

Research report

The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict

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Abstract

While numerous studies have implicated both anterior cingulate and prefrontal cortex in attentional control, the nature of their involvement remains a source of debate. Here we determine the extent to which their relative involvement in attentional control depends upon the levels of processing at which the conflict occurs (e.g., response, non-response). Using a combination of blocked and rapid presentation event-related functional magnetic resonance imaging techniques, we compared neural activity during incongruent Stroop trial types that produce conflict at different levels of processing. Our data suggest that the involvement of anterior cingulate and right prefrontal cortex in attentional control is primarily limited to situations of response conflict, while the involvement of left prefrontal cortex extends to the occurrence of conflict at non-response levels. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Although generally agreed that anterior regions of the attentional network are responsible for top-down control of activity within the network, the exact regions exerting such control remain a source of debate. While several models assume attentional control is supported by a single structure such as the anterior cingulate cortex (ACC) or dorsolateral prefrontal cortex (PFC) [17,22,25,20], recent studies have suggested the involvement of both regions [10], possibly possessing complementary roles [1,2,14]. The emerging perspective from these latter studies is that the ACC may be involved in evaluatory processes, monitoring for the occurrence of conflict within the attentional network [14,7,3]. In contrast, the dorsolateral (BA 9 and

BA 46) and posterior inferior PFC (BA 44) may be involved in maintaining an attentional set by modulating activity within posterior processing systems and facilitating selection of task relevant representations within working memory [1] (for a similar perspective see Ref. [14]).

Here we consider the extent to which the relative involvement of the ACC and PFC (dorsolateral and posterior inferior) depends upon the level(s) of processing at which the need for attentional control arises. While most studies of attentional control examine the involvement of the ACC and PFC by manipulating whether or not conflict can occur during task performance, we took the approach of varying the stages of processing at which conflict can occur. This was accomplished using the Stroop task, a paradigm in which competition has been shown to occur at multiple levels of performance (i.e., both response and non-response levels) [15].

In the Stroop task, participants identify the ink color in which a word is printed while ignoring its identity. Although seemingly uncomplicated, the word itself is a potentially strong source of interference to color identification. Engagement of the systems dedicated to processing words (e.g., orthography to phonology, orthography to

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semantics) is relatively automatic, requiring little or no attention [15]. Thus representations (e.g., semantic or phonological) arising from the word processing systems can compete for processing resources. Such competition is especially heightened when the word names a color. In this case, each processing system (i.e., word system, color system) can lead to the activation of not only the semantic and phonological representations associated with a particular color, but also associated responses. Inadvertent contributions from the word processing system are evident, as words incongruent with the ink color degrade performance whereas those congruent facilitate performance compared to neutral trials. Attentional selection is required to ensure that performance is based upon the task-relevant processing of the ink's color rather than the task-irrelevant color associated with the word's identity, a function typically attributed to both the PFC (dorsolateral and posterior inferior) and ACC [2,11,5,19].

We reasoned that if the ACC's involvement in attentional control is mainly limited to situations in which competition is present at the response level, then its activity during the attentionally demanding incongruent condition should be disproportionately influenced by whether or not response competition can occur. To test this idea, we varied whether an incongruent trial could produce interference at both the response and non-response levels, or just the non-response levels. More specifically, we manipulated whether the incongruent color word named a color in the response set (an eligible response) or a color outside of the response set (an ineligible response). Incongruent response-eligible words can be potentially strong sources of interference, due to their ability to introduce competing phonological and semantic representations related to color, as well as competing representations of the response output. In contrast, incongruent-ineligible words can only produce interference at the level of semantics and phonology, since the word does not name a potential response. To examine the degree of interference engendered by both incongruent ineligible and incongruent eligible trials, we compared activation to that which occurs during neutral trials, in which the word contains no color information or associated responses (e.g., LOT).

It is important to note that the inclusion of neutral trials allowed us to determine the extent to which a region's involvement in attentional control is dependent upon the presence of conflict at the response level. Relative to neutral trials, incongruent-eligible trials can produce conflict at both response and non-response levels. In contrast, incongruent-ineligible trials only differ from neutral trials in their ability to generate conflict at non-response levels, as neither incongruent-ineligible words nor neutral words are associated with an eligible response. Therefore, if activity within a brain region increases for incongruent trials that name an eligible response relative to neutral trials but not for incongruent trials that name an ineligible response, then that region's involvement in attentional control is primarily limited to the presence of conflict at

the response level. On the other hand, if a region shows increased activity for both types of incongruent trials, even when the color word does not name a possible response, then its involvement in attentional control is clearly not limited to situations of conflict at the level of response.

Given that the ACC's involvement in attentional control appears to be dependent upon the presence of response competition [1,18,25], we expected to find little to no activity during incongruent-ineligible trials when compared to neutral trials, but increased activity on incongruent-eligible trials. In contrast, dorsolateral and posterior inferior prefrontal cortices, which have been shown to be involved in attentional control when conflict arises at non-response levels trials [1,14], should be activated for both incongruent trial types when compared to neutral.

