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RESEARCH ARTICLE

Negative priming: a meta-analysis of fMRI studies

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Abstract A phenomenon termed negative priming is defined as an increase in reaction time and/or decrease in performance during instances in which current target stimuli are employed as distractor stimuli in the previous trial. A recent qualitative review on negative priming reported neural regions of interest underlined by activity within the right middle frontal gyrus and left middle temporal gyrus; however, these areas of interest have not been tested and supported by using coordinate-based, quantitative meta-analysis. We compiled functional magnetic resonance imaging studies that examined neural correlates of priming tasks using perceptual, conceptual and lexical primes. Effect-size signed differential mapping was used to perform a neuroimaging meta-analysis on the negative priming effect. Results from fourteen studies (245 participants; 85 foci) show concordance across studies in the right middle frontal gyrus and the left superior temporal gyrus, as suggested by the previous review; however, results also yielded concordance within the anterior cingulate cortex. Our data support the extant hypothesis and offer new insights into the neural mechanisms of the negative priming effect.

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Introduction

Ignored irrelevant stimuli may substantially impact the processing of subsequent relevant stimuli. A delay in response time when responding to target features that served as distractor features in previous encounters has been termed negative priming. This impairment of sequential priming has been suggested to reflect a phenomenon of stimulus–response (S–R) binding. When exposed to repetitions of S–R representations neural computations gradually decrease in activation (i.e., repetition suppression; see Henson et al. 2014; Henson and Rugg 2003). However, changes in S–R bindings are marked by an increase in activation within the same regions, namely the right inferior frontal cortices and left inferior temporal (Horner and Henson 2012; Dobbins et al. 2004; Henson and Rugg 2003). It has been hypothesized that changes in S–R bindings trigger these cortical regions to become re-engaged once previously learned responses are no longer appropriate. Negative priming may occur from such mechanism of S–R binding (Henson et al. 2014), affecting processes during the initial exposure of stimuli (i.e., when identifying perceptual or conceptual information of the stimulus) as well as processes during the retrieval phase (i.e., during response selection; Henson et al. 2014). Theoretical models for these processes have been suggested: the distractor inhibitory model describes this delay in response time as the result of an inhibitory mechanism, which inhibits irrelevant features during the prime phase yet continues to inhibit relevant stimuli features during the probe phase when they are encoded (Houghton

and Tipper 1994, 1998; Tipper and Cranston 1985; Tipper 2001). However, an alternative mechanism is explained by the episodic retrieval memory hypothesis, which emphasizes the retrieval phase suggesting that negative priming occurs due to conflicting semantic representations in episodic memory retrieval between the prime and probe phase (de Zubicaray et al. 2006, 2008; Neill and Valdes 1992). This latter model states that when a target feature similar or identical to the prime distractor serves as a retrieval cue to the prime episode, a delay in response time occurs from resolving the mismatch between prime and probe. In support of both models, it has been suggested that negative priming may involve more than one cognitive process irrespective of task modality in which identification or spatial localization features are manipulated (D'Angelo et al. 2016; Fox 1995; May et al. 1995).

Many functional magnetic resonance imaging (fMRI) studies have examined the brain correlates of negative priming (e.g., Frings et al. 2015; Ungar et al. 2010; Krüger et al. 2007; Egner and Hirsch 2005). A recent qualitative review suggests that key brain areas implicated in negative priming are within the right middle frontal and left middle temporal gyri (Frings et al. 2015), as in the case for S–R bindings (Horner and Henson 2012; Dobbins et al. 2004; Henson and Rugg 2003); however, this hypothesis has not yet been tested quantitatively using fMRI meta-analysis tools. For this study, we perform a quantitative meta-analysis on eligible studies that examined the negative priming effect with fMRI to create a statistical parametric map based on effect-size signed differential mapping (ES-SDM; Radua et al. 2012). The most commonly used meta-analysis method for fMRI is activation likelihood estimation (ALE) method; however, ALE requires a minimum number of 17–20 experiments for sufficient power (Eickhoff et al. 2017). ES-SDM meta-analysis tools adopt features of ALE, yet incorporates peak coordinates across multiple studies to increase statistical power. Furthermore, concordant clusters from the meta-analysis map can be further tested for replicability using jackknife sensitivity analysis. We expected to reveal replicable activation and provide stereotaxic coordinates associated with negative priming within the right middle frontal and left middle temporal gyri.

