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Review article

The neural bases of expressive suppression: A systematic review of functional neuroimaging studies

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ABSTRACT

Expressive suppression refers to the inhibition of emotion-expressive behavior (e.g., facial expressions of emotion). Although it is a commonly used emotion regulation strategy with well-documented consequences for well-being, little is known about its underlying mechanisms. In this systematic review, we for the first time synthesize functional neuroimaging studies on the neural bases of expressive suppression in non-clinical populations. The 12 studies included in this review contrasted the use of expressive suppression to simply watching emotional stimuli. Results showed that expressive suppression consistently increased activation of frontoparietal regions, especially the dorsolateral and ventrolateral prefrontal cortices and inferior parietal cortex, but decreased activation in temporo-occipital areas. Results regarding the involvement of the insula and amygdala were inconsistent with studies showing increased, decreased, or no changes in activation. These mixed findings underscore the importance of distinguishing expressive suppression from other forms of suppression and highlight the need to pay more attention to experimental design and neuroimaging data analysis procedures. We discuss these conceptual and methodological issues and provide suggestions for future research.

1. Introduction

Our ability to regulate emotions – to influence which emotions we have, when we have them, and how we experience and express these emotions – is central to our health and well-being (Gross, 1998a). Some of the emotion regulation strategies that we use alter the emotional response before it has been fully generated (e.g., reappraising the meaning of the situation in which the emotion is generated), whereas others modulate the already-generated emotional response (e.g., suppressing emotion-expressive behavior) (Gross, 2015). It is now clear that different emotion regulation strategies have quite different consequences, with some strategies being generally adaptive (such as cognitive reappraisal), and other strategies being generally maladaptive (such as expressive suppression) (Gross, 1998b; McRae and Gross, 2020). Given the differential impact of different strategies, researchers have sought to elucidate the biological bases of specific emotion regulation strategies. To date, most of these efforts have focused on reappraisal (which has been the target of well over a hundred studies and multiple meta-analyses), while we know little about the underlying mechanisms of response-focused emotion regulation strategies such as expressive suppression.

1.1. Expressive suppression

Expressive suppression refers to the inhibition of ongoing emotion-expressive behavior (Gross, 1998a), for example, keeping a neutral face when feeling annoyed. It differs from other response-focused strategies in that it is not targeted at regulating the subjective experience (e.g., trying to feel less anxious) or physiological response (e.g., trying to be less aroused) but only at the behavioral expression as such.

Research on expressive suppression involves either the measurement of the habitual use of expressive suppression or the manipulation of expressive suppression (McRae and Gross, 2020). Habitual use of expressive suppression refers to an individual's tendency to choose expressive suppression as an emotion regulation strategy. It can be operationalized as trait expressive suppression measured with

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questionnaires (e.g., the Emotion Regulation Questionnaire; Gross and John, 2003) or as the frequency of using expressive suppression in one's daily life measured with ecological momentary assessment (McMahon and Naragon-Gainey, 2020). Manipulation of expressive suppression is typically conducted in a laboratory environment by exposing participants to specific stimuli (e.g., negative pictures) and explicitly telling them to suppress their emotional behavior (e.g., expression of emotions on the face), which is then compared to a contrast condition (e.g., looking at negative pictures without regulating one's emotions). The degree to which a participant can follow these instructions reflects emotion regulation ability or success (McRae and Gross, 2020).

Laboratory studies involving the manipulation of expressive suppression demonstrate that the use of this strategy has a broad range of affective, cognitive, social, physiological, and health-related consequences. When exposed to negative stimuli, people are often unable to reduce their negative emotional experience using expressive suppression (Gross and Levenson, 1993, 1997), although there are exceptions to these findings (e.g., Goldin et al., 2008). However, when positive emotions are induced, people can successfully reduce their positive emotional experience by using expressive suppression (Gross and Levenson, 1997), although again not all studies have found this to be the case (e.g., Kalokerinos et al., 2015). In a large meta-analysis (Webb et al., 2012), expressive suppression had a large effect on regulating emotions, but this only applied to suppressing the expression, not the experience or physiological responses, of emotion. Expressive suppression influences cognitive function as well. Several studies report worse recollection of emotional events (e.g., videos and conversations) when people are asked to suppress the expression of emotions (Dillon et al., 2007; Richards and Gross, 2000, 2006).

In the social domain, those who are asked to suppress their emotional expressions are liked less, considered more hostile and withdrawn by others, and their conversation partners display less affiliative and more hostile behavior towards the suppressors (e.g., Butler et al., 2003, 2007). Similarly, in romantic relationships individuals suppressing the expression of their emotions are considered less responsive, display less intimate behavior (i.e., touch) and trigger negative emotions in their partner (Ben-Naim et al., 2013; Peters and Jamieson, 2016).

Although it may not outwardly look so, people who suppress expressive behavior display increased sympathetic activation (Gross and Levenson, 1993; Hagemann et al., 2006; Roberts et al., 2008), suggesting that the technique is physiologically costly. Increased sympathetic arousal is induced even in those with whom suppressors are talking to (Ben-Naim et al., 2013; Butler et al., 2003; Peters et al., 2014). However, it should be noted that in some studies expressive suppression has been found to decrease cardiovascular activity and respiration rate (Dan-Glauser and Gross, 2011).

Studies on habitual expressive suppression using questionnaires or ecological momentary assessment provide further support for the adverse effects of using this strategy by demonstrating that the use of this strategy is associated with higher levels of negative affect, lower levels of positive affect, lower life satisfaction, lower optimism, lower self-esteem, increased rumination, lower eudaimonic well-being, poorer social support, lower relationship satisfaction, increased loneliness, increased cardiovascular disease risk, altered immune functioning, and even increased mortality (e.g., Appleton et al., 2013; Brans et al., 2013; Cameron and Overall, 2017; Chapman et al., 2013; Fernandes and Tone, 2021; Gross and John, 2003; Hu et al., 2014; Lopez et al., 2020; Preece et al., 2021; Sasaki et al., 2021). Because of all these effects, expressive suppression is typically considered a maladaptive emotion regulation strategy. In fact, its use is associated with psychopathology, such as clinical and non-clinical social anxiety, depression, PTSD, eating disorders, and suicidal ideation, (Aldao et al., 2010; Boden et al., 2013; Dryman and Heimberg, 2018; Forkman et al., 2014; Khan et al., 2021). In line with this, prospective studies have demonstrated that the use of expressive suppression predicts depressive symptoms six months later (in adolescents; Tsai et al., 2017) and more pronounced paranoia in everyday life in healthy adults (Nittel et al., 2019). However, there is also evidence in the other direction, i.e., depressive symptoms predicting increased use of expressive suppression (De France et al., 2019; Larsen et al., 2013). As such, it is unclear whether expressive suppression is a risk factor for the development of future clinical disorders or a symptom of psychopathology.

Nevertheless, in certain contexts the use of expressive suppression can also be adaptive. For example, expressive suppression has negative outcomes for people from Western cultures but not necessarily for people from Eastern cultures or for those holding Asian values (Butler et al., 2007; Fernandes and Tone, 2021; Hu et al., 2014; Soto et al., 2011; Yuan et al., 2014). Similarly, social norms may require the suppression of expressing one's emotions (Butler and Gross, 2004), such as trying to show less positive emotions when winning a competition (Kalokerinos et al., 2014). Expressive suppression may also be adaptive for certain professions, such as for physicians and clinical practitioners, who may use suppression of their facial expressions in response to negative stimuli (e.g., observing pain in others) to optimally perform their job (Anderson et al., 2021; Decety et al., 2010; Hojat et al., 2009), although, to our knowledge, empirical studies directly testing this have yet to be performed.

1.2. *The neural correlates of emotion regulation*

According to neurobiological models of emotion regulation (Ochsner et al., 2012; Ochsner and Gross, 2014), emotion regulation is thought to be associated with cognitive control processes involving prefrontal and parietal cortical areas. The dorsolateral prefrontal cortex (DLPFC), an area involved in working memory, may serve to hold strategy-relevant content and regulation goals in one's mind. Together with the DLPFC, the inferior parietal cortex is suggested to reflect top-down attentional processes (e.g., shifting focus from negative stimuli towards regulation goals and content in working memory). Additionally, dorsal regions of the anterior cingulate cortex (ACC) are considered important for monitoring the success of the regulation process. The ventrolateral prefrontal cortex (VLPFC) helps select appropriate responses and inhibit irrelevant ones. The dorsomedial prefrontal cortex (DMPFC) may also contribute to emotion regulation by helping to pay attention to and make judgements about the emotional value of various stimuli, from self to others to objects.

These control-related regions are thought to modulate sub-cortical (amygdala, ventral striatum) and cortical (insula) emotion-generation or valuation systems by either down-regulating or up-regulating activity in these areas, depending on the goal (i.e., to increase or to decrease emotional responsivity) and emotion regulation strategy. The amygdala, ventral striatum, and insula – together with other regions activated in response to emotional stimuli, such as the ACC, thalamus, hypothalamus, and regions in the brainstem – are considered part of the so-called salience network (Seeley, 2019) which is central to responding to relevant internal or external stimuli and attributing emotional valence to these stimuli. Although increased amygdala activation is often associated with negative emotions, such as fear and disgust, this structure is involved in both negative and positive emotions (Costafreda et al., 2008; Sergerie et al., 2008) as well as in motivational salience (Lindquist et al., 2012) and arousal more broadly (Hamann, 2012; Kragel and LaBar, 2016). The ventral striatum is associated with motivation and reward processing (Berridge and Kringelbach, 2008). The insula, especially the anterior insula, has been consistently found to be involved in interoception – the awareness of one's bodily states – which is considered an important aspect of emotional experience (Zaki et al., 2012).

