbens	x	x	x			
Caudate nucleus	x	x	x		x	x
Putamen	x	x	x		x	x
Globus pallidus	x	x	x	x	x	
Thalamus	x		x			
Amygdala	x		x	x		
Midbrain	x	x	x	x		
Orbitofrontal cortex	x		x	x	x	
(Anterior) insula	x		x	x	x	x
Frontomedian cortex	x		x	x	x	x
(Anterior) cingulate cortex	x	x	x	x	x	x
Subcallosal area	x		x	x		
Frontolateral cortex	x				x	x
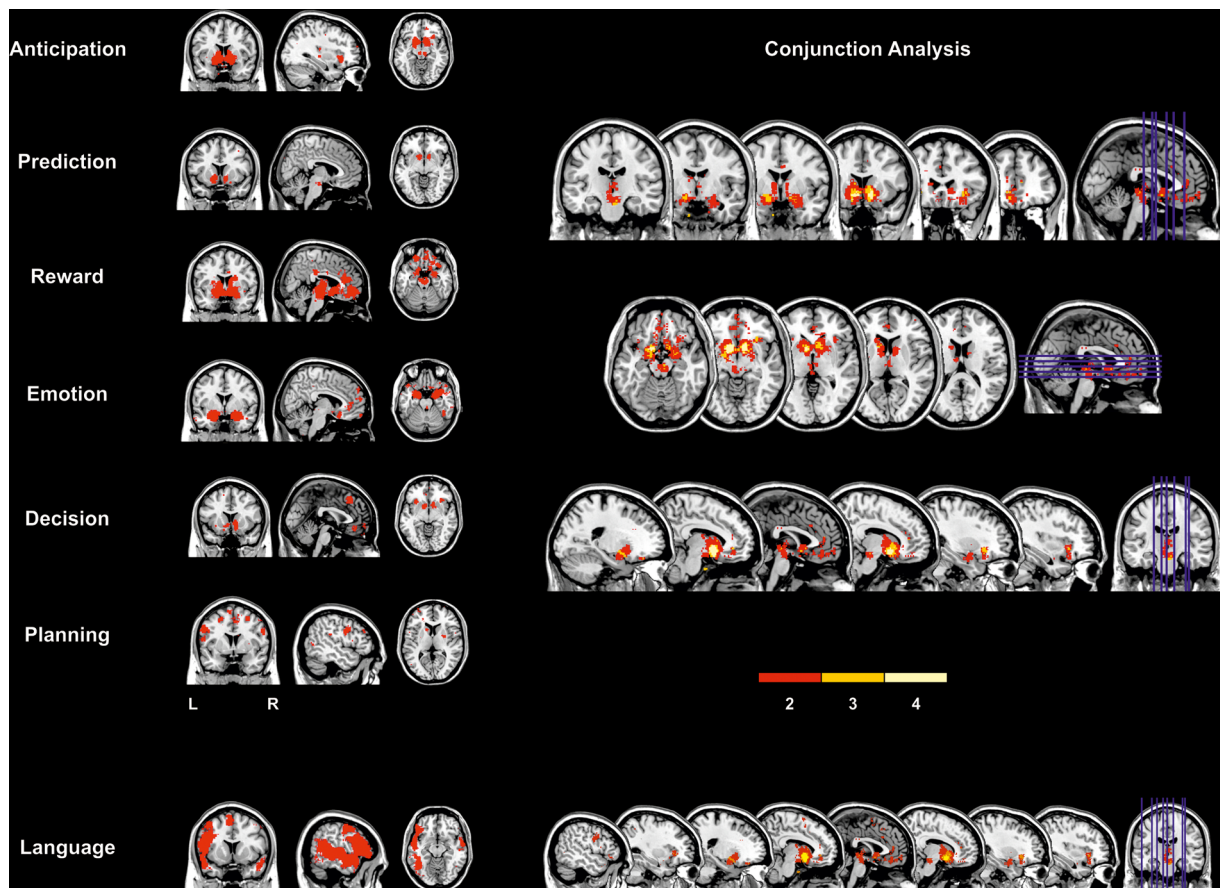
Fig. 7. Neural networks related to mental functions as revealed by the neurosynth database. *Left panel:* Maps illustrate regions were activation occurs more consistently for studies that mention the term than for studies that do not. *Right panel:* Conjunction analysis indicating regions were neural networks overlap for two, three or four mental functions. Upper three rows show conjunction for the neural correlates of anticipation, prediction, reward, emotion, decision and planning. Lower row shows conjunction between these mental functions and, additionally, language. Note that the right sagittal slices are exactly the same compared to the sagittal slices of the first conjunction analysis. The two left additional slices show the now more pronounced cluster in the left anterior insula and a new cluster in the left frontolateral cortex, i.e. around the inferior frontal junction area. L left, R right.
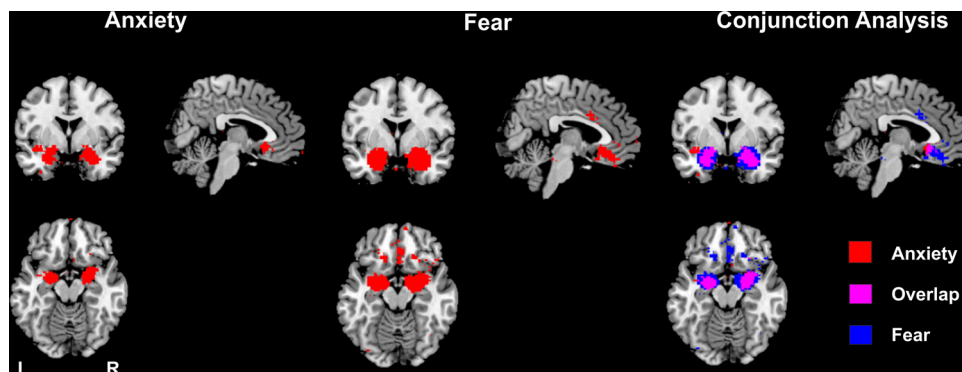
Fig. 8. Neural networks related to anxiety and fear as revealed by the neurosynth database. Maps illustrate regions were activation occurs more consistently for studies that mention the term than for studies that do not. Conjunction analysis shows regions were neural networks overlap for both, anxiety and fear. L left, R right.

and externalizing psychopathologies in youths (Han et al., 2001). In adolescents these failures in turn may trigger the development of negative AF, which are, in turn, related to the development of negative symptoms (Rector et al., 2005).

Moreover, in adult patients suffering from depression, reward anticipation has frequently been studied as alterations in reward processing that have been posited as an early developing risk factor (Davey et al., 2008). Here, melancholic symptoms, as one sub-type of depression, seem to be linked to altered reward processing as recently shown

by Liu et al. (Liu et al., 2016). The authors reported a negative correlation between frontal electroencephalogram (EEG) asymmetry during reward anticipation and melancholic symptoms. Interestingly, the association of melancholic symptoms with reduced neural reward anticipation was not influenced by depression severity. Hence, melancholic symptoms, and not depression scores in general, seem to be specifically associated with anticipatory reward deficits reflected in altered frontal EEG asymmetry.

For bipolar patients, only a handful of studies investigating reward

anticipation have been published, albeit with controversial findings regarding striatal and orbitofrontal involvement (e.g., (Nusslock et al., 2012) vs. (Caseras et al., 2013)). Most recent data indicate greater ACC activity in euthymic bipolar patients with regard to reward anticipation, potentially reflecting compensatory mechanisms counteracting a hyperactive behavioral activation system (Kollmann et al., 2017).