2. Methods

2.1. Participants

Sixteen right-handed, native English speakers from the university community participated in our experiment (ages: 18 to 30 years). All were without a history of neurological insult.

2.2. Stimuli and experimental design

Our Stroop task was programmed using Mel V2.0 and presented using an IBM-PC compatible computer. The ink colors used were blue, green and yellow. The words used for incongruent-eligible trials were 'BLUE', 'GREEN' and 'YELLOW' while those for incongruent-ineligible trials were 'RED', 'ORANGE' and 'BROWN'. Our neutral word sets consisted of words unrelated to color that were matched with the incongruent words for frequency and length (e.g., 'LOT').

Each participant was involved in a single functional magnetic resonance imaging (fMRI) run, consisting of two incongruent-ineligible blocks alternated with two incongruent-eligible blocks. All blocks contained 48 trials, half of which were neutral trials and half of which were incongruent (see Refs. [2] and [6], for a discussion of the benefits of this approach). The blocks were separated from one another by 10 s. Each block type (incongruent-eligible, incongruent-ineligible) contained a unique set of neutral words matched to each unique set of incongruent words (ineligible in one block, eligible in the other).

Within each block, trials occurred at a rate of one every 2 s. A trial began with the presentation of a fixation cross for 300 ms, followed by the word for 1200 ms, and then a 500 ms blank screen.

2.3. fMRI testing and imaging methods

A GE Signa (1.5 T) MRI system equipped for echo-planar imaging (EPI) was used for data acquisition. For

each run, a total of 224 EPI images using the BOLD technique was acquired (Time of recognition (TR)=2000 ms, Echo time (TE)=40 ms, flip angle=90°), each consisting of 10 contiguous slices (thickness=8 mm, in-plane resolution=3.75 mm), parallel to the AC-PC line. A high-resolution three-dimensional (3D) anatomical set (T1-weighted 3D spoiled gradient echo images) was collected for each participant for the purpose of landmark selection. T1-weighted images of our functional acquisition slices were collected as well. The head coil was fitted with a bite bar to minimize head motion. Stimuli were presented on a goggle system designed by Magnetic Resonance Technologies, and participants were instructed to identify the ink color of each word as quickly and as accurately as possible via a three-button response pad. Prior to data analysis, images were motion corrected using AIR V3.0.

2.4. Experimental design: hybrid blocked/rapid sequence event-related design

Our experimental approach integrated recently developed event-related fMRI techniques [9,4] with a blocked fMRI approach. The blocked comparison compared levels of neural activity during blocks of incongruent-eligible trials with that observed during blocks of incongruent-ineligible trials. We used rapid presentation event-related analysis techniques to extract the differences between incongruent and neutral trials within each block type (eligible, ineligible). Prior work has shown these methods to be feasible for an inter-trial interval of 2 s [9,4].

2.5. Image processing for blocked analysis

Images in the data series were intensity normalized, convolved with a 3D Gaussian kernel (FWHM=8 mm×8 mm×8 mm, kernel width=7×7 voxels), temporally denoised using an ID-wavelet transform (visu-shrink, number of levels=4) and linearly detrended.

2.6. Image processing for event-related analyses

Images in the data series were intensity normalized and linearly detrended. Next, the mean intensity for the time series at each voxel was calculated and subtracted out. Selective averaging [9] was carried out within each set of half cycles. Thus, for the 'A' block, we calculated an average hemodynamic response separately for neutral and incongruent (ineligible) trials. Then, for the 'B' block, we calculated an average hemodynamic response separately for both the neutral and incongruent (eligible) trials. The images in each time series were transformed in Talairach space and convolved with a 3D Gaussian kernel (FWHM=8 mm×8 mm×8 mm, kernel width=7×7 voxels).

2.7. Exploratory analysis: incongruent vs. neutral

The goal of this exploratory event-related analysis was to identify brain areas sensitive to the presence of competition regardless of the level of processing. More specifically, we compared the hemodynamic responses for incongruent trials (averaged over eligible and ineligible) with neutral trials. The two hemodynamic responses (neutral, incongruent) for each participant were entered into a voxel-wise repeated-measures analysis of variance (ANOVA) carried out across subjects (factors: condition, time point). The condition×time point interaction was used to generate activation maps ($P<0.0025$, uncorrected; criteria for peaks: $P<0.001$).

2.8. Exploratory analysis: incongruent-eligible vs. incongruent-ineligible

This exploratory blocked analysis identified brain areas sensitive to the presence of competition specifically at the response level. For each participant, the Kolmogorov–Smirnov statistical test was used to generate statistical maps for the comparison of incongruent-eligible vs. incongruent-ineligible blocks. Statistical maps were then converted to Z-score maps and transformed into a common stereotaxic space [23]. A map was generated in which each voxel's score indicated the percent of subjects for which the Z-score exceeded 2.32 ($P<0.01$). Voxels showing activity in a majority of participants (9/16 or better) were then selected for generation of activation maps (according to the binomial distribution, for an $n=16$, the voxel-wise probability for falsely meeting this criteria is $\sim 1 \times 10^{-14}$). MedX V3.0 was used for image processing and statistical analyses.