To date, most studies have investigated the down-regulation of emotions induced by negative stimuli. The number of studies on the neural correlates of specific emotion regulation strategies varies greatly. Cognitive change, and specifically cognitive reappraisal, is by far the most studied emotion regulation strategy with several meta-analyses focusing on the neural correlates of using this strategy (Buhle et al., 2014; Diekhof et al., 2011; Messina et al., 2015). In contrast, the neural bases of expressive suppression have received much less attention (e.g., Cutuli, 2014). Only one meta-analysis has compared different strategies, including suppression (Morawetz et al., 2017). However, the authors did not distinguish different forms of suppression – experiential suppression (suppressing the subjective experience of emotion), physiological suppression (suppressing the physiological arousal induced by emotion), and expressive suppression. This is problematic because, by definition, expressive suppression is specifically about suppressing the expression, but not the experience, of emotion. Although the different types of suppression are all aimed at modulating the emotional response in one way or another, the neurobiological mechanisms underlying these may differ.

Like other emotion regulation strategies, expressive suppression seems to involve the frontoparietal cognitive control system. However, it is unclear to what extent, and in which direction, the activation of the amygdala and insula are modulated. Because expressive suppression has often been found to increase, not decrease, physiological arousal, increased activation of amygdala, as well as insula, would be expected (Gross, 2015; Ochsner et al., 2012; Ochsner and Gross, 2014). However, in the study by Dörfel et al. (2014), the use of expressive suppression (as compared to other emotion regulation strategies) was the most effective in downregulating amygdala activity while having no effect on the insula.

A better understanding of the neural bases of expressive suppression may help shed light on the mixed findings regarding the extent to which this strategy is effective in down-regulating the experience of negative emotions and whether it involves enhanced physiological arousal. It may also help shed light on the contexts in which the use of this emotion regulation strategy is adaptive (Kalokerinos et al., 2014) or maladaptive (Butler et al., 2003). Ultimately, this research may help clarify the role expressive suppression plays in psychopathology and well-being, and where potential interventions could be targeted.

1.3. The present research

In this systematic review, we synthesize and discuss functional neuroimaging studies that have specifically focused on the suppression of emotion expression in non-clinical populations. The aim is to answer the following questions: (1) What are the neural correlates of using expressive suppression as an emotion regulation strategy when exposed to emotional stimuli? (2) What methodological issues can explain the mixed findings? (3) What should future research take into account when investigating expressive suppression?

We focus on healthy participants due to the evidence that clinical populations are characterized by dysfunctional emotion regulation and, as such, altered neural activity in emotion- and regulation-related brain areas (e.g., Gaebler et al., 2014; Rive et al., 2013). Also, we are specifically interested in experimental laboratory-based studies manipulating expressive suppression (as opposed to habitual use). It is not obvious what conclusions can be drawn from the structural correlates of habitual or trait suppression due to the causal directionality and the third variable problem. For example, the habitual use of expressive suppression may affect the volume or connectivity of certain brain structures, but it may also be that brain structures (which in turn may be influenced by, for example, genes) affect how one uses expressive suppression for emotion regulation. Conceptually, it is important to make a clear distinction between expressive suppression ability when exposed to emotional stimuli (by manipulating expressive suppression) and trait expressive suppression, partly because the former enables us to understand the causality of using specific emotion regulation strategies.

2. Method

2.1. Search strategy

The databases PubMED, Scopus, and Web of Science were used to search for relevant articles published from as far back as the databases allowed until the 29th of August 2021. Two strings of keywords were used for both searches. The first keyword string was [“expressive suppression” AND neuronal OR neural OR fMRI OR “magnetic resonance imaging” OR MRI OR “positron emission tomography” OR PET OR neuroimaging]. The second keyword string was [“emotion regulation” AND suppression AND neuronal OR neural OR fMRI OR “magnetic resonance imaging” OR MRI OR “positron emission tomography” OR PET OR neuroimaging].

2.2. Inclusion and exclusion criteria

Studies were included if they fulfilled the following criteria: (1) Empirical studies published in peer-reviewed journals. (2) Studies including only healthy participants (studies with clinical samples were included only if results from a healthy control group were presented). (3) Studies including only adult participants (i.e., at least 18 years old). (4) Studies in which participants were instructed to use expressive suppression as an explicit emotion regulation strategy when presented with stimuli, which was contrasted to simply watching the same stimuli without using any regulation strategies. (5) Studies that used either functional magnetic resonance imaging (fMRI) or positron emission tomography (PET). The exclusion criteria were: (1) Studies that did not explicitly report which emotion regulation strategy was used. (2) Studies that used any other form of suppression. (3) Studies that did not use fMRI or PET. Studies using solely structural neuroimaging were excluded because the aim was to review the neural correlates of using expressive suppression when exposed to emotion-inducing stimuli. Studies using electroencephalography and event-related potentials were excluded because these methods focus more on the temporal aspects of neural activation and are limited to investigating only cortical activity.

With regard to outcomes, we specifically focused on changes in the activation of brain areas in response to emotion-inducing stimuli for the contrast expressive suppression vs watching the emotional stimuli. Additionally, we extracted information regarding the contrast watching emotional vs watching neutral stimuli.

2.3. Selection process and search results

First, one of the authors (J.S.) carried out database searches using the keyword strings mentioned above. The search resulted in 662 articles that were imported into Rayyan, a web-based application for systematic reviews (Mourad et al., 2016). After having removed the duplicates, 326 articles remained (see PRISMA flow diagram, Fig. 1; Moher et al., 2009). In the first phase, two authors (J.S. and P.S.) independently screened the titles and abstracts of the articles based on the inclusion and exclusion criteria. The blind mode of the application ensured that the authors remained unaffected by each other’s decisions. Once the decisions regarding whether to include or exclude the article were made, the blind mode was turned off and inter-rater reliability calculated. After the initial screening phase, the authors agreed on 308 articles and disagreed on 18, leading to inter-rater reliability of 94.5 % (Cohens $\kappa = 0.837$, $p <$ .001). Reasons for disagreement were method, sample, publication type, and the type of the emotion regulation strategy investigated. If there was any doubt, articles were included in the second (full text) screening phase to ensure no relevant study is left out. Relevant meta-analyses were then scanned by one of the authors to find possible relevant studies that were not found during database search. Only one such study was found, leading to 77 articles selected for a full reading. In the second phase, two authors (J.S. and P.S.), again independently and in the blind mode, read the full texts of these articles and decided whether to include

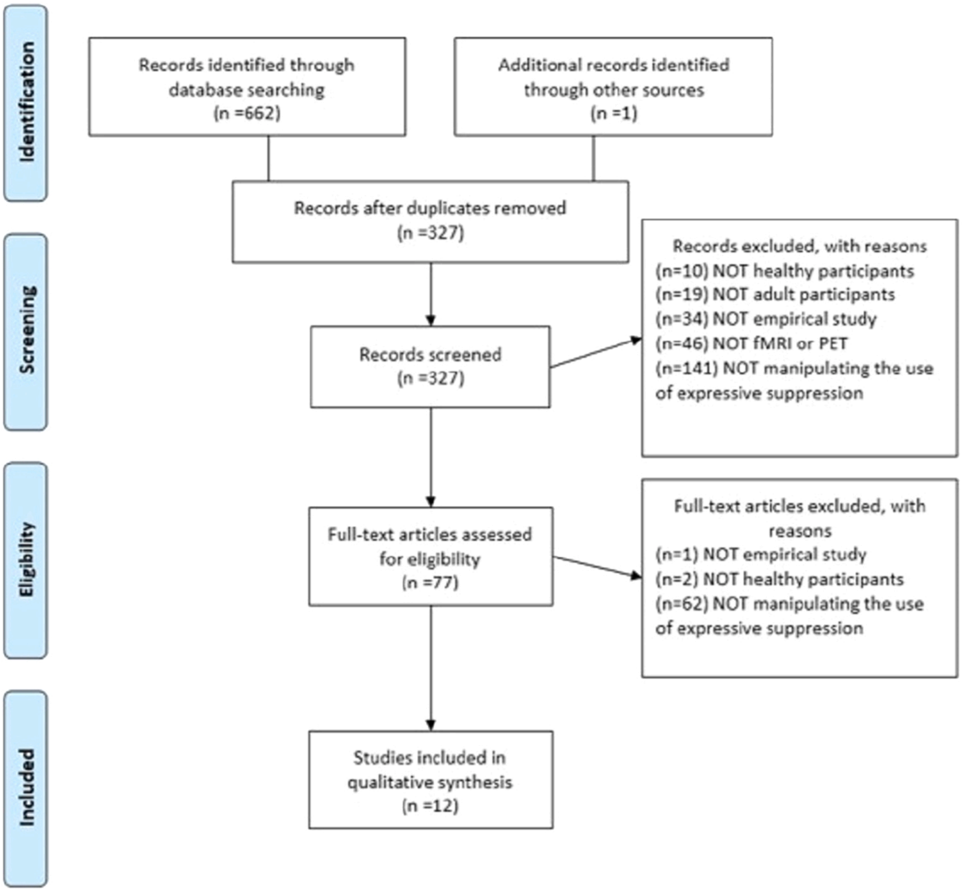

Fig. 1. PRISMA Flow Diagram Illustrating the Study Screening and Selection Process.

or exclude each article. The authors agreed on including 12 articles, excluding 61 articles, and disagreed about the inclusion of four articles. Thus, the inter-rater reliability was 94.8 % (Cohen's $\kappa = 0.828$, $p < .001$). Disagreements were due to the following reasons: (a) journal not indexed in any of the major databases; (b) lack of a control condition/group; (c) inappropriate control condition/group; (d) two groups (healthy and clinical samples) were not analyzed separately. After discussion, the authors decided to exclude these four articles. As a result, 12 studies were included in this systematic review.