In schizophrenia, deficits in the experience of anticipatory pleasure or pleasure related to future activities, but not in consummatory pleasure or pleasure experienced "in the moment" have been reported frequently (Kring and Elis, 2013). Interestingly, first-episode and chronically ill patients are similarly impaired and both groups show significant correlations between an anticipation deficit and negative symptomatology. In particular, studies investigating anticipatory pleasure deficits in schizophrenia have focused on neurocognitive deficits such as imagination, maintaining an image, or remembering the past (see (Kring and Elis, 2013)). Moreover, AF are important factors in the development of negative symptoms in schizophrenia (Rector et al., 2005). The subtle cognitive deficits, that might be present in children and adolescents who later develop schizophrenia, increase the risk of recurrent failures (Zammit et al., 2004). Another approach stems from the cognitive model of negative symptoms which emphasizes the role of dysfunctional beliefs and their association with negative symptoms that are likely to lead to social withdrawal or diminished engagement (Beck et al., 2013; Couture et al., 2011). More recent studies assessing AF with experience sampling methods not only support the anticipatory deficit for pleasure but further indicate stronger anticipation of negative emotions in patients (Brenner and Ben-Zeev, 2014; Engel et al., 2016).

Disturbed reward anticipation plays an important role in addiction as well. Some theoretical models explaining addiction are based on expectancy or anticipation (*e.g., outcome expectancy model* (Marlatt, 1985)). In particular, the anticipation of psychoactive substances has an emotional and motivational effect toward substance use (Jedras et al., 2019). Substance anticipation or expectancy improves the attentional biases for substance-related cues (Jedras et al., 2019). Attentional bias in turn is related to relapse in drug seeking after a period of abstinence (Marissen et al., 2006). For instance, expecting alcohol enhances the attentional bias for alcohol-related cues (Jones et al., 2012). At the neuronal level, reward expectancies or anticipation lead to an adaptation in the dopamine brain circuitry (*i.e.*, reward brain network which includes the nucleus accumbens and ventral tegmental area and some subregions of the PFC such as OFC and DLPFC (Smith et al., 2011). In individuals suffering from addiction, excessive reward expectancies or anticipation induced by drug-related cues trigger an increase in dopamine activity within the reward system. Alterations of the dopamine level lead to subjective feelings (*i.e.*, AF) such as the expectation of imminent consumption of psychoactive substances, which refers to an important motivation factor of substance use (Volkow et al., 2011). Besides altered expectancy or anticipation of addiction-related substances, addicted individuals also show disturbed anticipation of addiction-unrelated rewards. A recent meta-analysis (Luijten et al., 2017) revealed a consistent hypoactivation in the (ventral) striatum, a core region of the reward system, during monetary reward anticipation in addicted populations (substance and gambling addictions) compared to controls. Interestingly, during reward outcome, individuals with substance addiction showed increased activation in the ventral striatum. The authors speculate that disturbed reward learning may lie at the

core of addiction since addicted individuals seem to have difficulties in predicting reward from non-addiction related rewards.

Threat anticipation and anticipation of negative events have also been investigated within the context of mental disorders, in anxiety disorders. Neuroimaging studies have shown that activity in brain regions such as the amygdala, PFC, insula and ACC increases during the anticipation of negative events. While emotional reactivity can be adaptive to some extent, excessive negative anticipation may affect the development and maintenance of psychiatric symptoms (Galli et al., 2014). Sustained anticipatory anxiety, for instance, constitutes one core symptom of generalized anxiety disorder further facilitating the development and maintenance of anxiety symptoms (Zinbarg et al., 2006). Previous research on sustained anticipatory anxiety in rodents and healthy adults points to a neural dissociation of phasic and sustained brain responses to threat anticipation (Davis et al., 2010; Herrmann et al., 2016). While the amygdala seems to be particularly essential for phasic threat, reactivity of the bed nucleus of the stria terminalis is stronger for sustained threat (Avery et al., 2016). More recent findings from patients diagnosed with generalized anxiety disorder further extend this dissociation to a clinical sample as altered responses during threat anticipation in amygdala and the bed nucleus of the stria terminalis have been observed, though with different time courses (Buff et al., 2017).

In patients with borderline personality disorder cued anticipation of both, negative and positive events as well as ambivalent events has been investigated (Scherpiet et al., 2014). Authors reported hypoactivation of left dACC and left MCC but hyperactivation of the pregenual ACC, left lingual gyrus and left PCC during anticipation of negative events in patients with borderline personality disorder compared to controls. When anticipating stimuli with unknown valence, patients with borderline personality disorder showed reduced activation in a widespread network, including, amongst others, the left MCC extending to the medial PFC, left precentral gyrus, and right DLPFC. Interestingly, no group differences were found for anticipation of positive events (Scherpiet et al., 2014) (Table 3).

7. Linguistics

To better understand the range of verbally articulated feelings that are expressed in the English language, a small task team within the Human Affectome Project led a computational linguistics research effort to identify feeling words (Siddharthan et al., 2018). Results were extracted from the Google n-gram corpus (which includes roughly 8 million books (Younes and Reips, 2019) and then manually annotated by more than one hundred researchers from this project. This resulted in 9 proposed categories of feelings and a new affective dataset that identifies 3664 word senses as feelings. Of relevance to this review is a category related to Actions and "Prospects", which was defined as follows:

"Feelings related to goals, tasks and actions (e.g. purpose, inspired), including feelings related to planning of actions or goals (e.g., ambitious), feelings related to readiness and capacity of planned actions (e.g. ready, daunted), feelings related to levels of arousal, typically involving changes to heart rate, blood pressure, alertness, etc., physical and mental states of calmness and excitement (e.g. relaxed, excited, etc.), feelings related to a person's approach, progress or unfolding circumstances as it relates to tasks/

Table 3

Breakdown of the valence, associated anticipatory feeling, the known neural circuits involved, and related mental disorders.

Valence	Anticipatory Feeling	Neural Correlates	Related Mental Disorder
Positive	Anticipation of Reward	Reduced activation of the (ventral) striatum	Depression, schizophrenia, substance use, borderline personality disorder
Negative	Anticipation of Threat, Negative Events	Increased activation of amygdala, PFC, ACC, and Insula	Depression, anxiety disorder, borderline personality disorder

Category	Assigned Subcategories with Examples
General Arousal	Excited (*e.g.*, passionless, calm, serene, aroused, stirred, excited)
Factors Influencing Goals	Extreme need (*e.g.*, destitute, desperate, panicked) Duty-bound (*e.g.*, obligated, bound, consigned) Externally Influenced (*e.g.*, instigated, coerced, persuaded) Internal (*e.g.*, unselfish, covetous, emulous, fated)
Sense of Purpose	Purpose (*e.g.*, meaningless, adrift, empty, purposive, key)
Strategy	Creativity (*e.g.*, uninspired, uninventive, inspired, imaginative) Time allocated to decision (*e.g.*, spontaneous, impulsive)
Planning	Risk (*e.g.*, defenceless, unsafe, secure, steady) Readiness (*e.g.*, inexperienced, amateur, capable, qualified) Pessimism/Optimism (*e.g.*, uncertain, doomed, optimistic, upbeat, confident) Busy (*e.g.*, idle, busy) Logic (*e.g.*, irrational, sensible)
Decision to Act	Inclination (*e.g.*, timid, hesitant, undecided, predisposed, inclined)
	See supplemental materials for detailed list of word senses and synonyms

Fig. 9. Summary of the feeling words clustered in categories.

goals within the context of the surrounding environment (e.g. organized, overwhelmed, surprised, cautious, etc.), feelings related to prospects (e.g. afraid, anxious, hopeful, tense, etc.)."

This subset of the results included about 1137 feeling words, including 130 words that appeared to express AF within the context of planning (250 words). 49 anticipatory feeling words were exclusively related to feelings of fear and anxiety (e.g., apprehensive, trepidation, worried, afraid), whereas 73 words expressed feelings of optimism/pessimism (e.g, confident, assured, sure / doubt, foreboding, doomed), and several smaller clusters of words expressed feelings related to risk, readiness, busyness and logic/rationality. Although it was not within the scope of this effort to undertake a formal analysis of this dataset, we reviewed these feelings words and we attempted to roughly organize the words into discernable categories (Fig. 9). Caution should be exercised in the interpretation of this table since it was created only to give us an initial sense of how feeling words related to one another. The individual word senses can be found in the supplemental data accompanying this review.