Materials and methods

The literature was searched by entering keywords: (1) negative priming and fMRI; (2) "previous trial" and fMRI; and (3) "preceding trial" and fMRI into web of knowledge database (http://www.webofknowledge.com), a commonly used search database to compile relevant studies and which collapses multiple searches into a single search to omit duplicate articles. This search includes articles up to March 1,

2017. These separate searches yielded a total of 129 articles, which were subjected to a series of criteria to identify articles that investigated negative priming using fMRI and were suitable for the analysis. We excluded: (1) studies that did not report fMRI contrasts; (2) contrasts that did not report foci in standard stereotactic coordinate space (either Talairach or Montreal Neurological Institute, MNI); (3) articles that did not use whole-brain analysis or contrasts purely based on region of interest (ROI) analysis; (4) contrasts generated using fixed effects analyses; and (5) contrasts isolated from unhealthy adults. Fourteen articles survived the exclusion criteria, which reported within group whole-brain results from healthy participants in MNI or Talairach space. See Fig. 1 for PRISMA flowchart of article selection.

An indication of negative priming effect is an increase in response time between prime and probe trials with dissimilar/opposite features. All articles were selected based on this difference in response time, with the exception of two articles that directly investigated the negative priming effect using the same task contrast; Egner and Hirsch (2005) reported no difference between reaction times of negative priming and Stroop interference conditions despite showing correlations between individual reaction time scores and dorsolateral prefrontal cortex activation; and Steel et al. (2001) reported a difference in prime and probe phase, reflecting negative priming, but did not explicitly report response time.

Foci within each article included a single contrast that was subtracted by a corresponding control condition. Whole-brain foci from each study were extracted using the same threshold to fulfill the ES-SDM effect-size assumption (Radua et al. 2012). A total of 85 foci from 14 articles were included in the meta-analysis. Three articles utilized a modified Stroop task and subtracted brain activity related to instances of Stroop interference from instances of negative priming (Ungar et al. 2010; Egner and Hirsch 2005; Steel et al. 2001). Three articles used a visuospatial negative priming task, in which the location of a specific target served as the distractor target on the previous trial (Krüger et al. 2007; Manoach et al. 2007; Wright et al. 2006). Five articles used lexical stimuli, of which words (e.g., tool, panda, window) served as both prime and probe (Wallentin et al. 2014; Sass et al. 2012; Eugène et al. 2010; Nee and Jonides 2008; Leung et al. 2008). Two articles used the original Tipper's identity negative priming task (Tipper 1985), which superimposes pictures representing related or unrelated categories (de Zubicaray et al. 2006, 2008). Contrasts for these articles included semantically ignored cases (e.g., ignored stimuli and target objects were categorically related) and a control involving unrelated superimposed objects. In another article, primed cue stimuli on the current trial differed in color from the probe trial on the previous trial (Pessoa et al. 2009). It is important to note that although few of these articles did not