3. Results

3.1. *Description of included studies*

Table 1 provides an overview of the sample characteristics and methodology of included studies. Most of the studies included young adults with the mean age between 21 and 25 years. Three studies included older participants (Katsumi et al., 2020; Van der Meer et al., 2014; Van der Velde et al., 2015) . The studies had a total of 448 participants, with the majority of them being women (72.8 %). Five out of the twelve studies relied solely on female samples (Chen et al., 2017; Dörfel et al., 2014; Goldin et al., 2008; Vanderhasselt et al., 2013a; Vrtička et al., 2011). Three of these studies justified the inclusion of females only by referring to evidence that the strength of the emotional response differs between genders (Chen et al., 2017; Goldin et al., 2008; Vrtička et al., 2011). Regarding cultural background, four studies included only US participants (Hayes et al., 2010; Goldin et al., 2008; Katsumi and Dolcos, 2018; Katsumi et al., 2020), three studies participants from China (Anderson et al., 2021; Chen et al., 2017; Li et al., 2021), five studies samples from the European Germanic cultures (Germany, Belgium, Netherlands, Switzerland; Dörfel et al., 2014; Vanderhasselt et al., 2013a; Van der Meer et al., 2014; van der Velde et al., 2015; Vrtička et al., 2011), and one study both the US and Chinese samples (Anderson et al., 2021).

In almost all the studies, emotional responses were induced by pictures from the International Affective Picture System (IAPS; Lang et al., 1997) or from other sources (Hayes et al., 2010; Katsumi and Dolcos, 2018; Katsumi et al., 2020). All but two studies used negative and neutral stimuli only. In the studies by Li et al. (2021) and Vrtička et al. (2011) positive stimuli were used in addition to negative and neutral stimuli. Whereas Vrtička et al. (2011) analyzed the responses to negative and positive stimuli separately, Li et al. (2021) merged the responses to these valenced stimuli. Only one study used film clips displaying disgust-eliciting scenes (e.g., surgical procedures) as stimuli (Goldin et al., 2008). This study investigated the activation of brain areas during three distinct temporal stages (first 0–4.5 s, second 4.5–10.5 s, and third 10.5–15 s) of the 15 s film clips. While half of the studies gave some examples of the content of the stimuli (Chen et al., 2017; Goldin et al., 2008; Hayes et al., 2010; Katsumi and Dolcos, 2018; Li et al., 2021; Vrtička et al., 2011), the others only referred to them as negative or neutral (Anderson et al., 2021; Dörfel et al., 2014; Katsumi et al., 2020; Vanderhasselt et al., 2013a; Van der Meer et al., 2014; van der Velde et al., 2015). In the study by Anderson et al. (2021) pictures of faces displaying neutral and pain expressions were used in addition to pictures from the IAPS. The reliability of inducing negative emotions was ensured by either having participants rate the valence of the stimuli, or by relying on normative ratings or ratings from earlier studies. Four of the studies explicitly mentioned matching pictures for complexity and/or social content (i.e., humans present in the pictures) (Anderson et al., 2021; Hayes et al., 2010; Katsumi and Dolcos, 2018; Vrtička et al., 2011).

Except for one study (Dörfel et al., 2014), all employed a

Table 1
Sample characteristics, study design, and procedure of included studies.

Study	Participants	Mean (SD) age	Design	Emotion-inducing stimuli	Instructions for expressive suppression	Instructions for contrast condition
Anderson et al. (2021)	N = 60 (30 women) from China (n = 30) and US (n = 30)	21.2 (3.3)	Within-subject	108 pictures depicting faces with painful or neutral expressions. 108 negative or neutral pictures from the IAPS	"Keep your face still while looking at the picture so that someone watching your face would not be able to know what you are feeling"	"Look at the picture directly and respond naturally"
Chen et al. (2017)	N = 52 (52 women), of whom 47 in the final analyses from China	21.0 (1.4)	Within-subject	240 pictures (120 negative, 120 neutral) from the Chinese Affective Picture System (adapted from the IAPS)	Participants were instructed to "keep their face still while viewing pictures so that someone watching their face would not be able to detect what was being experienced subjectively".	Participants were asked to "view the pictures attentively and experience the emotions freely if generated".
Dörfel et al. (2014)	N = 74 (74 women), of whom 22 in the expressive suppression group, from Germany	23.2 (range 18–39)	Between-subject	60 negative or neutral pictures from the IAPS	"Keep your face still while looking at the picture so that someone watching your face will not be able to detect what you are experiencing subjectively"	"Look at the following picture directly and permit feeling your emotions"
Goldin et al. (2008)	N = 17 (17 women) from the US	22.7 (3.5)	Within-subject	40 film clips (30 disgust-inducing and 10 neutral)	Participants were instructed to "keep their face still while viewing films so that someone watching their face would not be able to detect what was being experienced subjectively"	"Watch" (not specified)
Hayes et al. (2010)	N = 25 (11 women) from the US	21.6 (2.5)	Within-subject	160 pictures (120 negative, 40 neutral) from the IAPS plus from researchers' own database	Participants were instructed to "not let any emotion you are feeling show on your face"	"Simply look at the picture and let any emotions you're feeling unfold naturally"
Katsumi and Dolcos (2018)	N = 23 (15 women) from the US	23.4 (3.7)	Within-subject	180 pictures (90 negative, 90 neutral) from the IAPS plus additional neutral pictures from other sources	Participants were instructed to "view and rate the […] images, while trying to suppress experience and expression of emotional responses triggered by the images"	Participants were asked to "view the images and rate their subjective emotional experience triggered by the images"
Katsumi et al. (2020)	N = 33 (21 women), of whom 17 younger adults[a] and 16 older adults, from the US	Younger: 23.3 (4.1) Older: 68.6 (7.0)	Within-subject	180 pictures (90 negative, 90 neutral) from IAPS plus additional neutral pictures from other sources	Participants were instructed to "view and rate the […] images, while trying to inhibit the experience and expression of emotional responses triggered by the images"	Participants were asked to "view the images and rate their subjective emotional experience triggered by the images"
Li et al. (2021)	N = 32 (16 women) from China	19.6 (1.3)	Within-subject	45 pictures (15 negative, 15 positive, 15 neutral) from the OASIS	Participants were asked to "inhibit potential behavioral or physiological responses, e.g. facial expressions, respiration, and heart rate, related to an emotional stimulus"	"Participants passively viewed the images and reacted freely to the emotional content without trying to modulate their emotions"
Vanderhasselt et al., 2013a	N = 42 (42 women) from Belgium	21.3 (2.3)	Within-subject	63 negative pictures from the IAPS	Participants were instructed to "suppress displaying their feelings elicited by the picture. They were told that it was important that people in their environment would not be able to see what they were feeling"	Participants were instructed to "simply look at the pictures, feel their natural feelings and not change anything"
Van der Meer et al. (2014)	N = 20 (6 women) from the Netherlands	35.5 (11.7)	Within-subject	88 pictures (66 negative, 22 neutral) pictures from the IAPS	"Suppress the emotion elicited by the picture […] someone else should not be able to read the emotion on the subject's face (i.e., keeping a poker face".	"Look at the picture and experience the elicited emotion"
van der Velde et al. (2015)	N = 51 (23 women) from the Netherlands	37.1 (10.3)	Within-subject	88 pictures (66 negative, 22 neutral) from the IAPS	Participants were instructed to "refrain from expressing their emotions, in a way that bystanders would not be able to read their emotions by looking at their face"	Participants were instructed to "look closely at the picture and not change the way they were feeling"
Vrtička et al. (2011)	N = 19 (19 women) from Switzerland	24.8 (4.0)	Within-subject	240 emotional (60 social positive, 60 social negative, 60 nonsocial positive, 60 nonsocial negative) and 40 neutral (20 with humans, 20 without humans) pictures from the IAPS or from the Internet	Do not "display any felt emotions that could become visible on the outside (e.g., through breathing frequency, heart rate, skin conductance responses, and facial expression"	Participants were instructed to "watch and evaluate the depicted emotional scenarios as if they corresponded to real situations to which they would be personally exposed"

Note. ES = expressive suppression; IAPS = International Affective Picture System; OASIS = Open Affective Standardized Image Set; SD = standard deviation.

[a] Data from younger participants overlaps with the data from Katsumi and Dolcos (2018).

within-subject design. In the study by Dörfel et al. (2014), participants were randomized into one of four groups that were instructed to use different emotion regulation strategies. In all the other studies, some form of block-design was used. Common procedures were employed in all studies: participants were instructed to either use an emotion regulation strategy or to simply look at the stimuli, while being presented with neutral or emotional stimuli. The stimuli were pseudo-randomized so as to not induce longer-lasting mood (as a result of presenting several negative pictures consecutively). Studies differed with respect to stimulus presentation time, with some studies having short presentation times, e.g., 2 s (Chen et al., 2017; Vrtička et al., 2011) and others up to 10–15 s (Goldin et al., 2008; Vanderhasselt et al., 2013a).

Instructions for expressive suppression were almost identical, with only small variations. All studies instructed participants to suppress displays of emotion on the face or in general. Two studies added the instruction to also suppress the experience of emotion (in addition to suppressing the expression of emotion) (Katsumi and Dolcos, 2018; Katsumi et al., 2020) and two the instruction to suppress the physiological response, such as respiration and heart rate (Li et al., 2021; Vrtička et al., 2011). Compliance with following the instructions was directly controlled in only one study. Specifically, Goldin et al. (2008) filmed participants with a video camera while they were using expressive suppression. Two coders (blind to the experimental condition) then evaluated the extent of emotional expressiveness on participants' faces. In the other studies, participants were either falsely informed about the presence of control measurements (e.g., cameras) (Vanderhasselt et al., 2013a; Vrtička et al., 2011), had to report the extent to which they followed the instructions by filling in self-report scales (Chen et al., 2017; Dörfel et al., 2014; Li et al., 2021), or compliance was not controlled at all (Anderson et al., 2021; Hayes et al., 2010; Katsumi and Dolcos, 2018; Katsumi et al., 2020; Van der Meer et al., 2014; van der Velde et al., 2015). The contrast conditions were similar in all studies with instructions to simply watch the emotional stimuli and let emotions unfold naturally. Three studies explicitly asked participants to be attentive or to look at the stimuli carefully (Anderson et al., 2021; Chen et al., 2017; Van der Velde et al., 2015).

Table 2
Description of neuroimaging analysis methods used in included studies.