Interestingly, this initial, cursory review revealed that many of these terms are rarely studied by neuroscientists. Feeling words that are most commonly used as keywords in neuroscience research are related to the planning category (e.g., optimism and pessimism). In general, authors in the field of biomedical and cognitive sciences are more inclined to use emotion-words rather than feeling-words, because they prefer to refer to physiological and subcortical states, and concepts that are easily measured through behavior and standardized tests (*i.e.*, rather than subjective feeling states). This likely explains why words in these subcategories are concepts that are not frequently found in the neuroscience literature.

Undeniably, languages are rich in emotional words and metaphorical expressions, leading one to assume a tight connection between words and felt emotions. However, as we outlined in section 2, the assumption that language and emotion processes are linked on a neural level has only recently been established (for an overview see section 2 and e.g., (Herbert et al., 2018; Kissler et al., 2006). The meta-analysis conducted within this review (see section 5) provided a first step in showing how the identified brain networks that play a major role in processes relevant for AF are related to language. While this initial review of these feeling words is only a preliminary effort, it revealed a much more nuanced domain of AF than those that are currently being researched. Our working definition of AF (shown below) acknowledges that AF can be expressed in language and subjectively described. This dataset could therefore be useful to help researchers identify additional AF that might be worthy of exploration to deepen our understanding of the feelings in this domain.

8. Conclusions

In the literature, AF and anticipation were generally used as umbrella terms that encompassed many different phenomena, from cognitive processes to physiological, emotional and behavioral outputs of animals, humans and even non-living systems. Because the meaning of term AF differed depending on the study framework, it was important to develop a more precise definition of AF. In absence of a unifying definition or theory available to guide our understanding of AF, in the present review, we developed a working definition of AF, where we define AF as a state of awareness of physiological and neurocognitive changes that occur within an organism during a specific process of adapting to future events- anticipation, and proposed their role in facilitating this process of adapting to future events. The efforts to create a precise definition of AF included narrowing down components of similar processes and states such as anticipation and cognitive functions underlying prediction. We approached AF as a multi-component construct that encompasses expectancy and anticipation, as well as interoceptive signals and physiological signals as bodily cues of AF. Furthermore we considered the individual differences that influence AF, including personal beliefs, dispositional traits (e.g., optimism, hope and pessimism, and worry), as well as alterations of AF in mental disorders and possible strategies for regulating AF. Addressing the lexical hypothysis that states that all dispositional characteristics are encompassed in the human language (Crowne, 2007), we proposed that AF can be expressed in language and subjectively described by expressive-linguistic components.

Having defined AF as a multi-component construct, we approached AF and its components from different perspectives. We considered the neural correlates of AF and the factors contributing to AF by summarizing neuroimaging studies with respect to the brain structures and networks that are assumed to play a crucial role in AF. Evidence from animal and human research and changes observed in mental disorders and their consequences for individual well-being, were discussed in order to produce an interdisciplinary overview of AF and its interoceptive, physiological, affective, cognitive and expressive-linguistic components. Furthermore, a meta-analysis and a sequential conjunction analysis were performed across hundreds of imaging studies in order to detect key neural networks of mental processes relevant for AF.

In a review of the literature to date, we highlighted how certain anticipatory capabilities exist in many animal species, and that in rodents, the suprachiasmatic nucleus and prefrontal cortex (play a key role in AF and other anticipatory processes; we then proceeded to illustrate the role of bodily-related stimulus processing in AF, and its neural correlates, mainly the posterior insula, the insular cortex (anterior insula) and amygdala.

Assessing literature on the neural mechanisms associated with

dispositional factors underlying AF, such as optimism and pessimism, we have shown that optimism and hope are related to ventromedial prefrontal cortex activity associated with self-referential processing, as well as inferior frontal gyrus and dorsomedial prefrontal regions associated with cognitive control; while activity in the medial thalamus, right inferior and left posterior insula, right IFG and nucleus ruber is associated with having a pessimistic outlook. Furthermore, we have shown that activity in the amygdala, prefrontal cortex, insula and ACC increase during the anticipation of threats, negative events and stimuli, while reward processing involves frontal control regions while also activating primary reward regions in the striatum.

Finally, we considered how alterations of AF may function as a potential risk factor for several mental disorders. Specifically, disturbed reward anticipation as well as altered anticipation of negative events/threats have been linked to psychopathology such as addictive behavior, psychosis or anxiety. On a neural level, the ventral striatum, amygdala, cingulate cortex and prefrontal areas play a crucial role in altered AF.

The results reported in the present review highlighted three brain regions, namely the insula, vmPFC and amygdala, involved in future oriented feelings and cognition. Moreover, these areas were confirmed by the meta-analysis that found the nucleus accumbens, caudate nucleus, putamen, globus pallidus, thalamus, amygdala, midbrain, orbitofrontal cortex, anterior insula, frontomedian cortex and anterior cingulate cortex to be the brain regions most consistently present in imaging studies related to the topic we reviewed.

We completed the review with an initial, cursory review of feeling words that are articulated in the English language; this analysis revealed a very nuanced list of AF constructs that have not yet been explored in neuroscience research. While a formal linguistics analysis of AF words was outside of the scope of this review, the fact that so many AF constructs appear in the English language is provocative and leaves the door open for a much broader range of AF research in the future.

Perhaps one of the most important contributions of this review was the working definition of AF that allowed separating AF from similar constructs, as this seemed to be a recurring problem in the studies reviewed in this article. The AF and components related to AF, as described in the definition, were successfully delienated in this resume; the fact that these components were present in up to date literature, further validates our approach to precising the construct of AF.

The working definition, the interdisciplinary summary of studies on AF and the linguistic analysis of this concept in neuroscience articles are all key features that will hopefully facilitate future research of AF.

Author contributions

All authors contributed equally and substantially to this work with specific contributions as follows: LL developed the study concept design, drafted the Linguistic section and critical revisions of the manuscript. ES drafted the final manuscript, and CH, BF, OD and LL provided critical revisions of the manuscript. CH and BF drafted the Abstract, Highlights, the working definition of AF, and drafted and revised the Introduction and parts of the Linguistic section. OD and ES drafted and finally revised the Abstract, Highlights, the Working definition of AF, and drafted and revised the Introduction and parts of the Linguistic section and Conclusions. CH and CW drafted and revised the AF and bodily-related stimulus processing section and CH drafted and revised the AF, bodily-related stimulus processing and language section. OD and ES drafted and revised section Anticipation vs. AF: Evidence from other species, section Pessimism, Worry, Neural correlates of negative anticipation. ERS, CB, MLS and FA drafted the section on Hope, Optimism and Neural correlates of positive anticipation US, ANZ, LAKL and BD drafted the AF regulation and Alterations of AF. MLS drafted and revised the section: Extracting neural correlates of AF and associated mental functions with quantitative and conjunction meta-analyses. SWB and JR developed the design and finalized most figures. OD

and LL analyzed the feeling words for the Linguistic section. All authors approved the final version of the manuscript for submission.

Declaration of Competing Interest

The authors disclose no conflicts of interest.

References

Abramson, L.Y., Metalsky, G.I., Alloy, L.B., 1989. Hopelessness depression: a theory-based subtype of depression. Psychol. Rev. 96, 358–372.

Ainge, J., Tamosiunaite, M., Worgotter, F., Dudchenko, P., 2012. Hippocampal place cells encode intended destination, and not a discriminative stimulus, in a conditional T-maze task. Hippocampus 22, 534–543.

Alarcon, G.M., Bowling, N.A., Khazon, S., 2013. Great expectations: a meta-analytic examination of optimism and hope. Pers. Individ. Dif. 54, 821–827.