Fig. 1 PRISMA flowchart. Chart visually displays initial search, exclusion criteria and resulting articles used in ES-SDM meta-analysis
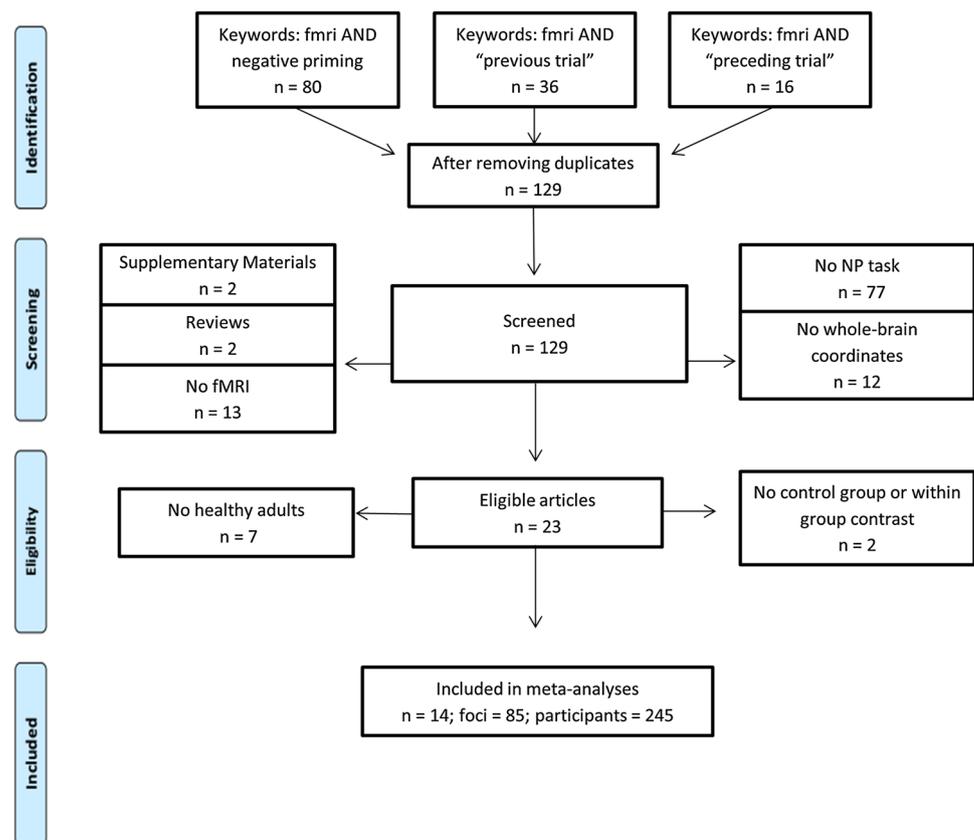
explicitly state that they were directly investigating negative priming, they were included in the meta-analysis because the data showed an increase in response time between the irrelevant prime phase and the relevant probe phase that had dissimilar stimuli features (Wallentin et al. 2014; Sass et al. 2012; Pessoa et al. 2009; Manoach et al. 2007). None of the articles reported deactivations; hence, all foci represented increases in activation.

Software and analysis

An ES-SDM meta-analysis was performed using the software from the Seed-based d Mapping project (http://www.sdmproject.com). Based on activation likelihood estimation, this analysis combines statistical parametric t-maps and peak coordinates of clusters from multiple studies to increase statistical power (see Radua et al. 2012 for more details). Effect-size brain maps and variances are derived from reported t-statistics (or converted from F, p values or z-scores). The full width at half maximum (FWHM) in SDM was set at the default (20 mm) to control for false positives (see Radua et al. 2012). Resulting statistical maps were thresholded at $p = 0.005$. Replicability of each area was assessed by performing a jackknife sensitivity analysis also thresholded at $p = 0.005$. This analysis repeats the meta-analysis as many times as the number of studies that

have been included (i.e., 14 times), removing each study per analysis. The rationale of this test is that if an area remains significant in all or most of the combinations of studies, it is considered highly replicable (Radua and Mataix-Cols 2009). ALE values were overlaid onto the "colin brain" anatomical template normalized to Talairach space using Mango image viewer software (http://rii.uthscsa.edu/mango/mango.html).

Results

Eighty-five coordinates from fourteen articles, which passed our criteria, were included in the analysis. Table 1 summarizes participant demographics, negative priming task, magnitude of negative priming effect (response time difference in ms), and contrast selection. A total of 245 participants (56.08% male) with a mean age of 28.25 years took part in these studies. All but one article (Steel et al. 2001) explicitly reported recruiting only right-handed volunteers.

The analysis revealed four clusters that were significantly concordant across studies (Fig. 2; Table 2). Beginning with the largest cluster, the meta-analysis revealed clusters centered within the right middle frontal gyrus [Brodmann area (BA) 6/8], left superior temporal gyrus (BA 38/48), anterior cingulate gyrus (BA 24), and left precuneus (BA 5). Jackknife sensitivity analysis revealed 100% replicability within

Table 1 List of articles included in analysis with task-specific contrasts isolating the negative priming effect