Study	WB/ ROI	ROI type	Corrected p for	CDT (uncorr.)	Final thres-hold	Additional constrains/ details	Software for statistical estimation
Anderson et al. (2021)[a]	WB		Voxel	–	p < .05, FDR	k > 50	FSL
Chen et al. (2017)	WB		Voxel	–	p < .001, FWE	k > 10	SPM8
	AMY (1st step)	Anatomical ROI	Cluster	p < .001	p < .01, FWE	“Watch negative vs. watch neutral” contrast	AFNI, (AlphaSim)
	AMY (2nd step)	Voxels above threshold within the anatomical ROI	–	–	–	Mean % signal for “main effect of strategy”, ANOVA	–
Dörfel et al. (2014)	WB		Voxel	–	p < .05, FWE		SPM8
	AMY	Anatomical ROI	Voxel	–	p < .05, FWE		
Goldin et al. (2008)	WB		Cluster	p < .0025	p < .001, FWE		AFNI, (AlphaSim)
	WB (for split time components)		Cluster	p < .005	p < .005, FWE		
Hayes et al. (2010)	WB		Cluster	z > 2.3	p < .05, FWE		FSL (Monte-Carlo / TFCE)
	AMY	Anatomical ROI			p < .05, FWE		
Katsumi and Dolcos (2018)	WB		Cluster	p < .005	p < .05, FWE		AFNI (3dClustSim)
	MTL (AMY, HC, PHC); PFC	Anatomical ROIs (separate analyses)	Cluster	p < .005	p < .05, FWE		
Katsumi et al. (2020)	WB		Cluster	p < .005	p < .05, FWE		AFNI (3dClustSim)
	MTL (AMY, HC, PHC); PFC	Anatomical ROIs (separate analyses)	Cluster	p < .005	p < .05, FWE		
Li et al. (2021)	WB		Voxel	–	p < .001, FWE; p < .05, FWE for contrast involving “Suppression”	k > 20	SPM12
Vanderhasselt et al., 2013a	WB		Voxel	–	p < .05, FWE	k > 5	SPM5
	AMY; PCG	Anatomical ROIs	(Not specified)				
Van der Meer et al. (2014)	WB (control group)		Cluster	p < .001	p < .05, FWE		SPM5
Van der Velde et al. (2015)	WB		Cluster	p < .001	p < .05, FWE		SPM8
	AMY	Not specified	Cluster	p < .001	p < .05, FWE		
Vrticka et al. (2011)	WB, only one sample t-tests[b]		Voxel	–	P < 001, uncorr	k > 5	SPM2
	AMY, only one sample t-tests[b]	Functional	Voxel	–	P < 005, uncorr	k < 5	

Note. This table lists only those methods that are relevant for the results of the present review. CDT = Cluster defining threshold (primary voxel-wise uncorrected threshold used in cluster-based analysis); k = cluster extent (voxels); ROI = region of interest analysis; WB = whole brain analysis. AMY = amygdala; HC = hippocampus; MTL = medial temporal lobe; PHC = parahippocampal cortex; PCG = precentral gyrus; PFC = prefrontal cortex.

[a] Anderson et al. (2021) also applied the multivariate pattern analysis derived Picture Induced Negative Emotion Signature (PINES; Chang et al., 2015) to their data.

[b] In Vrticka et al. (2011), the voxel mean values of survived clusters from one sample t-tests were taken to further analysis outside of SPM (with SPSS).

Most studies presented instructions before the stimuli (e.g., Katsumi and Dolcos, 2018), whereas three studies presented instructions (for both expressive suppression and contrast conditions) during or after having presented the stimuli (Hayes et al., 2010; Van der Meer et al., 2014; van der Velde et al., 2015). One study gave participants time to prepare a regulation strategy before the stimuli were presented (mean time 4.5 s; Vanderhasselt et al., 2013a). These participants were also asked to think that they would be successful in their emotion regulation and were told that it would improve their regulation if they prepared.

Regarding the measurement and analysis of neural activity, all studies used fMRI. Four studies relied on whole brain (WB) analysis together with an a priori amygdala region of interest (ROI) analysis (Chen et al., 2017; Dörfel et al., 2014; Hayes et al., 2010; van der Velde et al., 2015). Two studies used WB analysis together with prefrontal cortex and medial temporal lobe structures as ROIs (Katsumi and Dolcos, 2018; Katsumi et al., 2020), one study WB analysis together with precentral gyrus and amygdala as ROIs (Vanderhasselt et al., 2013a), and in one study ROIs (e.g., amygdala, insula) were determined on the basis of WB analysis (Vrtička et al., 2011). Four studies used only WB analysis (Anderson et al., 2021; Goldin et al., 2008; Li et al., 2021; Van der Meer et al., 2014). It should be mentioned that four studies also used functional connectivity analyses (Chen et al., 2017; Li et al., 2021; Katsumi and Dolcos, 2018; Katsumi et al., 2020), but because mostly these analyses addressed other research questions, these results are not presented here. For more information on the methodological details of fMRI analyses, see Table 2.

3.2. *Neural activation while watching negative stimuli*

To understand the extent to which emotional stimuli were effective in modulating neural activity, the contrast of watching negative versus neutral stimuli is presented. It is important to note that not all studies reported these results (Katsumi and Dolcos, 2018; Van der Meer et al., 2014). When watching negative (or emotional, Li et al., 2021) stimuli, as compared to neutral stimuli, there was activation in the VLPFC (Anderson et al., 2021; Dörfel et al., 2014; Goldin et al., 2008; Li et al., 2021; van der Velde et al., 2015), DLPFC (Anderson et al., 2021; Dörfel et al., 2014; Goldin et al., 2008; Vrtička et al., 2011) and DMPFC (Anderson et al., 2021; Dörfel et al., 2014; Goldin et al., 2008; van der Velde et al., 2015). Activation was also evident in other cortical areas including the insula, hippocampus, inferior parietal lobule (IPL), and cingulate cortex. Activation in the temporo-occipital cortices (e.g., lingual gyrus, fusiform gyrus) was found in almost all studies. Subcortically, studies reported amygdala (Anderson et al., 2021; Chen et al., 2017; Dörfel et al., 2014; Goldin et al., 2008; Hayes et al., 2010; van der Velde et al., 2015), caudate (Anderson et al., 2021; Chen et al., 2017; Goldin et al., 2008; van der Velde et al., 2015; Vrtička et al., 2011) and thalamic activation (Dörfel et al., 2014; Goldin et al., 2008). For more details, see Table 3. Thus, as expected, negative emotional stimuli (versus neutral stimuli) produced activity in areas belonging to the salience network.

Table 3
Neural activation while watching negative stimuli compared to watching neutral stimuli.

Study	Watch Negative > Watch Neutral
Anderson et al. (2021)[a]	Faces: BL superior frontal gyrus, BL anterior cingulate, BL lateral frontopolar cortex/middle frontal gyrus/superiro frontal gyrus, BL inferior frontal gyrus (opercular, orbital aspects), R inferior frontal gyrus (triangular aspect), anterior insula/rolandic operculum, BL precentral sulcus, BL supramarginal gyrus, BL posterior cingulate gyrus, BL middle temporal gyrus, R inferior temporal gyrus, L cuneus, BL lateral occipital cortex, R collateral sulcus (lingual/fusiform gyrus), BL thalamus, BL caudate/pallidum, BL cerebellum IAPS: BL lateral frontopolar cortex/superior frontal sulcus, L medial frontal pole, BL superior frontal gyrus/medial frontal gyrus/precentral sulcus/inferior frontal gyrus/anterior insula/hippocampus/amygdala/thalamus/caudate/midbrain, L middle frontal gyrus, BL intraparietal sulcus, BL anterior cingulate gyrus, BL posterior middle temporal gyrus/supramarginal gyrus/lateral and polar occipital cortices/fusiform gyrus/bilateral cerebellum, BL posterior cingulate gyrus[b]
Chen et al. (2017)	R angular gyrus, BL fusiform gyrus, R middle temporal gyrus, L inferior temporal gyrus, L middle occipital gyrus, L hippocampus, L caudate, L thalamus, BL amygdala
Dörfel et al. (2014)	BL inferior orbitofrontal gyrus/insula/amygdala, R precentral gyrus/inferior frontal gyrus operculum/middle frontal gyrus, L precentral gyrus/inferior frontal gyrus operculum, BL superior frontal gyrus medial, BL anterior cingulate gyrus, R SMA, L inferior parietal gyrus/postcentral gyrus, R inferior parietal gyrus/superior parietal gyrus, L supramarginal gyrus/postcentral gyrus, L hippocampus, BL middle occipital gyrus/middle temporal gyrus/inferior occipital gyrus/fusiform gyrus, R cerebellum, L hippocampus/thalamus
Goldin et al. (2008)	L inferior frontal gyrus/insula, medial PFC, R DMPFC, L inferior frontal gyrus/DLPFC, BL middle frontal gyrus/DLPFC, R inferior frontal gyrus, L precentral gyrus, L superior frontal gyrus/medial PFC, L inferior temporal gyrus, R superior temporal gyrus/ R insula, R superior parietal lobule, L postcentral gyrus, L lingual gyrus, BL amygdala, BL caudate body, L hypothalamus, R thalamus (pulvinar)
Hayes et al. (2010)	R frontal pole, R angular gyrus, BL posterior cingulate cortex, R insular cortex, L fusiform gyrus, L subcallosal cortex, BL amygdala, BL midbrain
Katsumi and Dolcos (2018)	N/A (Reported only the watch negative > suppress contrast)
Katsumi et al. (2020)[c]	BL inferior frontal gyrus, BL middle frontal gyrus, L superior frontal gyrus, BL medial frontal gyrus, BL insula, BL anterior cingulate, L cingulate gyrus, L precentral gyrus, R postcentral gyrus, L posterior cingulate, L inferior parietal lobule, L superior parietal lobule, BL precuneus, BL middle temporal gyrus, BL fusiform gyrus, R middle occipital gyrus, R superior temporal gyrus, BL amygdala, BL hippocampus, L parahippocampus, BL entorhinal cortex, L globus pallidus, R caudate, R putamen, BL brainstem
Li et al. (2021)	Emotional (positive and negative) > neutral: BL inferior frontal gyrus pars opercularis/triangularis, BL SMA, BL superior occipital gyrus/middle occipital gyrus,
Van der Meer et al. (2014)	N/A (Reported only suppress > watch negative and watch negative > suppress contrasts)
van der Velde et al. (2015)	BL superior medial frontal gyrus, L middle inferior frontal gyrus, BL inferior frontal gyrus, L anterior insula, L SMA, L middle cingulate gyrus, L precuneus, BL inferior and superior parietal gyrus, BL supramarginal gyrus, BL angular gyrus, R fusiform gyrus/middle and inferior temporal gyrus, L middle temporal gyrus/middle occipital gyrus, L calcarine sulcus/occipital cortex, R occipital cortex, BL hippocampus, R amygdala, L amygdala (after SVC), R caudate, BL brainstem
Vanderhasselt et al., 2013a	N/A (Did not include neutral pictures)
Vrtička et al. (2011)	BL medial orbitofrontal cortex, BL rostro-ventral anterior cingulate cortex, BL DLPFC, BL superior anterior temporal gyrus, BL posterior cingulate cortex, BL temporo-parietal junction.