Alvarez-Buylla, A., Theelen, M., Nottebohm, F., 1988. Birth of projection neurons in the higher vocal center of the canary forebrain before, during, and after song learning. Proc. Natl. Acad. Sci. U.S.A. 85, 8722–8726.

Angeles-Castellanos, M., Salgado-Delgado, R., Rodriguez, K., Buijs, R.M., Escobar, C., 2008. Expectancy for food or expectancy for chocolate reveals timing systems for metabolism and reward. Neuroscience 155, 297–307.

Antle, M.C., Silver, R., 2009. Neural basis of timing and anticipatory behaviors. Eur. J. Neurosci. 30, 1643–1649.

Augustyn, A., Bauer, P., Duignan, B., Eldridge, A., Gregersen, E., McKenna, A., Zelazko, A., 2012. Feeling. Encyclopaedia Britannica.

Avery, S.N., Clauss, J.A., Blackford, J.U., 2016. The human BNST: functional role in anxiety and addiction. Neuropsychopharmacology 41, 126–141.

Balakhonov, D., Rose, J., 2017. Crows rival monkeys in cognitive capacity. Sci. Rep. 7, 8809.

Balsam, P., Sanchez-Castillo, H., Taylor, K., Van Volkinburg, H., Ward, R.D., 2009. Timing and anticipation: conceptual and methodological approaches. Eur. J. Neurosci. 30, 1749–1755.

Barrett, L.F., Quigley, K.S., Hamilton, P., 2016. An active inference theory of allostasis and interoception in depression. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 371.

Barsalou, L.W., 2008. Grounded cognition. Annu. Rev. Psychol. 59, 617–645.

Baur, V., Hanggi, J., Langer, N., Jancke, L., 2013. Resting-state functional and structural connectivity within an insula-amygdala route specifically index state and trait anxiety. Biol. Psychiatry 73, 85–92.

Bayern, A., Danel, S., Auersperg, A.M.I., Mioduszewska, B., Kacelnik, A., 2018. Compound tool construction by New Caledonian crows. Sci. Rep. 8, 15676.

Bechara, A., Damasio, H., Tranel, D., Damasio, A.R., 1997. Deciding advantageously before knowing the advantageous strategy. Science 275, 1293–1295.

Beck, A.T., Grant, P.M., Huh, G.A., Perivoliotis, D., Chang, N.A., 2013. Dysfunctional attitudes and expectancies in deficit syndrome schizophrenia. Schizophr. Bull. 39, 43–51.

Berteau-Pavy, F., Park, B., Raber, J., 2007. Effects of sex and APOE e4 on object recognition and spatial navigation in the elderly. Neuroscience 147, 6–17.

Biederman, S., Biedermann, D., Wenzlaff, F., Kurjak, T., Nouri, S., Auer, M., Wiedemann, K., Briken, P., Haaker, J., Lonsdorf, T., Fuss, J., 2017. An elevated plus-maze in mixed reality for studying human anxiety-related behavior. BMC Biol. 15, 125.

Blair, K.S., Otero, M., Teng, C., Jacobs, M., Odenheimer, S., Pine, D.S., Blair, R.J., 2013. Dissociable roles of ventromedial prefrontal cortex (vmPFC) and rostral anterior cingulate cortex (rACC) in value representation and optimistic bias. Neuroimage 78, 103–110.

Blair, K.S., Otero, M., Teng, C., Geraci, M., Ernst, M., Blair, R.J.R., Pine, D.S., Grillon, C., 2017. Reduced optimism and a heightened neural response to everyday worries are

specific to generalized anxiety disorder, and not seen in social anxiety. Psychol. Med. 47, 1806–1815.

Blancas, A., Gonzalez-Garcia, S.D., Rodriguez, K., Escobar, C., 2014. Progressive anticipation in behavior and brain activation of rats exposed to scheduled daily palatable food. Neuroscience 281, 44–53.

Bowman, E.M., Aigner, T.G., Richmond, B.J., 1996. Neural signals in the monkey ventral striatum related to motivation for juice and cocaine rewards. J. Neurophysiol. 75, 1061–1073.

Bradley, K.A.L., Case, J.A.C., Freed, R.D., Stern, E.R., Gabbay, V., 2017. Neural correlates of RDoC reward constructs in adolescents with diverse psychiatric symptoms: a reward Flanker Task pilot study. J. Affect. Disord. 216, 36–45.

Breiter, H.C., Aharon, I., Kahneman, D., Dale, A., Shizgal, P., 2001. Functional imaging of neural responses to expectancy and experience of monetary gains and losses. Neuron 30, 619–639.

Brenner, C.J., Ben-Zeev, D., 2014. Affective forecasting in schizophrenia: comparing predictions to real-time Ecological Momentary Assessment (EMA) ratings. Psychiatr. Rehabil. J. 37, 316–320.

Bruininks, P., Malle, B.F., 2005. Distinguishing hope from optimism and related affective states. Motiv. Emot. 29, 327–355.

Bryan, F.B., Cvengros, J.A., 2004. Distinguishing hope and optimism: Two sides of a coin, or two separate coins? J. Soc. Clin. Psychol. 23, 273–302.

Bubic, A., von Cramon, D.Y., Schubotz, R.I., 2010. Prediction, cognition and the brain. Front. Hum. Neurosci. 4, 25.

Buff, C., Brinkmann, L., Bruchmann, M., Becker, M.P.I., Tupak, S., Herrmann, M.J., Straube, T., 2017. Activity alterations in the bed nucleus of the stria terminalis and amygdala during threat anticipation in generalized anxiety disorder. Soc. Cogn. Affect. Neurosci. 12, 1766–1774.

Caba, M., Gonzalez-Mariscal, G., 2009. The rabbit pup, a natural model of nursing-anticipatory activity. Eur. J. Neurosci. 30, 1697–1706.

Carlson, J.M., Greenberg, T., Rubin, D., Mujica-Parodi, L.R., 2011. Feeling anxious: anticipatory amygdalo-insular response predicts the feeling of anxious anticipation. Soc. Cogn. Affect. Neurosci. 6, 74–81.

Carneiro, B.T., Araujo, J.F., 2012. Food entrainment: major and recent findings. Front. Behav. Neurosci. 6, 83.

Carter, R.M., Macinnes, J.J., Huettel, S.A., Adcock, R.A., 2009. Activation in the VTA and nucleus accumbens increases in anticipation of both gains and losses. Front. Behav. Neurosci. 3, 21.

Carver, C.S., Scheier, M.F., 2014. Dispositional optimism. Trends Cogn. Sci. (Regul. Ed.) 18, 293–299.

Caseras, X., Lawrence, N.S., Murphy, K., Wise, R.G., Phillips, M.L., 2013. Ventral striatum activity in response to reward: differences between bipolar I and II disorders. Am. J. Psychiatry 170, 533–541.

Cerliani, L., Thomas, R.M., Jbabdi, S., Siero, J.C., Nanetti, L., Crippa, A., Gazzola, V., D'Arceuil, H., Keysers, C., 2012. Probabilistic tractography recovers a rostrocaudal trajectory of connectivity variability in the human insular cortex. Hum. Brain Mapp. 33, 2005–2034.

Chua, P., Krams, M., Toni, I., Passingham, R., Dolan, R., 1999. A functional anatomy of anticipatory anxiety. Neuroimage 9, 563–571.

Couture, S.M., Blanchard, J.J., Bennett, M.E., 2011. Negative expectancy appraisals and defeatist performance beliefs and negative symptoms of schizophrenia. Psychiatry Res. 189, 43–48.

Craig, A.D., 2002. How do you feel? Interoception: the sense of the physiological condition of the body. Nature reviews 3, 655–666.

Craig, A.D., 2009. How do you feel–now? The anterior insula and human awareness. Nature reviews 10, 59–70.

Craig, A.D., Chen, K., Bandy, D., Reiman, E.M., 2000. Thermosensory activation of insular cortex. Nat. Neurosci. 3, 184–190.