Article	N	Age (SD, range)[a]	Foci	Task	Delay in RT[b]	Contrast
Egner and Hirsch (2005)	17	23.5 (17–33)	2	Stroop task	n.s.	Negative priming > Stroop interference
Eugène et al. (2010)	12	(18–60)	1	Lexical priming	22.4	Ignored repetition > new words
Krüger et al. (2007)	12	26.4, (20–33)	4	Visuospatial priming task	~5	Ignored repetition > control
Leung et al. (2008)	8	24.4 (1.9, 22–28)	2	Lexical priming task	23.4	Neutral incongruent > control
Manoach et al. (2007)	21	34.2	3	Anti-saccade task	10	Anti-saccade/pro-saccade > pro-saccade/ pro-saccade
Nee and Jonides (2008)	16	(19–26)	6	Lexical priming	23.07	Interference-ignore probes > control-ignore probes
Pessoa et al. (2009)	20	32 (5)	10	Priming task	13	Switch > non-switch (color-cue)
Sass et al. (2012)	16	24.88 (2.06)	7	Lexical priming task	26	Unrelated > related
Steel et al. (2001)	7	(22–30)	14	Stroop task	n/r	Negative priming > Stroop interference
Ungar et al. (2010)	15	43 (6)	1	Stroop task	30.62	Negative priming > Stroop interference
Wallentin et al. (2014)	58	22 (19–38)	20	One back lexical task	~160	Conceptual shift > conceptual non-shift
Wright et al. (2006)	15	25.9 (6.9, 18–45)	10	Visuospatial Priming	26	Ignored repetition > new location
de Zubicaray et al. (2006)	13	25.4 (6.2)	3	Negative priming task	31	Semantic ignored > new items
de Zubicaray et al. (2008)	15	24 (5.2)	2	Negative priming task	28.9	Semantic ignored > new items

Contrasts were extracted from articles investigating negative priming from various tasks

n.s. not significant, *n/r* not reported

[a] Age is reported in mean and standard deviation (SD) or range when available

[b] Response time reported in milliseconds
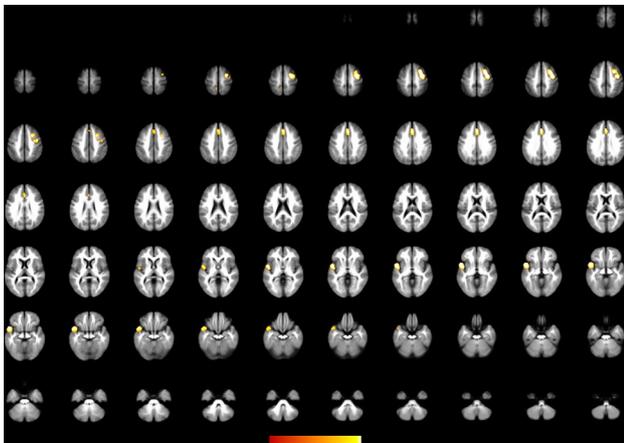
Fig. 2 Rendered ES-SDM activation maps showing neural correlates of negative priming. ES-SDM meta-analysis demonstrating regions with highest likelihood of activation for negative priming

the right middle frontal gyrus, left superior temporal gyrus, and anterior cingulate gyrus, yet only 64.2% of the analyses yielded left precuneus activation.

Discussion

We examined the neural correlates of negative priming phenomena by using ES-SDM meta-analysis which takes into account peak coordinates of statistical parametric maps derived from fMRI studies (Radua et al. 2012). Based on a recent review on negative priming (Frings et al. 2015), we hypothesized that negative priming involves activation of the right middle frontal gyrus and left middle temporal gyrus. We confirmed this hypothesis in part, by demonstrating replicable right middle frontal and left superior temporal cortical activation; however, our analysis also revealed a similarly replicable cluster within the anterior cingulate gyrus.

The largest cluster observed in the right middle frontal gyrus is centered on the frontal eye fields (BA 8) and extends into BA 6. Activity within these areas is implicated in regulation of perceptual conflict (Kim et al. 2012; also see Badre 2008), response preparation (Schulz et al. 2011), and motor planning during spatial mental operations (Hanakawa et al. 2002). In a review article, BA 6 was suggested to coordinate temporal sequences associated between external stimuli and internally generated actions (Krieghoff et al. 2011; see also Lee and Quessy 2003). According to these inferences, this cluster may be related to readjusting internally generated controlled actions when faced with disparate externally driven stimuli.

In addition to its implication in processing competing features, the right middle frontal gyrus has also been implicated in response inhibition, which assesses conflict associated with potential responses (Dambacher et al. 2014a; McNab et al. 2008; Zheng et al. 2008; Chevrier et al. 2007; Aron and Poldrack 2006; Garavan et al. 2002).