3.3. *Neural activation while using expressive suppression during exposure to negative stimuli*

All studies used fMRI and compared the use of expressive suppression to simply watching or attending to negative (or emotional, Li et al., 2021) stimuli. Eleven studies reported data on the contrast expressive suppression versus watching negative stimuli and nine of those reached significant thresholds (see Table 4 and Fig. 2). In the nine studies reaching significant thresholds, eight reported increased right DLPFC activation (Anderson et al., 2021; Dörfel et al., 2014; Goldin et al., 2008; Hayes et al., 2010; Katsumi et al., 2020; Vanderhasselt et al., 2013a; Van der Velde et al., 2015; Vrtička et al., 2011), although in one study this applied to younger participants only (Katsumi et al., 2020). Two studies also reported increased activation in the left DLPFC (Anderson et al., *Note.* BL= bilateral; L= left; R= right. ACC = anterior cingulate cortex; DLPFC = dorsolateral prefrontal cortex; DMPFC = dorsomedial prefrontal cortex; PFC = prefrontal cortex; SMA = supplementary motor area; SVC = small volume correction.

[a] Because the authors reported only a few peaks in the table, omitting others located distantly within extended clusters, the results were updated using images made publicly available by the authors at https://neurovault.org/collections/XKWLLVBQ/

[b] Anderson et al. (2021) also used multivariate pattern analysis by focusing on the Picture Induced Negative Emotion Signature (PINES; Chang et al., 2015), which includes positive predictive weights in the amygdala, anterior insula, dorsomedial prefrontal cortex, presupplementary motor area, and posterior cingulate cortex. The authors reported increased PINES responses to watching negative, as compared to neutral, images.

[c] Includes both younger and older adults.

2021; Vanderhasselt et al., 2013a). Li et al. (2021), who combined both positive and negative stimuli, reported activation only in the left (but not right) DLPFC. VLPFC activation increased in six studies but was less restricted to one hemisphere only (Anderson et al., 2021; Goldin et al., 2008; Hayes et al., 2010; Li et al., 2021; Vanderhasselt et al., 2013a; Van der Velde et al., 2015). Only one study reported increased DMPFC activation (Goldin et al., 2008). In the study by Goldin et al. (2008), these three prefrontal areas (DLPFC, VLPFC, DMPFC) showed increased activation only after 10–15 s of stimulus exposure. Increased activation of VMPFC was also reported in one study only (Anderson et al., 2021).

Several other cortical areas also showed activation during expressive suppression (as compared to watching negative stimuli). Increased activation in the inferior regions of the parietal lobule, such as the supramarginal gyrus and angular gyrus, was consistently found (Anderson et al., 2021; Dörfel et al., 2014; Goldin et al., 2008; Hayes et al., 2010; Vanderhasselt et al., 2013a; Van der Velde et al., 2015). Three studies reported increased activation also in the precuneus (PreC; Anderson et al., 2021; Goldin et al., 2008; Vanderhasselt et al., 2013a). Activation either in the anterior (ACC; Anderson et al., 2021), middle (MCC; Hayes et al., 2010; Van der Velde et al., 2015) or posterior cingulate cortex (PCC; Anderson et al., 2021) was also observed, although the latter pertained to painful facial expressions only. Three studies reported increased activation in the anterior insula (Goldin et al., 2008; Hayes et al., 2010; Van der Velde et al., 2015). Interestingly, in two studies the activation in anterior insula was downregulated (Anderson et al., 2021; Vrtička et al., 2011).

The opposite contrast – watching negative stimuli versus suppressing the expression of emotion – yielded increased (mostly bilateral) amygdala activation in seven studies (Anderson et al., 2021; Chen et al., 2017; Dörfel et al., 2014; Hayes et al., 2010; Katsumi and Dolcos, 2018; Katsumi et al., 2020; Vrtička et al., 2011). This suggests that expressive suppression was successful in downregulating amygdala activity in these studies. However, it is important to note that three studies showed no impact of suppression on amygdala activity (Li et al., 2021; Van der Meer et al., 2014; van der Velde et al., 2015) and one showed increased amygdala activation during suppression (Goldin et al., 2008). Although Vrtička and colleagues (2011) also reported downregulation of amygdala activation during suppression, this was true for social stimuli only. Similarly, Anderson et al. (2021) showed that amygdala activation was downregulated for pictures of faces but not for other pictures. Finally, significant downregulation of activation in temporo-occipital cortex (TOC; e.g., lingual gyrus, fusiform gyrus, and cuneus) during expressive suppression was reported in several studies (Anderson et al., 2021; Dörfel et al., 2014; Goldin et al., 2008; Li et al., 2021; Van der Meer et al., 2014; Van der Velde et al., 2015; Vrtička et al., 2011).

A few studies reported changes in activation in motor areas (i.e., supplementary motor area, SMA; pre-and postcentral gyri, PPCG) as well as in the caudate, but the direction of change was inconsistent (Anderson et al., 2021; Li et al., 2021; van der Velde et al., 2015).

4. Discussion

We investigated the neural correlates of expressive suppression. As a result of a systematic review of functional neuroimaging studies, we identified twelve articles in which participants were asked to suppress the expression of emotion induced by emotional stimuli as compared to simply watching the stimuli. In this section, we will discuss the results and methodological issues of these studies as well as point to future research directions.

4.1. The involvement of cognitive control regions in expressive suppression

In almost all of the reviewed studies, suppressing outward signs of emotion when exposed to negative stimuli, as compared to simply watching these negative stimuli, resulted in increased activation of regions comprising the frontoparietal control network, such as the DLPFC, VLPFC, and IPL. Especially the right DLPFC was involved in expressive suppression. Right-lateralized PFC activation has previously been reported in studies in which participants have been instructed to decrease, rather than increase, their emotional response (Kim and Hamann, 2007; Ochsner et al., 2004). Moreover, the right lateral PFC has been shown to be unique to down-regulating negative emotions (Kim and Hamann, 2007). This is in line with a bulk of studies displaying hemispheric asymmetry in the processing of emotions, according to which the right hemisphere is more involved in the processing of negative affect (or avoidance-related emotions), while the left hemisphere is associated with positive affect (or approach-related emotions) (Kelley et al., 2017). These hemispheric differences in the processing of emotions differing on the dimension of valence (or approach-avoidance) may also help explain why Li et al. (2021), who pooled positive and negative stimuli, reported suppression-related activation in the left DLPFC. However, it should be noted that the right lateral PFC, including both DLPFC and VLPFC, has been suggested to be a domain-general area related to a variety of phenomena involving inhibition, such as emotion regulation and behavioral inhibition (Aron et al., 2014; Bari and Robbins, 2013; Depue et al., 2016; Gable et al., 2018).

Increased activity in lateral prefrontal and parietal areas is also reported in studies investigating other emotion regulation strategies (Ochsner et al., 2012). For example, Dörfel and colleagues (2014) compared the neural basis of three families of emotion regulation strategies – cognitive change, attentional deployment, and expressive suppression – and found that regions in the lateral PFC and IPL seem to comprise a common regulation network. The involvement of these areas may thus also reflect holding strategy-relevant content information in mind (i.e., in the form of working memory) to enable the continual implementation of an emotion regulation technique (facial neutrality in the case of expressive suppression). Furthermore, especially in the right hemisphere, the frontoparietal control network is closely coupled with attention networks (Dixon et al., 2018; Wang et al., 2014) which may help focus attention on task-relevant information. As suggested by Dörfel et al. (2014), activation of parietal areas, or more specifically the supramarginal gyrus, may also reflect the ongoing monitoring and awareness of one's facial expression.

However, expressive suppression did not involve (at least not consistently) the more medial control-related areas considered part of the emotion regulation network, such as the ACC and DMPFC. This is in line with a recent meta-analysis of fMRI studies suggesting that these regions are specifically implicated in cognitive reappraisal, but not in other emotion regulation strategies (Morawetz et al., 2017). Moreover, studies investigating the functional and structural correlates of the habitual use of expressive suppression (Giulani et al., 2011; Vanderhasselt et al., 2013b) have also failed to find the involvement of medial prefrontal cortical areas.

Table 4
Neural activation while using expressive suppression during exposure to negative stimuli compared to watching negative stimuli.