Critchley, H.D., 2009. Psychophysiology of neural, cognitive and affective integration: fMRI and autonomic indicants. Int. J. Psychophysiol. 73, 88–94.

Critchley, H.D., Wiens, S., Rotshtein, P., Ohman, A., Dolan, R.J., 2004. Neural systems supporting interoceptive awareness. Nat. Neurosci. 7, 189–195.

Crowne, D.P., 2007. Personality Theory. Oxford University Press, Don Mills, Ontario.

Damasio, A., Tranel, D., Damasio, H.C., 1991. Somatic markers and the guidance of behavior: theory and preliminary testing. In: Levin, H.S., Eisenberg, H.M., Benton, aL B. (Eds.), Frontal Lobe Function and Dysfunction. Oxford University Press, New York.

Davey, C.G., Yucel, M., Allen, N.B., 2008. The emergence of depression in adolescence: development of the prefrontal cortex and the representation of reward. Neurosci. Biobehav. Rev. 32, 1–19.

Davidson, R.J., Sutton, S.K., 1995. Affective neuroscience: the emergence of a discipline. Curr. Opin. Neurobiol. 5, 217–224.

Davis, M., Walker, D.L., Miles, L., Grillon, C., 2010. Phasic vs sustained fear in rats and humans: role of the extended amygdala in fear vs anxiety. Neuropsychopharmacology 35, 105–135.

Dawson, M.E., Schell, A.M., Courtney, C.G., 2011. The skin conductance response, anticipation, and decision-making. J. Neurosci. Psychol. Econ. 4, 111–116.

Dillon, D.G., Holmes, A.J., Jahn, A.L., Bogdan, R., Wald, L.L., Pizzagalli, D.A., 2008. Dissociation of neural regions associated with anticipatory versus consummatory phases of incentive processing. Psychophysiology 45, 36–49.

Dolcos, S., Hu, Y., Iordan, A.D., Moore, M., Dolcos, F., 2016. Optimism and the brain: trait optimism mediates the protective role of the orbitofrontal cortex gray matter volume against anxiety. Soc. Cogn. Affect. Neurosci. 11, 263–271.

Dosenbach, N.U., Fair, D.A., Miezin, F.M., Cohen, A.L., Wenger, K.K., Dosenbach, R.A., Fox, M.D., Snyder, A.Z., Vincent, J.L., Raichle, M.E., Schlaggar, B.L., Petersen, S.E., 2007. Distinct brain networks for adaptive and stable task control in humans. Proc. Natl. Acad. Sci. U.S.A. 104, 11073–11078.

Dreyer, F.R., Pulvermuller, F., 2018. Abstract semantics in the motor system? - an event-related fMRI study on passive reading of semantic word categories carrying abstract emotional and mental meaning. Cortex 100, 52–70.

Drozd, R., Cieslak, P.E., Rychlik, M., Rodriguez Parkitna, J., Rygula, R., 2016. Cognitive judgment Bias interacts with risk based decision making and sensitivity to dopaminergic challenge in male rats. Front. Behav. Neurosci. 10, 163.

Eichenbaum, H., 2014. Time cells in the hippocampus: a new dimension for mapping memories. Nature reviews 15, 732–744.

Engel, M., Fritzsche, A., Lincoln, T.M., 2016. Anticipation and experience of emotions in patients with schizophrenia and negative symptoms. An experimental study in a social context. Schizophr. Res. 170, 191–197.

Erk, S., Abler, B., Walter, H., 2006. Cognitive modulation of emotion anticipation. Eur. J. Neurosci. 24, 1227–1236.

Ernst, M., Nelson, E.E., McClure, E.B., Monk, C.S., Munson, S., Eshel, N., Zarahn, E., Leibenluft, E., Zametkin, A., Towbin, K., Blair, J., Charney, D., Pine, D.S., 2004. Choice selection and reward anticipation: an fMRI study. Neuropsychologia 42, 1585–1597.

Fairfield, B., Mammarella, N., Di Domenico, A., 2015. Motivated goal pursuit and working memory: Are there age-related differences? Motiv. Emot. 39, 201–215.

Friston, K., 2010. The free-energy principle: a unified brain theory? Nature Rev. 11, 127–138.

Gallagher, M.W., Lopez, S.J., 2009. Positive expectancies and mental health: identifying the unique contributions of hope and optimism. J. Posit. Psychol. 4, 548–556.

Galli, G., Griffiths, V.A., Otten, L.J., 2014. Emotion regulation modulates anticipatory brain activity that predicts emotional memory encoding in women. Soc. Cogn. Affect. Neurosci. 9, 378–384.

Garber, J., Hollon, S.D., 1991. What can specificity designs say about causality in psychopathology research? Psychol. Bull. 110, 129–136.

Garrett, N., Sharot, T., Faulkner, P., Korn, C.W., Roiser, J.P., Dolan, R.J., 2014. Losing the rose tinted glasses: neural substrates of unbiased belief updating in depression. Front. Hum. Neurosci. 8, 639.

Grieves, R., Wood, E., Dudchenko, P., 2016. Place cells on a maze encode routes rather than destinations. eLife 5, e15986.

Grupe, D.W., Nitschke, J.B., 2013. Uncertainty and anticipation in anxiety: an integrated neurobiological and psychological perspective. Nature reviews 14, 488–501.

Han, S.S., Weisz, J.R., Weiss, B., 2001. Specificity of relations between children's control-related beliefs and internalizing and externalizing psychopathology. J. Consult. Clin. Psychol. 69, 240–251.

Hassani, O.K., Cromwell, H.C., Schultz, W., 2001. Influence of expectation of different rewards on behavior-related neuronal activity in the striatum. J. Neurophysiol. 85, 2477–2489.

Hecht, D., 2013. The neural basis of optimism and pessimism. Exp. Neurobiol. 22, 173–199.

Herbert, C., Kissler, J., 2010. Motivational priming and processing interrupt: startle reflex modulation during shallow and deep processing of emotional words. Int. J. Psychophysiol. 76, 64–71.

Herbert, C., Herbert, B.M., Pauli, P., 2011. Emotional self-reference: brain structures involved in the processing of words describing one's own emotions. Neuropsychologia 49, 2947–2956.

Herbert, C., Sfarlea, A., Blumenthal, T., 2013. Your emotion or mine: labeling feelings alters emotional face perception-an ERP study on automatic and intentional affect labeling. Front. Hum. Neurosci. 7, 378.

Herbert, C., Ethofer, T., Fallgatter, A.J., Walla, P., Northoff, G., 2018. Editorial: The Janus Face of Language: Where Are the Emotions in Words and Where Are the Words in Emotions? Front. Psychol. 9, 650.

Herrmann, M.J., Boehme, S., Becker, M.P., Tupak, S.V., Guhn, A., Schmidt, B., Brinkmann, L., Straube, T., 2016. Phasic and sustained brain responses in the amygdala and the bed nucleus of the stria terminalis during threat anticipation. Hum. Brain Mapp. 37, 1091–1102.

Herwig, U., Kaffenberger, T., Baumgartner, T., Jancke, L., 2007. Neural correlates of a' pessimistic' attitude when anticipating events of unknown emotional valence. Neuroimage 34, 848–858.

Hinz, A., Conrad, I., Schroeter, M.L., Glaesmer, H., Brähler, E., Zenger, M., Kocalevent, R.-D., Herzberg, P.Y., 2018. Psychometric properties of the Satisfaction with Life Scale (SWLS), derived from a large German community sample. Qual. Life Res. 1–10.

Hollen, L.I., Radford, A.N., 2009. The development of alarm call behaviour in mammals and birds. Anim. Behav. 78, 791–800.

Ishii, H., Ohara, S., Tobler, P.N., Tsutsui, K., Iijima, T., 2012. Inactivating anterior insular cortex reduces risk taking. J. Neurosci. 32, 16031–16039.