Table 2 Significant regions of negative priming (thresholded at $p < 0.005$; FWHM 20 mm)

Region	BA[a]	x	y	z	SDM-Z	p	Voxels[b]	Jackknife
R middle frontal gyrus	8 (6)	28	5	54	2.606	2.086e−6	1029	100
L superior temporal gyrus	38 (48)	−52	6	−6	2.232	1.336e−4	969	100
R. anterior cingulate gyrus	24	2	28	34	2.145	2.719e−4	515	100
L precuneus	5	−6	−44	60	1.800	2.647e−3	22	64.2

Jackknife replicability is represented as percentage

BA Brodmann area, *SDM-Z* signed differential mapping z-score, *L* left, *R* right

[a]Peak coordinates with overlapping BA areas (in brackets)

[b]2 mm × 2 mm × 2 mm

Further evidence derives from electrical stimulation studies that demonstrate an impairment to stop an initiated response when disrupting the right prefrontal cortex (Dambacher et al. 2014b; Chambers et al. 2006).

Given the evidence that the right inferior frontal gyrus coordinates temporal sequences of actions, one may speculate that this frontal area reflects maintaining the task goal to inhibit relevant stimuli features during the probe phase, supporting the distractor inhibitory model; however, the role of the right inferior frontal gyrus may also serve as evidence for the episodic memory retrieval model since the right middle frontal gyrus is also implicated in response inhibition, which requires the retrieval of previous responses. Therefore, from the current meta-analysis we cannot deduce whether the right middle frontal gyrus is specifically relevant for readjusting internally generated controlled actions and/or inhibition of responses during negative primed trials. This remains to be determined in targeted empirical investigations.

We also observe concordant activity in the left superior temporal gyrus. The left temporal cortex together with the prefrontal cortex has been inferred to underlie inhibitory control (Wright et al. 2006). For example, Wright et al. (2006) administered a visuospatial priming task and found activation within prefrontal and temporal areas bilaterally, proposed to reflect a neural mechanism of inhibitory control. By using the classic identity negative priming task (Tipper 1985), which utilizes superimposed categorically related target and to-be-ignored stimuli, others have reported and interpreted activity of the anterior temporal cortex as the representation of abstract semantic knowledge (de Zubicaray et al. 2006), a prominent function of the temporal cortex (McClelland and Rogers 2003). Therefore, activity of the temporal cortex may indicate support for either inhibitory or memory retrieval accounts of negative priming, analogously to frontal activity. However, it is important to note that inhibitory control may not necessarily reflect the same cognitive process as residual inhibition from previous trials. Thus, additional experimentation is required before determining the mechanistic role of the temporal cortex in negative priming.

An alternative hypothesis suggests that negative priming may be a phenomenon of S–R binding (Henson et al. 2014). The results of our study support evidence for this claim since retrieval of previously encoded S–R bindings with disparate stimuli responses has been shown to increase activation within the left inferior temporal gyrus and the right inferior frontal gyrus (Horner and Henson 2012; Dobbins et al. 2004; Henson and Rugg 2003). Some have even suggested specific roles for these regions with respect to S–R binding. For example, changes in activity within the temporal cortex are thought to reflect facilitation/interference of perceptual processes (see Henson 2012; Henson et al. 2002; Henson 2003; Blaxton 1999), whereas changes in frontal activity may reflect facilitation/interference of conceptual components (Henson 2012; Wagner et al. 1997, 2000). However, due to the small sample size, it is not possible to compare and deduce the functional roles of these regions in terms of the perceptual and conceptual components of S–R binding. Therefore, further neuroimaging studies are required to test whether these areas account for specific models of negative priming or reflect perceptual and conceptual changes in S–R bindings.

In addition to the our expectations, the analysis revealed high replicability within the anterior cingulate cortex, an area associated with set-shifting (Bissonette et al. 2013) and activity prior to responses when conflicting stimuli features are presented (Kim et al. 2012; Carter and Van Veen 2007; Botvinick et al. 2004; van Veen and Carter 2002; Botvinick et al. 1999; Carter et al. 1998). Specifically, the anterior cingulate cortex is associated with detection of conflicting features, proposed to be part of a conflict monitoring system that may account for the increase in response time for trials primed with opposing stimuli features (e.g., Etkin et al. 2006; Egner and Hirsch 2005; Wright et al. 2005). Critically, activation of the anterior cingulate cortex activation may have resulted from the contrast itself rather than the negative priming phenomenon since ignored repetition condition minus typical control condition would also yield some degree of conflict. Some research articles on negative priming have controlled for this by using the Stroop task subtracting