	DLPFC	VLPFC	DMPFC	VMPFC	SMA	PPCG	ACC	MCC	PCC	IPL/ IPC	PreC	Insula	TOC	Amygdala	Caudate
Increased activity during suppression as compared to watching negative stimuli (contrast: suppress > watch negative)															
Anderson et al. (2021) faces[a]	↑BL			↑BL		↑BL	↑BL		↑R	↑BL	↑BL		↑BL		↑R
Anderson et al. (2021) IAPS	↑R	↑R		↑R			↑R			↑BL			↑BL		
Dörfel et al. (2014)	↑R									↑BL					
Goldin et al. (2008)	↑R	↑BL	↑R							↑BL	↑L	↑R[b] (ant.)	↑BL	↑R[c]	
Hayes et al. (2010)	↑R	↑BL						↑R		↑BL		↑BL (ant.)			
Katsumi and Dolcos (2018)	–	–	–	–		–	–	–	–	–	–	–	–	–	–
Katsumi et al. (2020)[d]	↑R (younger)[e]														
Li et al. (2021)[f]	↑L	↑L			↑BL	↑L							↑BL		
Vanderhasselt et al., 2013a	↑BL	↑R								↑R	↑R				
Van der Meer et al. (2014)	–	–	–	–		–	–	–	–	–	–	–	–	–	–
van der Velde et al. (2015)	↑R	↑BL						↑BL		↑BL		↑BL (ant.)			
Vrtička et al. (2011)	↑R														
Decreased activity during suppression as compared to watching negative stimuli (contrast: watch negative > suppress)															
Anderson et al. (2021) faces[g,i]					↓BL	↓BL	↓L			↓L		↓BL (post.)	↓BL	↓BL	
Anderson et al. (2021) IAPS[h,i]	↓L		↓L		↓BL	↓BL	↓L				↓L	↓L (ant.)	↓BL		↓BL
Chen et al. (2017)														↓BL	
Dörfel et al. (2014)													↓BL	↓L	
Goldin et al. (2008)													↓L		
Hayes et al. (2010)														↓BL	
Katsumi and Dolcos (2018)														↓BL	
Katsumi et al. (2020)	↓R (older)[e]													↓BL	
Li et al. (2021)[j]										↓R			↓BL		
Van der Meer et al. (2014)													↓L		
van der Velde et al. (2015)						↓L							↓BL		
Vrtička et al. (2011)	↓R											↓R (ant. for negative stimuli; mid. for nonsocial stimuli)	↓L	↓R (social stimuli)	

Note. Chen et al. (2017) did not report any results for the contrast suppress > watch negative, whereas Vanderhasselt et al., 2013a did not report any results for the contrast watch negative > suppress.
↑ = increased activation; ↓ = decreased activation. ant. = anterior; mid. = middle; post. = posterior. BL = bilateral; L = left; R = right.
DLPFC = dorsolateral prefrontal cortex; VLPFC = ventrolateral prefrontal cortex; DMPFC = dorsomedial prefrontal cortex; VMPFC = ventromedial prefrontal cortex; SMA = supplementary motor area; PPCG = precentral and/or postcentral gyrus (not divided into lateral and medial parts); ACC = anterior cingulate cortex; MCC = middle cingulate cortex; PCC = posterior cingulate cortex; IPL/IPC = inferior parietal lobule/inferior parietal cortex; PreC = precuneus; TOC = temporo-occipital cortex.

[a] Because the authors reported only a few peaks in the table, omitting others located distantly within extended clusters, the results were updated using images made publicly available by the authors at https://neurovault.org/collections/XKWLLVBQ/

[b] In the paper, Goldin et al. (2008) reported activation in the left anterior insula (in Table 1). However, after personal communication with the authors of the paper, the first author of the paper confirmed that the activation occurred in the right (not left) anterior insula.

[c] Activation greater only marginally ($p = .08$)

[d] Katsumi et al. (2020) only reported results for explicit and implicit suppression combined

[e] The analyses combined both explicit and implicit expressive suppression, displaying greater activation in this region during suppression (as compared to watching the stimuli) in younger participants, but increased activation during watching the stimuli (as compared to suppression) in older participants. Importantly, there were no significant differences between explicit and implicit suppression conditions for either younger or older participants.

[f] Li et al. (2021) contrasted suppress > watch emotional (positive and negative)

[g] In Anderson et al. (2021) there was also increased activation in the BL putamen, midbrain, and cerebellum.

[h] In Anderson et al. (2021) there was also increased activation in the BL cerebellum

[i] In Anderson et al. (2021), results from the multivariate pattern analysis showed decreased Picture Induced Negative Emotion Signature (PINES; Chang et al., 2015) responses when engaging in expressive suppression, as compared to simply watching painful faces and negative IAPS pictures. The PINES includes positive predictive weights in the amygdala, anterior insula, dorsomedial prefrontal cortex, presupplementary motor area, and posterior cingulate cortex as well as negative predictive weights in the parahippocampal gyrus, superior temporal gyrus, temporoparietal junction, and caudate.

[j] These data was provided by the authors upon request. Also includes increased activation in the L superior parietal lobe

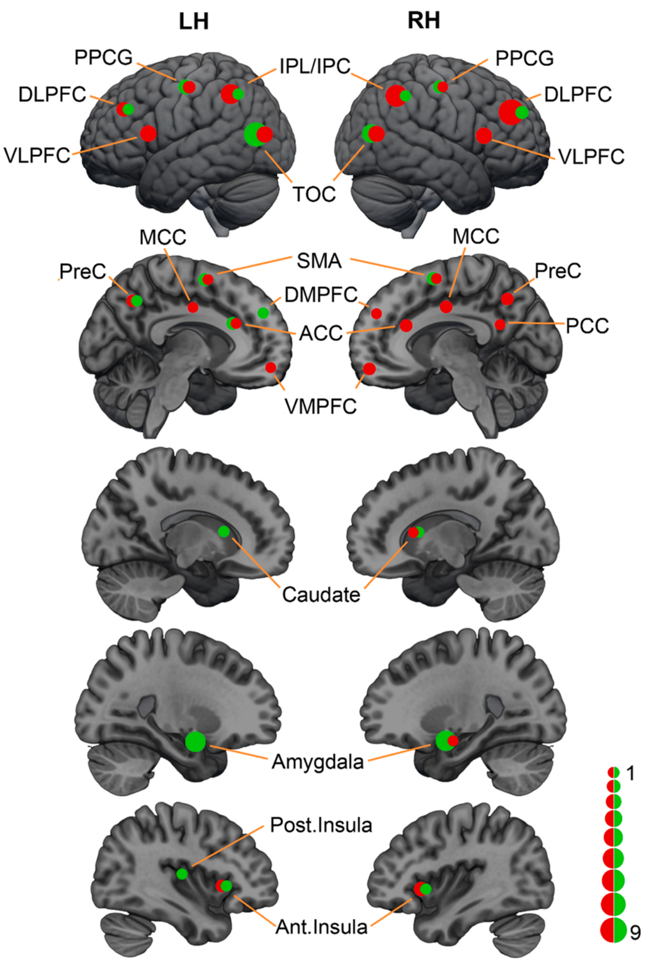

Fig. 2. An illustrative summary of neural activations and deactivations during expressive suppression. Note. Red = Increased activity during suppression as compared to watching negative stimuli (contrast: suppress > watch negative). Green = Decreased activity during suppression as compared to watching negative stimuli (contrast: watch negative > suppress). The size of the circle represents the number of studies reporting this finding (from 1 = one study to 9 = nine studies). ACC = anterior cingulate cortex; Ant. Insula = anterior insula; DLPFC = dorsolateral prefrontal cortex; DMPFC = dorsomedial prefrontal cortex; IPL/IPC = inferior parietal lobule/inferior parietal cortex; LH = left hemisphere; MCC = middle cingulate cortex; PCC = posterior cingulate cortex; Post. Insula = posterior insula; PPCG = pre-and post-central gyrus; PreC = precuneus; RH = right hemisphere; SMA = supplementary motor area; TOC = temporo-occipital cortex; VLPFC = ventrolateral prefrontal cortex; VMPFC = ventromedial prefrontal cortex.

4.2. *The involvement of emotion-generative regions in expressive suppression*

Given the findings that expressive suppression is associated with increased sympathetic arousal (Gross, 2015; Ochsner et al., 2012; Ochsner and Gross, 2014), one would expect to find increased amygdala activity. However, half of the studies observed decreased, not increased, amygdala activation during expressive suppression of negative emotions compared to the non-regulation contrast (Anderson et al., 2021; Chen et al., 2017; Dörfel et al., 2014; Hayes et al., 2010; Katsumi et al., 2020; Katsumi and Dolcos, 2018). Previous studies have demonstrated hemispheric differences in amygdala activation, with the left amygdala being involved in the cognitive processing of emotional information (i.e., appraisal of arousal) but right hemisphere in more automatic (i.e., physiological reaction) processing (Dyck et al., 2011; Gläscher and Adolphs, 2003; Phelps et al., 2001). The fact that, in the studies of the present review, expressive suppression mostly involved bilateral amygdala activation seems to suggest that this emotion regulation strategy influences both components of arousal.

Only one study reported (and then only marginally, $p = .08$) increased amygdala activation during expressive suppression compared to the non-regulation contrast (Goldin et al., 2008). Unlike other studies, here participants watched film clips. This was also the only study that elicited a specific emotional response (disgust). Previous studies using disgust-eliciting film clips have demonstrated increased sympathetic activation (or arousal) during expressive suppression (e.g., ; Gross and Levenson, 1993; Roberts et al., 2008; Soto et al., 2016), but increased sympathetic responding is also evident while suppressing during sadness-inducing films (Gross and Levenson, 1997). Three studies found no differences in amygdala activation during expressive suppression (Li et al., 2021; Van der Meer et al., 2014; van der Velde et al., 2015), but in one of those (Li et al., 2021), positive and negative stimuli were pooled.

Despite finding no differences in amygdala activation as a function of valence, Vrtička et al. (2011) demonstrated activation in bilateral amygdala depending on whether the pictures displayed social content (humans) or not. This increased activation in response to social (as compared to nonsocial) pictures was eliminated during expressive suppression, although this applied to the right amygdala only. Similar findings were reported by Anderson et al. (2021) who found decreased amygdala activation during suppression of faces but not of other stimuli. Previous studies have demonstrated the activation of the amygdala in response to a wide range of social stimuli, which is in line with the proposed role of amygdala in the processing of motivational salience (for reviews, see Adolphs, 2010; Bickart et al., 2014). Given the differential effects of suppression on social vs nonsocial stimuli, combining different stimulus content types (social and nonsocial) into one category may be one explanation for the inconsistent results between different studies.