Ishii, H., Tsutsui, K., Iijima, T., 2013. [Risk taking and the insular cortex]. Brain Nerve 65, 965–972.

James, W., 1890. Origin of right-handedness. Science 16, 275.

James, W., 1894. Physical basis of emotion. Psychol. Rev. 1.

Jedras, P., Jones, A., Stancak, A., Field, M., 2019. The effects of reward and loss anticipation on attentional bias for reward related stimuli. Appetite 133, 93–100.

Jones, A., Hogarth, L., Christiansen, P., Rose, A.K., Martinovic, J., Field, M., 2012. Reward expectancy promotes generalized increases in attentional bias for rewarding stimuli. Q. J. Exp. Psychol. 65, 2333–2342.

Kikusui, T., Nishizawa, D., Takeuchi, Y., Mori, Y., 2003. Conditioned fear-related ultrasonic vocalizations are emitted as an emotional response. J. Vet. Med. Sci. 65, 1299–1305.

Kim, H., Shimojo, S., O'Doherty, J.P., 2011. Overlapping responses for the expectation of juice and money rewards in human ventromedial prefrontal cortex. Cereb. Cortex 21, 769–776.

Kinsbourne, M., 1978. Asymmetry and the brain. Science 200, 651–652.

Kirsch, P., Schienle, A., Stark, R., Sammer, G., Blecker, C., Walter, B., Ott, U., Burkart, J., Vaitl, D., 2003. Anticipation of reward in a nonaversive differential conditioning

paradigm and the brain reward system: an event-related fMRI study. Neuroimage 20, 1086–1095.

Kissler, J., Assadollahi, R., Herbert, C., 2006. Emotional and semantic networks in visual word processing: insights from ERP studies. Prog. Brain Res. 156, 147–183.

Klein, D.C., Moore, R.Y., Reppert, S.M., 1991. Suprachiasmatic Nucleus: the Mind's Clock. Oxford University Press, USA.

Knudson, I., Melcher, J., 2016. Elevated acoustic startle responses in humans: relationship to reduced loudness discomfort level, but not self-report of hyperacusis. J Assoc Res Otalaryngol 17, 223–235.

Knutson, B., Greer, S.M., 2008. Anticipatory affect: neural correlates and consequences for choice. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 363, 3771–3786.

Knutson, B., Adams, C.M., Fong, G.W., Hommer, D., 2001a. Anticipation of increasing monetary reward selectively recruits nucleus accumbens. J. Neurosci. 21, RC159.

Knutson, B., Fong, G.W., Adams, C.M., Varner, J.L., Hommer, D., 2001b. Dissociation of reward anticipation and outcome with event-related fMRI. Neuroreport 12, 3683–3687.

Knutson, B., Fong, G.W., Bennett, S.M., Adams, C.M., Hommer, D., 2003. A region of mesial prefrontal cortex tracks monetarily rewarding outcomes: characterization with rapid event-related fMRI. Neuroimage 18, 263–272.

Knutson, B., Rick, S., Wimmer, G.E., Prelec, D., Loewenstein, G., 2007. Neural predictors of purchases. Neuron 53, 147–156.

Kollmann, B., Scholz, V., Linke, J., Kirsch, P., Wessa, M., 2017. Reward anticipation revisited- evidence from an fMRI study in euthymic bipolar I patients and healthy first-degree relatives. J. Affect. Disord. 219, 178–186.

Kress, L., Aue, T., 2017. The link between optimism bias and attention bias: a neurocognitive perspective. Neurosci. Biobehav. Rev. 80, 688–702.

Kring, A.M., Elis, O., 2013. Emotion deficits in people with schizophrenia. Annu. Rev. Clin. Psychol. 9, 409–433.

Kringelbach, M.L., 2005. The human orbitofrontal cortex: linking reward to hedonic experience. Nature reviews 6, 691–702.

Krupenye, C., Kano, F., Hirata, S., Call, J., Tomasello, M., 2016. Great apes anticipate that other individuals will act according to false beliefs. Science 354, 110–114.

Kuhl, J., Fuhrmann, A., 1998. Decomposing self-regulation and self-control: the volitional components checklist. In: Dweck, J.H.C. (Ed.), Motivation and Self-Regulation Across the Life Span. Cambridge University Press, New York, pp. 15–49.

Kulkarni, S.K., Singh, K., Bishnoi, M., 2007. Elevated zero maze: a paradigm to evaluate antianxiety effects of drugs. Methods Find. Exp. Clin. Pharmacol. 29, 343–348.

Kurth, F., Eickhoff, S.B., Schleicher, A., Hoemke, L., Zilles, K., Amunts, K., 2010. Cytoarchitecture and probabilistic maps of the human posterior insular cortex. Cereb. Cortex 20, 1448–1461.

Kuzmanovic, B., Rigoux, L., Vogeley, K., 2016. Brief report: reduced optimism Bias in self-referential belief updating in high-functioning autism. J. Autism Dev. Disord.

Laviola, G., Macri, S., Morley-Fletcher, S., Adriani, W., 2003. Risk-taking behavior in adolescent mice: psychobiological determinants and early epigenetic influence. Neurosci. Biobehav. Rev. 27, 19–31.

Levin, I.P., Xue, G., Weller, J.A., Reimann, M., Lauriola, M., Bechara, A., 2012. A neuropsychological approach to understanding risk-taking for potential gains and losses. Front. Neurosci. 6, 15.

Lindquist, K.A., MacCormack, J.K., Shablack, H., 2015. The role of language in emotion: predictions from psychological constructionism. Front. Psychol. 6, 444.

Lister, R.G., 1987. The use of a plus-maze to measure anxiety in the mouse. Psychopharmacology 92, 180–185.

Liu, H., Sarapas, C., Shankman, S.A., 2016. Anticipatory reward deficits in melancholia. J. Abnorm. Psychol. 125, 631–640.

Luijten, M., Schellekens, A.F., Kuhn, S., Machielse, M.W., Sescousse, G., 2017. Disruption of reward processing in addiction : an image-based meta-analysis of functional magnetic resonance imaging studies. JAMA Psychiatry 74, 387–398.

Macleod, A., 2017. Prospection, Well-being, and Mental Health. Oxford University Press, Oxford, UK.

MacLeod, A.K., 1994. Worry and explanation-based pessimism. In: Davey, G.C.L., Tallis, F. (Eds.), Worrying: Perspectives on Theory, Assessment and Treatment. John Wiley & Sons, Oxford, England, pp. 115–134.

MacLeod, A.K., Williams, J.M., Bekerian, D.A., 1991. Worry is reasonable: the role of explanations in pessimism about future personal events. J. Abnorm. Psychol. 100, 478–486.

Marissen, M.A.E., Franken, I.H.A., Waters, A.J., Blanken, P., van den Brink, W., Hendriks, V.M., 2006. Attentional bias predicts heroin relapse following treatment. Addiction 101, 1306–1312.

Marlatt, G., 1985. Cognitive factors in the relapse process. In: Marlatt, G., Gordon, J. (Eds.), Relapse Prevention: Maintenance Strategies in the Treatment of Addictive Behaviors. Guilford Press, New York, pp. 128–200.

Mayer, E.A., 2011. Gut feelings: the emerging biology of gut-brain communication. Nature reviews 12, 453–466.

McKay, R.T., Dennett, D.C., 2009. The evolution of misbelief. Behav. Brain Sci. 32, 493–510 discussion 510-461.

McLay, R.N., Freeman, S.M., Harlan, R.E., Kastin, A.J., Zadina, J.E., 1999. Tests used to assess the cognitive abilities of aged rats: their relation to each other and to hippocampal morphology and neurotrophin expression. Gerontology 45, 143–155.

Meier, L., Federspiel, A., Jann, K., Wiest, R., Strik, W., Dierks, T., 2018. Thirst-dependent activity of the insular cortex reflects its emotion-related subdivision: a cerebral blood flow study. Neuroscience 383, 170–177.