negative priming trials from Stroop interference trials (Ungar et al. 2010; Egner and Hirsch 2005; Steel et al. 2001), resulting in no suprathreshold activation in the anterior cingulate cortex. This suggests that anterior cingulate involvement needed in Stroop interference trials is similar to that required by the negative priming trials; perhaps indicating common processes. The majority of the studies included in the analysis used a more basic control task; thus, the question of whether conflict arises from sequential prime to probe stimuli reconfigurations or simply due to the contrast between ignored repetition versus control conditions cannot be addressed in the current study. As an example, Egner and Hirsch (2005) investigated whether prefrontal or anterior cingulate cortices could underlie processing of conflict related to negative priming. Despite revealing no difference in reaction time between negative priming and no priming trials (i.e., Stroop interference), the anterior cingulate cortex activated during incongruent trials while prefrontal cortex activation and individual performance of negative primed trials were positively correlated. Therefore, there is evidence to suggest that anterior cingulate cortex activity may arise from contrasting averaged incongruent versus control events, rather than from subsequent negatively primed trials.

Nevertheless, some have interpreted activation of the anterior cingulate cortex to support memory retrieval accounts of negative priming by monitoring conflicting encounters encoded in episodic memory (Nee and Jonides 2008; MacLeod et al. 2003). Notably, patients suffering from schizophrenia have hyperactivated anterior cingulate cortices during memory encoding and retrieval tasks (Ragland et al. 2009; Koch et al. 2008; Achim and Lepage 2005) and are unable to encode or retrieve primed stimuli from previous encounters (Holt et al. 2011; Bonner-Jackson et al. 2005). Therefore, dysfunction of the anterior cingulate cortex may explain the reduced negative priming effects in patients with schizophrenia (Frings et al. 2015; Ungar et al. 2010; Minas and Park 2007; Zimmermann et al. 2006). Moreover, reverse negative priming effects (i.e., facilitation instead of an impedance in performance when presented with negative primed stimuli) have been shown in patients with damage to the medial prefrontal cortex (Metzler and Parkin 2000), an area adjacent to the anterior cingulate cortex. This may suggest that damage to the anterior cingulate cortex may result to disinhibition of negatively primed stimuli, thereby facilitating negative primed trials. Therefore, the role of the anterior cingulate cortex deserves some focus to whether it has a crucial role in negative priming in terms of the conflict arising between trials, or whether this area increases in activation as a result of contrasting incongruent with congruent events.

Limitations

Despite the number of studies examining negative priming, only 14 studies survived our criteria. This sample size may be due to the fact that most studies do not report whole-brain contrasts related to negative priming (see Fig. 1). To compensate for the lower sample size, we performed our meta-analysis using ES-SDM because it offers an improved approach by comparing the standardized volume differences between conditions (as opposed to the raw differences), which accounts for small sample size bias (Radua and Mataix-Cols 2012). In addition, we applied jackknife sensitivity analysis to test the replicability of our findings. In terms of our methodology for article selection, some studies we included in the analysis did not specifically state that they investigated negative priming, and moreover, task modality varied across studies. Notably, all selected studies included in the meta-analysis reported a statistically significant increase in response time when comparing primed with non-primed stimuli, a key characteristic of a negative priming effect. The convergence of our quantitative meta-analysis results is consistent with the recent qualitative review (Frings et al. 2015), supporting the hypothesis that the proposed brain regions play a critical role in the negative priming phenomenon. Finally, although the meta-analysis technique is a useful tool for validating areas of interest involved in negative priming, we could not address particular questions relating to different task modalities or models of negative priming. Nevertheless, this quantitative approach confirms the relevance of these regions and can therefore be used for future neuroimaging studies investigating negative priming.

Conclusion

The current meta-analysis supports the hypothesis that the brain areas associated with negative priming across modalities are comprised of the right middle frontal and left superior temporal cortices. To account for the functional role of these areas, various studies have adopted models of negative priming, while others attribute these areas to index facilitation and interference of S–R bindings. In addition, the anterior cingulate cortex, an area not hypothesized to be consistent across negative priming studies, was highly replicable. Activation of the anterior cingulate cortex may serve as a conflict detection system that responds to disparate stimuli features and/or potential responses between subsequent trials or may be the result of contrasting incongruent with congruent trials. In a practical sense, our data may serve as targeted regions on interest for future fMRI studies with and without clinical populations that show reduced or reverse negative priming. In a theoretical sense, current models of

negative priming can benefit from understanding the association between behavioral and neural correlates in stereotaxic space.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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