Another explanation for the mixed findings may be the lack of task compliance: to regulate their emotional expression, participants may have paid less attention to, or even looked away from, the stimuli. The importance of controlling for task compliance is clearly illustrated by Ferri et al. (2013) who investigated the differences between attentional deployment versus not regulating emotions in response to stimuli. Participants were instructed to look at a non-arousing (as compared to arousing) portion of negative stimuli, but only in the study in which eye tracking data was collected from all participants was activity in the amygdala modulated. This suggests the need for controlling confounds associated with visual attention using, for example, eye tracking technology. No studies included in the current review controlled for this confound. It may well be the case that in the studies reporting increased or unchanged amygdala activation, the stimuli (e.g., the film clips in Goldin et al., 2008) were more effective in engaging participants' attention and preventing participants from attending away from the stimuli.

Alternatively, it could be argued that decreased amygdala activation may reflect reduced intensity of emotional experience, especially since two of the studies reporting reduced amygdala activation explicitly asked the participants to suppress not only the expression but also the experience of emotions (Katsumi and Dolcos, 2018; Katsumi et al., 2020). However, this argument runs into difficulties when taking into account participants' ratings of the stimuli (see Supplementary Materials for results). Contrary to the evidence concerning the ineffectiveness of expressive suppression in regulating emotional experience (e.g., Gross and Levenson, 1997; Kalokerinos et al., 2015; Webb et al., 2012), most studies in this review demonstrated lower ratings of negative emotional experience after participants suppressed the emotional expression evoked by the stimuli (as compared to simply watching the stimuli). Importantly, this occurred irrespective of whether amygdala activation decreased, increased, or was unchanged in the respective studies. These findings show that expressive suppression is in some contexts associated with decreased emotional experience and that we should be cautious when using amygdala activation as a proxy for the (in)effectiveness of expressive suppression.

The involvement of the insula in expressive suppression was not straightforward, with a few studies showing increased activation in anterior insula during suppression either bilaterally (Hayes et al., 2010; van der Velde et al., 2015) or unilaterally (Goldin et al., 2008), while others reported no differences in activity between suppression and simply watching stimuli (Dörfel et al., 2014; Katsumi and Dolcos, 2018; Li et al., 2021; Vanderhasselt et al., 2013a; Van der Meer et al., 2014). Moreover, two studies demonstrated reduced activation in the insula during suppression, although the involvement of the particular sub-regions differed depending on the type of stimuli used: left or right anterior insula for negative stimuli, middle insula for non-social stimuli, and posterior insula for facial stimuli (Anderson et al., 2021; Vrtička et al., 2011). Thus, it may well be that the content of stimuli, i.e., different number of stimuli with social vs non-social content used in different studies, may hold one explanation for these mixed findings. Furthermore, increased insula activation may reflect enhanced effort in monitoring and regulating one's emotional response. In line with this, Li et al. (2021) demonstrated that increased connectivity between the left insula and the left inferior frontal gyrus was associated with more successful expressive suppression.

Mixed findings regarding the amygdala and insula also may be due to the fact that expressive suppression entails a host of cognitive processes beyond the inhibition of expression itself. For example, people may be monitoring and be aware of their current emotional and bodily state, experiencing empathy for others (e.g., when the stimuli depict other individuals in adverse situations), all of which have been suggested to involve the anterior insula (Singer et al., 2009). In different studies participants may have been engaged in these processes to a different extent. Also, relatively stable individual differences, for example in trait emotion regulation or trait anxiety, as well as the differential involvement of the various sub-regions of amygdala and insula (Janak and Tye, 2015; Orem et al., 2019) may underlie conflicting results. All this calls for the need to investigate the specific circuits within these structures and to control for possible individual differences.

4.3. The involvement of other regions in expressive suppression

Activation in temporo-occipital areas related to visual processing (e.g., occipital gyri, fusiform gyrus, lingual gyrus) was generally higher when watching negative stimuli, as compared to using expressive suppression, or in other words, activity in these areas was downregulated when suppressing the expression of emotion. This could reflect an increased focus on oneself instead of the visual properties of the presented stimuli. While explicitly instructed to not look away from the picture in some studies (Vanderhasselt et al., 2013a), it is likely that during expressive suppression participants may have paid less attention to the stimuli, looked away, or even closed their eyes.

Another explanation for the lower levels of temporo-occipital activity during the use of expressive suppression, as compared to the non-regulation condition, may be a decrease in valence. In a meta-analysis by Lindquist et al. (2016) portions of temporo-occipital cortical regions, which the authors consider part of the salience network, responded to valenced stimuli, both negative and positive. Given that expressive suppression was successful in down-regulating negative emotional experience (rather than emotion expression only), reduced activity in these areas would be expected.

Reduced temporo-occipital activation could also occur due to the top-down control of the DLPFC over attentional and perceptual processes. By modulating or 'gating' perceptual input to temporo-occipital cortices, the DLPFC could influence early processing of the emotional aspects of visual stimuli, and by doing so, regulate emotion (Ligeza et al., 2016).

4.4. Methodological issues and future directions

The studies included in the current review are well aligned regarding the involvement of cognitive control regions in expressive suppression. There is less agreement, however, about whether and in what direction activity in emotion-generative regions is modulated. Here we discuss methodological issues that may underlie not only these disagreements but that also may limit the conclusions drawn based on the included studies and provide suggestions as to how to address these issues in future studies.

4.4.1. Sample composition

The samples used in the studies were heavily biased towards women, with several studies including female participants only (Chen et al., 2017; Dörfel et al., 2014; Goldin et al., 2008; Vanderhasselt et al., 2013a; Vrtička et al., 2011). Meta-analytic evidence based on functional neuroimaging studies demonstrates that women display stronger emotional reactivity to negative stimuli than men (Filkowski et al., 2017; Stevens and Hamann, 2012). Questionnaire-based studies have shown that men have a greater tendency to use habitual expressive suppression (Gross and John, 2003; Haga et al., 2009) and there is evidence that the neural basis of expressive suppression differs between men and women (Burr et al., 2019; Wang et al., 2017). Given these differences, it is unclear to what extent the findings of the studies included in this systematic review can be generalized to men.

Another issue regarding sample composition pertains to the fact that younger participants were heavily oversampled. The use of habitual expressive suppression has been shown to differ between younger and older people, although the direction of the relationship is inconsistent (Allen and Windsor, 2019). Studies in which individuals have been instructed to suppress stimulus-induced emotions are also mixed with some studies showing that older adults are worse in suppressing their facial expressions of emotion (Zsoldos et al., 2019) while others report no differences between younger and older participants (Livingstone and Isaacowitz, 2018; Shiota and Levenson, 2009; Vieillard et al., 2015). Nevertheless, as demonstrated by Katsumi et al. (2020), there are age-related differences in the engagement of the lateral PFC in expressive suppression with older adults relying less on lateral PFC, and more on medial frontal regions, than younger adults. Thus, the neural basis of expressive suppression seems to differ, at least to some extent, depending on age.

In addition to individual differences in gender and age, cultural background plays a role in expressive suppression. For example, questionnaire as well as laboratory studies have demonstrated that people with a more collectivistic cultural background (e.g., East Asian) are more likely to suppress the expression of their emotions than those with a more individualistic (e.g., European American) cultural background (Gross and John, 2003; Mauss et al., 2010). This is because suppressing one's emotional responses is considered to be in line with cultural display rules in more collectivistic cultures (Matsumoto et al., 2008). There is also evidence for cultural differences in neurophysiological responses to negative stimuli while using expressive suppression (Murata et al., 2013; Kraus and Kitayama, 2019). Given that most studies on the neural basis of expressive suppression have been conducted on people from Western cultural contexts, it remains unclear to what extent the findings can be generalized to those with a non-Western background. Moreover, although a few studies on expressive suppression have included non-Western samples (e.g., Chen et al., 2017; Li et al., 2021), or directly compared Western and non-Western samples (Anderson et al., 2021), future research is needed to delineate the precise cultural variables that influence the consequences and neural correlates of expressive suppression in different cultural contexts. For example, independent vs interdependent self-construal (Su et al., 2013) as well as other cultural dimensions (e.g., power distance, uncertainty avoidance, masculinity/femininity; Hofstede, 1980) may underlie differential effects of expressive suppression not only between Western and non-Western cultures but also among various Western cultures.

This, together with the issues addressed above, underscores the need to include more diverse samples with respect to gender, age, and cultural background.

4.4.2. Emotion induction

One important issue pertains to how emotions were induced in the studies. First, all but two studies used pictures from the IAPS to elicit an emotional response. Except for the normative valence and arousal ratings, most studies provided no, or only a few, details regarding the content of the pictures. Only four studies reported matching pictures across different conditions based on the content (Anderson et al., 2021; Hayes et al., 2010; Katsumi and Dolcos, 2018; Vrtička et al., 2011). Different effects of expressive suppression on emotions evoked by social vs nonsocial pictures (Anderson et al., 2021; Vrtička et al., 2011), demonstrates the importance to carefully consider, and equate, the (social) content of pictures.

Second, all except one study (Goldin et al., 2008) used stimuli that elicit different types of negative emotions but grouped them together in the analyses. This is problematic because different discrete emotions may differ in arousal and, in turn, may be better tailored for different emotion regulation strategies. Flexibility in using a particular emotion regulation strategy depending on the intensity of emotion may be a prerequisite for healthy emotion regulation (Sheppes et al., 2011). In fact, studies have shown that different discrete emotions are associated with the habitual use of different emotion regulation strategies. For example, expressive suppression is used more in response to sadness than to anger (Dixon-Gordon et al., 2015) but less in response to sadness than fear (Zimmermann and Iwanski, 2014). As such, suppression of different discrete emotions may also involve, at least to some extent, different neural mechanisms. Therefore, studies should investigate the similarities and differences in the neural basis of suppressing different types of emotions.