Menon, V., 2011. Large-scale brain networks and psychopathology: a unifying triple network model. Trends Cogn. Sci. (Regul. Ed.) 15, 483–506.

Menon, V., 2015. Salience network. In: Toga, A.W. (Ed.), Brain Mapping: An Encyclopedic Reference. Elsevier Inc.

Menon, V., Uddin, L.Q., 2010. Saliency, switching, attention and control: a network

model of insula function. Brain Struct. Funct. 214, 655–667.

Meyer, C., Padmala, S., Pessoa, L., 2018. Dynamic threat processing. J. Cogn. Neurosci. 1–21.

Miller, M.W., Patrick, C.J., 2000. Trait differences in affective and attentional responding to threat revealed by emotional Stroop interference and startle reflex modulation. Behav. Ther. 31, 757–776.

Miloyan, B., Suddendorf, T., 2015. Feelings of the future. Trends Cogn. Sci. (Regul. Ed.) 19, 196–200.

Mistlberger, R.E., 1994. Circadian food-anticipatory activity: formal models and physiological mechanisms. Neurosci. Biobehav. Rev. 18, 171–195.

Mistlberger, R.E., 2009. Food-anticipatory circadian rhythms: concepts and methods. Eur. J. Neurosci. 30, 1718–1729.

Moore, R.Y., 2013. The suprachiasmatic nucleus and the circadian timing system. Prog. Mol. Biol. Transl. Sci. 119, 1–28.

Morawetz, C., Bode, S., Baudewig, J., Heekeren, H.R., 2017. Effective amygdala-prefrontal connectivity predicts individual differences in successful emotion regulation. Soc. Cogn. Affect. Neurosci. 12, 569–585.

Morris, R., 1984. Developments of a water-maze procedure for studying spatial learning in the rat. J. Neurosci. Methods 11, 47–60.

Motzkin, J.C., Philippi, C.L., Wolf, R.C., Baskaya, M.K., Koenigs, M., 2015. Ventromedial prefrontal cortex is critical for the regulation of amygdala activity in humans. Biol. Psychiatry 77, 276–284.

Namkung, H., Kim, S.H., Sawa, A., 2017. The insula: an underestimated brain area in clinical neuroscience, psychiatry, and neurology. Trends Neurosci. 40, 200–207.

Niedenthal, P.M., Barsalou, L.W., Winkielman, P., Krauth-Gruber, S., Ric, F., 2005. Embodiment in attitudes, social perception, and emotion. Pers. Soc. Psychol. Rev. 9, 184–211.

Norem, J., 2007. Defensive pessimism, anxiety, and the complexity of evaluating self-regulation. Soc. Personal. Psychol. Compass 2 (121), 134.

Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., Panksepp, J., 2006. Self-referential processing in our brain–a meta-analysis of imaging studies on the self. Neuroimage 31, 440–457.

Nottebohm, F., Alvarez-Buylla, A., Cynx, J., Kirn, J., Ling, C.Y., Nottebohm, M., Suter, R., Tolles, A., Williams, H., 1990. Song learning in birds: the relation between perception and production. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 329, 115–124.

Nusslock, R., Almeida, J.R., Forbes, E.E., Versace, A., Frank, E., Labarbara, E.J., Klein, C.R., Phillips, M.L., 2012. Waiting to win: elevated striatal and orbitofrontal cortical activity during reward anticipation in euthymic bipolar disorder adults. Bipolar Disord. 14, 249–260.

O'Doherty, J.P., Deichmann, R., Critchley, H.D., Dolan, R.J., 2002. Neural responses during anticipation of a primary taste reward. Neuron 33, 815–826.

Parham, K., Willott, J.F., 1988. Acoustic startle response in young and aging C57BL/6J and CBA/J mice. Behav. Neurosci. 102, 881–886.

Paulus, M.P., Stein, M.B., 2006. An insular view of anxiety. Biol. Psychiatry 60, 383–387.

Paulus, M.P., Stein, M.B., 2010. Interoception in anxiety and depression. Brain Struct. Funct. 214, 451–463.

Pavlov, P.I., 2010. Conditioned reflexes: an investigation of the physiological activity of the cerebral cortex. Ann. Neurosci. 17, 136–141.

Pezzulo, G., Castelfranchi, C., 2009. Intentional action: from anticipation to goal-directed behavior. Psychol. Res. 73, 437–440.

Raber, J., Rola, R., LeFevour, A., Morhardt, D., Curley, J., Mizumatsu, S., VandenBerg, S.R., Fike, J.R., 2004. Radiation-induced cognitive impairments are associated with changes in indicators of hippocampal neurogenesis. Radiat. Res. 162, 39–47.

Rademacher, L., Krach, S., Kohls, G., Irmak, A., Grunder, G., Spreckelmeyer, K.N., 2010. Dissociation of neural networks for anticipation and consumption of monetary and social rewards. Neuroimage 49, 3276–3285.

Ran, Q., Yang, J., Yang, W., Wei, D., Qiu, J., Zhang, D., 2017. The association between resting functional connectivity and dispositional optimism. PLoS One 12, e0180334.

Rector, N.A., Beck, A.T., Stolar, N., 2005. The negative symptoms of schizophrenia: a cognitive perspective. Canadian journal of psychiatry. Can. Child Adolesc. Psychiatr. Rev. 50, 247–257.

Rich, E.L., Stoll, F.M., Rudebeck, P.H., 2018. Linking dynamic patterns of neural activity in orbitofrontal cortex with decision making. Curr. Opin. Neurobiol. 49, 24–32.

Riegler, A., 2001. The Role of Anticipation in Cognition. American Institute of Physics, pp. 534–541.

Rizk-Jackson, A., Acevedo, S., Inman, D., Howieson, D., Benice, T., Raber, J., 2006. Effects of sex on object recognition and spatial navigation in humans. Beh Brain Res 173, 181–190.

Rutz, C., Klump, B.C., Komarczyk, L., Leighton, R., Kramer, J., Wischnewski, S., Sugasawa, S., Morrissey, M.B., James, R., St Clair, J.J., Switzer, R.A., Masuda, B.M., 2016. Discovery of species-wide tool use in the Hawaiian crow. Nature 537, 403–407.

Sabatinelli, D., Bradley, M.M., Lang, P.J., 2001. Affective startle modulation in anticipation and perception. Psychophysiology 38, 719–722.

Sander, K., Frome, Y., Scheich, H., 2007. FMRI activations of amygdala, cingulate cortex, and auditory cortex by infant laughing and crying. Hum. Brain Mapp. 28, 1007–1022.

Sanger, D.J., Joly, D., 1985. Anxiolytic drugs and the acquisition of conditioned fear in mice. Psychopharmacology (Berl.) 85, 284–288.

Scherpiet, S., Bruhl, A.B., Opialla, S., Roth, L., Jancke, L., Herwig, U., 2014. Altered emotion processing circuits during the anticipation of emotional stimuli in women with borderline personality disorder. Eur. Arch. Psychiatry Clin. Neurosci. 264, 45–60.

Schier, L.A., Blonde, G.D., Spector, A.C., 2016. Bilateral lesions in a specific subregion of posterior insular cortex impair conditioned taste aversion expression in rats. J. Comp. Neurol. 524, 54–73.

Schneider, B., Koenigs, M., 2017. Human lesion studies of ventromedial prefrontal cortex. Neuropsychologia 107, 84–93.

Schomaker, L., 2004. Anticipation in cybernetic systems: a case against mindless anti-representationalism. IEEE International Conference: Systems, Man and Cybernetics 2037–2045.

Schultz, W., 1998. Predictive reward signal of dopamine neurons. J. Neurophysiol. 80, 1–27.

Schultz, W., Apicella, P., Scarnati, E., Ljungberg, T., 1992. Neuronal activity in monkey ventral striatum related to the expectation of reward. J. Neurosci. 12, 4595–4610.

Seeley, W.W., Menon, V., Schatzberg, A.F., Keller, J., Glover, G.H., Kenna, H., Reiss, A.L., Greicius, M.D., 2007. Dissociable intrinsic connectivity networks for salience processing and executive control. J. Neurosci. 27, 2349–2356.

Seth, A.K., 2013. Interoceptive inference, emotion, and the embodied self. Trends Cogn. Sci. (Regul. Ed.) 17, 565–573.

Sharot, T., 2011. The optimism bias. Curr. Biol. 21, R941–945.

Sharot, T., Riccardi, A.M., Raio, C.M., Phelps, E.A., 2007. Neural mechanisms mediating optimism bias. Nature 450, 102–105.

Sharot, T., Korn, C.W., Dolan, R.J., 2011. How unrealistic optimism is maintained in the face of reality. Nat. Neurosci. 14, 1475–1479.

Shephard, J.K., Grewal, S.S., Fletcher, A., Bill, D.J., Dourish, C.T., 1994. Behavioural and pharmacological characterisation of the elevated "zero-maze" as an animal model of anxiety. Psychopharma 116, 56–64.

Siddharthan, A., Cherbuin, N., Eslinger, P.J., Kozlowska, K., Murphy, N.A., Lowe, L., 2018. WordNet-feelings: a linguistic categorisation of human feelings. eprint 1–22 arXiv:1811.02435.

Sjöberg, L., 1998. Worry and risk perception. Risk Anal. 18, 85–93.

Smith, S.M., Fox, P.T., Miller, K.L., Glahn, D.C., Fox, P.M., Mackay, C.E., Filippini, N., Watkins, K.E., Toro, R., Laird, A.R., Beckmann, C.F., 2009. Correspondence of the brain's functional architecture during activation and rest. Proc. Natl. Acad. Sci. U.S.A. 106, 13040–13045.

Smith, K.S., Berridge, K.C., Aldridge, J.W., 2011. Disentangling pleasure from incentive salience and learning signals in brain reward circuitry. Proc Natl Acad Sci U S A 108, E255–264.

Spreckelmeyer, K.N., Krach, S., Kohls, G., Rademacher, L., Irmak, A., Konrad, K., Kircher, T., Grunder, G., 2009. Anticipation of monetary and social reward differently activates mesolimbic brain structures in men and women. Soc. Cogn. Affect. Neurosci. 4, 158–165.

St Clair, J.J.H., Klump, B.C., Sugasawa, S., Higgott, C.G., Colegrave, N., Rutz, C., 2018. Hook innovation boosts foraging efficiency in tool-using crows. Nat. Ecol. Evol. 2, 441–444.

Stephan, F.K., 2002. The "other" circadian system: food as a Zeitgeber. J. Biol. Rhythms 17, 284–292.

Strigo, I.A., Craig, A.D., 2016. Interoception, homeostatic emotions and sympathovagal balance. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 371.

Swanson, L.W., 1982. The projections of the ventral tegmental area and adjacent regions: a combined fluorescent retrograde tracer and immunofluorescence study in the rat. Brain Res. Bull. 9, 321–353.

Ueda, K., Okamoto, Y., Okada, G., Yamashita, H., Hori, T., Yamawaki, S., 2003. Brain activity during expectancy of emotional stimuli: an fMRI study. Neuroreport 14, 51–55.

van den Bos, R., 2017. Animal Anticipation: A Perspective. Springer, Cham.

Van Meer, P., Raber, J., 2005. Mouse behavioral analysis in systems biology. Biochem. J. 389, 593–610.

Vincent, J.L., Kahn, I., Snyder, A.Z., Raichle, M.E., Buckner, R.L., 2008. Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. J. Neurophysiol. 100, 3328–3342.

Vogt, B.A., 2005. Pain and emotion interactions in subregions of the cingulate gyrus. Nature reviews 6, 533–544.

Volkow, N.D., Wang, G.J., Fowler, J.S., Tomasi, D., Telang, F., 2011. Addiction: beyond dopamine reward circuitry. Proc Natl Acad Sci U S A 108, 15037–15042.

Vroom, V.H., 1964. Work and Motivation. Jossey-Bass, San Francisco, CA.

Wang, D., Liu, T., Shi, J., 2017a. Development of monetary and social reward processes. Sci. Rep. 7, 11128.

Wang, S., Xu, X., Zhou, M., Chen, T., Yang, X., Chen, G., Gong, Q., 2017b. Hope and the brain: trait hope mediates the protective role of medial orbitofrontal cortex spontaneous activity against anxiety. Neuroimage 157, 439–447.

Webber, E., McGraw, M.D.E., Beckwith, T., Cromwell, H., 2013. Ultrasonic vocalizations, predictability, and sensorimotor gating in the rat. Beh Brain Res 253, 32–41.

Weir, A.A., Chappell, J., Kacelnik, A., 2002. Shaping of hooks in New Caledonian crows. Science 297, 981.

Weller, J.A., Levin, I.P., Shiv, B., Bechara, A., 2007. Neural correlates of adaptive decision making for risky gains and losses. Psychol. Sci. 18, 958–964.

Wiebking, C., Duncan, N.W., Tiret, B., Hayes, D.J., Marjanska, M., Doyon, J., Bajbouj, M., Northoff, G., 2014. GABA in the insula - a predictor of the neural response to interoceptive awareness. Neuroimage 86, 10–18.

Wilson, T.D., Gilbert, D.T., 2005. Affective forecasting - knowing what to want. Curr. Dir. Psychol. Sci. 14, 131–134.

Wilson, R., Vacek, T., Lanier, D., Dewsbury, D., 1976. Open field behavior in muroid rodents. Behav. Biol. 17, 495–506.

Winkielman, P., Niedenthal, P., Wielgosz, J., Eelen, J., Kavanagh, L.C., 2015. Embodiment of cognition and emotion. In: Mikulincer, M., Shaver, P.R., Borgida, E., Bargh, J.A. (Eds.), APA Handbooks in Psychology®. APA Handbook of Personality and Social Psychology. American Psychological Association, pp. 151–175.

Wohr, M., Houx, B., Schwarting, R.K., Spruijt, B., 2008. Effects of experience and context on 50-kHz vocalizations in rats. Physiol. Behav. 93, 766–776.

Wright, H., Li, X., Fallon, N.B., Crookall, R., Giesbrecht, T., Thomas, A., Halford, J.C., Harrold, J., Stancak, A., 2016. Differential effects of hunger and satiety on insular cortex and hypothalamic functional connectivity. Eur. J. Neurosci. 43, 1181–1189.

Yang, J., Wei, D., Wang, K., Qiu, J., 2013. Gray matter correlates of dispositional optimism: a voxel-based morphometry study. Neurosci. Lett. 553, 201–205.

Yarkoni, T., Poldrack, R.A., Nichols, T.E., Van Essen, D.C., Wager, T.D., 2011. Frontiers: NeuroSynth: a New Platform for Large-scale Automated Synthesis of Human Functional Neuroimaging Data. Frontiers in Neuroinformatics.

Younes, N., Reips, U.D., 2019. Guideline for improving the reliability of Google Ngram studies: evidence from religious terms. PLoS One 14, e0213554.

Zammit, S., Allebeck, P., David, A.S., Dalman, C., Hemmingsson, T., Lundberg, I., Lewis, G., 2004. A longitudinal study of premorbid IQ Score and risk of developing schizophrenia, bipolar disorder, severe depression, and other nonaffective psychoses. Arch. Gen. Psychiatry 61, 354–360.

Zinbarg, R.E., Craske, M.G., Barlow, D.H., 2006. Mastery of Your Anxiety and Worry (MAW): Therapist Guide. Oxford University Press, New York.

Zink, C.F., Pagnoni, G., Martin-Skurski, M.E., Chappelow, J.C., Berns, G.S., 2004. Human striatal responses to monetary reward depend on saliency. Neuron 42, 509–517.