Third, emotion induction has also been limited to the use of stimuli inducing negative emotions with only two studies including positive stimuli (Li et al., 2021; Vrtička et al., 2011). Thus, more research on the neural basis of suppressing positive emotions is needed.

In general, using IAPS pictures as stimuli for emotion regulation studies has both advantages and disadvantages. Although the content of the specific pictures included in the studies may differ, there is at least some form of control for stimuli which makes the studies more easily comparable. However, this comes at the cost of external validity. In everyday life it is rarely exposure to pictures that leads us to regulate our emotions. Also, these pictures may not induce enough arousal to demand the regulation effort amenable to measurement with neuroimaging methods. Although the normative ratings of arousal of the selected pictures were towards the higher end of the scale (i.e., average ratings were around 6 on a 9-point scale), given the lack of arousal ratings in the studies reviewed, it is not clear to what extent these stimuli were experienced as arousing by the participants in these studies. By using more self-relevant stimuli (Salas et al., 2012) or employing virtual-reality technology (Parsons, 2015) we may be better able to simulate real-life situations, albeit still in a controlled manner, where emotions are generated and emotion regulation is needed and used. It is also important to ask participants to rate the extent to which they experienced arousal when exposed to the stimuli. To avoid the possible effect of such an appraisal process itself, this could be performed after the scanning procedure.

4.4.3. Experimental instructions

Another methodological issue relates to experimental instructions. Instructions for expressive suppression were generally similar across studies. Participants were asked to refrain from facial expressions or to conceal emotion behavior so that an outside observer could not tell what they are feeling. Nevertheless, in three studies participants were instructed to also suppress the experience (Katsumi and Dolcos, 2018; Katsumi et al., 2020) or physiological (Li et al., 2021) responses. Although in one study participants were asked to specifically suppress the expression of emotion, additional instructions specified that emotion should not be visible on the outside through facial expression, breathing frequency, heart rate, or skin conductance (Vrtička et al., 2011). This may have led the participants to suppress not only the expression, but also physiological reactivity, associated with the emotion. Because expressive suppression is specifically about inhibiting the expression, not the experience of, or physiological activity related to, emotions, it is unclear to what extent the findings of these three studies can be considered specific to expressive suppression as such.

Timing of the instructions is also relevant. According to the process model of emotion regulation, antecedent-focused emotion regulation strategies that are directed at modulating the emotion-generation process before the emotional response has been fully induced should be more effective than those modulating the already generated emotional response (Gross, 1998a, 2015). As such, presenting regulation instructions before showing the stimuli enables the participant to prepare the regulation strategy already before the emotional response has been generated. This may be more efficient in modulating the emotional response than when instructions to regulate are given only after the stimuli have been shown and related emotions induced (Webb et al., 2012). Since most studies presented instructions before showing the stimuli, this may have influenced the generation of an emotional response, rather than simply modulating the already generated response. Lower ratings of negative emotional experience in the suppression condition provide support for this argument. As a result, the neural activation observed in these studies may not be specific to the suppression of emotion expression as such but can also reflect the suppression of emotion generation more broadly. Relatedly, stimulus presentation times should be long enough to enable both emotion generation and the successful application of expressive suppression. In fact, as demonstrated by Goldin et al. (2008), suppression modulated cortical activity only during the late period (10.5 – 15 s) of stimulus presentation. Given that almost all studies used stimulus durations of a few seconds only (less than 10 s), it is likely that the suppression effect may not have been activated, making it difficult to detect suppression-related neural activity. This is even more problematic in studies that presented instructions after the stimulus had been displayed for some time, leaving even less time for suppression to take shape. More research is needed to study the effects of the timing of instructions as well as stimulus duration on both the behavioral and neural basis of expressive suppression.

Similarly, the instructions used for the control condition also need to be carefully considered. It is important to emphasize that participants should express the emotions as they would naturally do. Although not instructed to regulate their emotions, participants in an experiment are in a social environment (with researchers they do not know) and so permitting emotions to flow freely may be difficult. It is likely that, in such a setting, participants unintentionally suppress their emotional expression, especially if they are inside an MRI scanner. In fact, there is evidence that participants show less negative facial emotional expression in the presence of an experimenter (Lee and Wagner, 2002) and, therefore, this condition may reflect implicit expressive suppression (Zsoldos et al., 2019). None of the studies in the systematic review seem to have included such instructions.

Furthermore, instructing someone to naturally feel their emotion without trying to change anything (as done in Li et al., 2021; van der Velde et al., 2015; Vanderhasselt et al., 2013a) may lead to participants adopting a strategy of acceptance. Emotional acceptance has been shown to reduce distress (Ellard et al., 2017) and is a central element of mindfulness meditation (Teper and Inzlicht, 2013). Indeed, acceptance is even conceptualized as an explicit emotion regulation strategy (Goldin et al., 2019). Comparing (the neural correlates of) two emotion regulation strategies (expressive suppression vs acceptance, or explicit vs implicit suppression) is different from comparing emotion regulation with a non-regulation condition and may mask any differences between the latter. Therefore, a clear conceptual and operational distinction between the different types of emotion regulation is essential.

4.4.4. Adequate controls

In addition to carefully crafted instructions, adequate controls need to be implemented when carrying out the studies. First, it is important to ensure that participants actually look at and attend to the stimuli. This enables the experimenter to assess whether the emotion regulation effect occurs due to expressive suppression or some other strategy, such as attentional deployment. For this, eye-tracking technology can be used. Second, it is necessary to measure whether and to what extent participants implement the instructed emotion regulation strategy and suppress their emotional expression. In most studies, participants' decreased ratings of emotional experience were considered evidence of compliance. This is surprising, given that expressive suppression is not about the experience but about the expression of emotion. Although in some studies participants rated the success of using expressive suppression (Dörfel et al., 2014), it is likely that people do not have very good awareness of their expressive behavior. More objective measures, such as video-recordings (e.g., filming faces and coding facial expressions) or electromyography (i.e., via electrodes measuring facial muscle activity) would be beneficial.

4.4.5. Neuroimaging data acquisition, processing, and analysis

As can be seen in Table 2, there was substantial heterogeneity in fMRI data processing and analysis methodology. In general, whereas the scanning and processing parameters were adequate for whole-brain analysis, they rarely approximated those suitable for separating amygdalar signal. As a result, almost all studies that reported amygdala modulation used a spatially constrained approach, such as average ROI value or small volume correction (SVC) voxelwise analysis. On the one hand, the use of ROI- or SVC-based approaches is justified because it is difficult to detect changes in amygdala activation with commonly used fMRI study parameters. On the other hand, ROI- and SVC-based approaches have their own drawbacks that may yield unreliable results (Gentili et al., 2021). For example, studies in this review employing ROI analyses often used questionable thresholds (Eklund et al., 2016; Woo et al., 2014) and some also suffered from circular analysis, i.e., ROI was defined functionally, and data were extracted, and analyses performed, on the same non-independent data (Kriegeskorte et al., 2009). While a threshold-forming strategy based on arbitrary choice of cluster-forming threshold was considered acceptable at earlier times, when some of these studies were conducted, the most popular contemporary alternatives – the threshold-free cluster enhancement method (Smith and Nichols, 2009), which avoids the problem of arbitrary thresholding – was not employed in any of the studies.

Additionally, univariate analyses focus on the most significantly activated voxels in a particular brain area. However, it is unlikely that emotions, and relatedly, the effect of expressive suppression on these, are represented by specific nodes in the brain. Thus, future studies should consider using multivariate analysis techniques, such as multivariate pattern analysis, which are sensitive to distributed patterns of activation across cortical and subcortical regions (Kragel and LaBar, 2016). Such multivariate analyses are increasingly used in neuroimaging research to identify the neural signatures of particular processes. For example, the Picture Induced Negative Emotion Signature (PINES) developed by Chang et al. (2015) was shown to outperform ROI-based analyses approaches and functional connectivity-derived network maps. Only one study on expressive suppression has used such an approach: Anderson et al. (2021) demonstrated that the use of this emotion regulation strategy decreases the PINES responses to negative images.

In general, we need to move towards using more standardized processing, analysis, and reporting procedures. Many excellent recommendations have been put forward (Gentili et al., 2021; Müller et al., 2018; Woo et al., 2014). In the least, articles should report (a) the criteria for selecting certain thresholds and these should enable to control for false positives, (b) brain atlases used to define the names of brain structures (in addition to the names of standardized anatomical spaces, such as MNI or Talaraich), (c) not only the main peak(s) of activation, but all structures covered by each activation cluster. Ideally, the researchers could share unthresholded whole-brain statistical images in an online database (e.g., Neurovault.org; Gorgolewski et al., 2015) or, better yet, the full data (e.g., OpenfMRI.org, Poldrack et al., 2013). This would also enable to conduct quantitative meta-analytic studies according to the best-practice recommendations in the future (Müller et al., 2018).

In summary, to advance the field of emotion regulation, it is necessary to be conceptually and methodologically more precise than has been the case for most studies up to date. Maintaining a clear distinction between expressive suppression (which targets the behavior component of emotion) and other forms of suppression (e.g., those targeting emotional experience) is necessary in order to interpret the psychological and neurobiological results. With these distinctions in mind, as well as with more careful consideration of the sample composition, stimuli, instructions, controls, and neuroimaging methodology used in studies, we can move forward in the pursuit of unraveling what lies behind the 'poker face'.

5. Conclusion

We conducted a systematic review on the neural correlates of expressive suppression. The systematic search resulted in 12 functional neuroimaging studies contrasting the use of expressive suppression to simply watching emotional (mostly negative) stimuli. Results showed that expressive suppression consistently increased activation of lateral prefrontal and inferior parietal areas and decreased activation of temporo-occipital areas. The effect of expressive suppression on the activity of the insula and amygdala remains inconclusive due to inconsistent results. These discrepancies may result from conceptual and methodological issues that need to be addressed in future studies.

Data availability

No data was used for the research described in the article.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neubiorev.2022.104708.

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