2.9. Secondary analysis of regions identified in exploratory analyses

We first defined our regions of interest as a set of spherical volumes in Talairach space (radius=2 voxels or 4 mm), each centered around a peak [16] obtained from our exploratory analyses. For each region, we tested for the presence of event-related responses for each type of incongruent trial (ineligible, eligible) when compared to neutral trials by entering the average difference waveforms into a correlation analysis. The correlation analysis made use of idealized hemodynamic response described by Ref. [4] and a lag parameter.

3. fMRI results

3.1. Incongruent vs. neutral

As in prior studies of the Stroop task [2,5,11,19], the comparison of incongruent vs. neutral trials (regardless of

eligibility) revealed the presence of a distributed network of structures supporting attentional control, including bilateral ACC/preSMA, bilateral middle frontal gyrus, left inferior frontal gyrus, and left superior and inferior parietal lobules (see Table 1 and Fig. 1).

Further analysis of neural activity within these regions found differences in their relative involvement during the two incongruent trial types. To identify those regions specifically related to response selection, we determined which regions exhibited significantly greater activity on response-eligible than neutral trials, but exhibited no significant difference in activity between response-ineligible and neutral trials. The areas so identified were the anterior cingulate/preSMA, the right middle frontal gyrus, and the left superior parietal lobe. To delineate regions whose activity was linked to non-response levels, we identified regions that yielded significant increases in activity relative to neutral trials for both incongruent trial types. Regions so identified were the left middle frontal gyrus, left precuneus and left superior parietal lobule. As shown in Table 1, many of these regions exhibit greater activation response to incongruent-eligible than incongruent-ineligible trials relative to neutral trials. Although one might suggest that this pattern indicates involvement of these brain regions in response selection as well, it is important to note that this pattern could be generated solely by differences in attentional demands at the non-response level(s). For example, interference generated by semantic priming is greater for response-eligible than response-ineligible words (see Refs. [21] and [15], for a longer discussion of this issue). Regardless, the distinction between activation for response-eligible and response-ineligible trials for these areas is not as clear-cut with regards to sensitivity to response conflict as that observed for the anterior cingulate, right middle frontal gyrus, and left superior parietal lobule.

3.2. Incongruent-eligible vs. incongruent-ineligible

When compared to the incongruent-ineligible blocks, the incongruent-eligible blocks produced consistent increases in activity throughout most of the attentional network. Structures identified in this analysis included the right ACC (dorsal)/preSMA, bilateral middle frontal gyrus, right inferior frontal gyrus, right superior frontal gyrus, left superior parietal lobule and left precuneus cortex (see Table 2).

Further analysis of neural activity within this network confirmed differences in the nature of involvement of the different brain regions in attentional control. For ACC (BA 32/6), the right inferior frontal gyrus (BA 44), right superior frontal gyrus (BA 8/9), right superior parietal lobule (BA 7) and the right middle frontal gyrus (BA 9), significant responses relative to neutral trials were only detectable during incongruent-eligible trials, indicating their involvement in task performance is primarily limited to the response level. Overall, these findings are consistent with those of the first exploratory analysis. In contrast, when compared with neutral trials, significant increases in activity were noted for both incongruent trial types (eligible, ineligible) within the left middle frontal gyrus (BA 9/6), left precuneus cortex (BA 7) and left superior parietal lobule (BA 7), though differing in magnitude (incongruent-eligible > incongruent-ineligible). This pattern suggests involvement in selection at the non-response level.

In order to verify that our findings concerning ACC and LMFG are not dependent on assumptions concerning the hemodynamic response, we used repeated-measures ANOVA to test for differences between each of the incongruent trial types (eligible, ineligible) and neutral trials as a function of time. The results were consistent with those of the correlation analysis [eligible vs. neutral:

Table 1
Talairach coordinates and results of event-related analysis for regions identified in exploratory comparison of incongruent > neutral

Significant activations							
Location	BA	X	Y	Z	Inc. vs. neutral -log (Prob)	Eligible vs. neutral -log (Prob)	Ineligible vs. neutral -log (Prob)
<i>Areas exhibiting response-related activity</i>							
R. middle frontal gyrus	9	40	8	42	3.29	2.108	n.s.
Anterior cingulate cortex/pre-SMA	32/6	0	10	44	4.43	3.155	n.s.
L. superior parietal lobule	7	-24	-68	40	5.41	2.959	n.s.
<i>Areas exhibiting non-response-related activity</i>							
L. middle frontal gyrus	9/6	-42	2	36	6.70	2.770	2.061
L. inferior frontal gyrus*	44/45	-34	20	24	5.37	1.553	1.627
L. inferior parietal lobule*	7	-34	-52	44	4.13	2.155	1.721
L. inferior parietal lobule*	39/40	-42	-46	46	3.81	2.921	1.239

Note: $-\log(0.050)=1.301$, $-\log(0.005)=2.301$, $-\log(0.001)=3.000$. *Regions revealed by comparison of incongruent vs. neutral, but not incongruent-eligible vs. incongruent-ineligible.

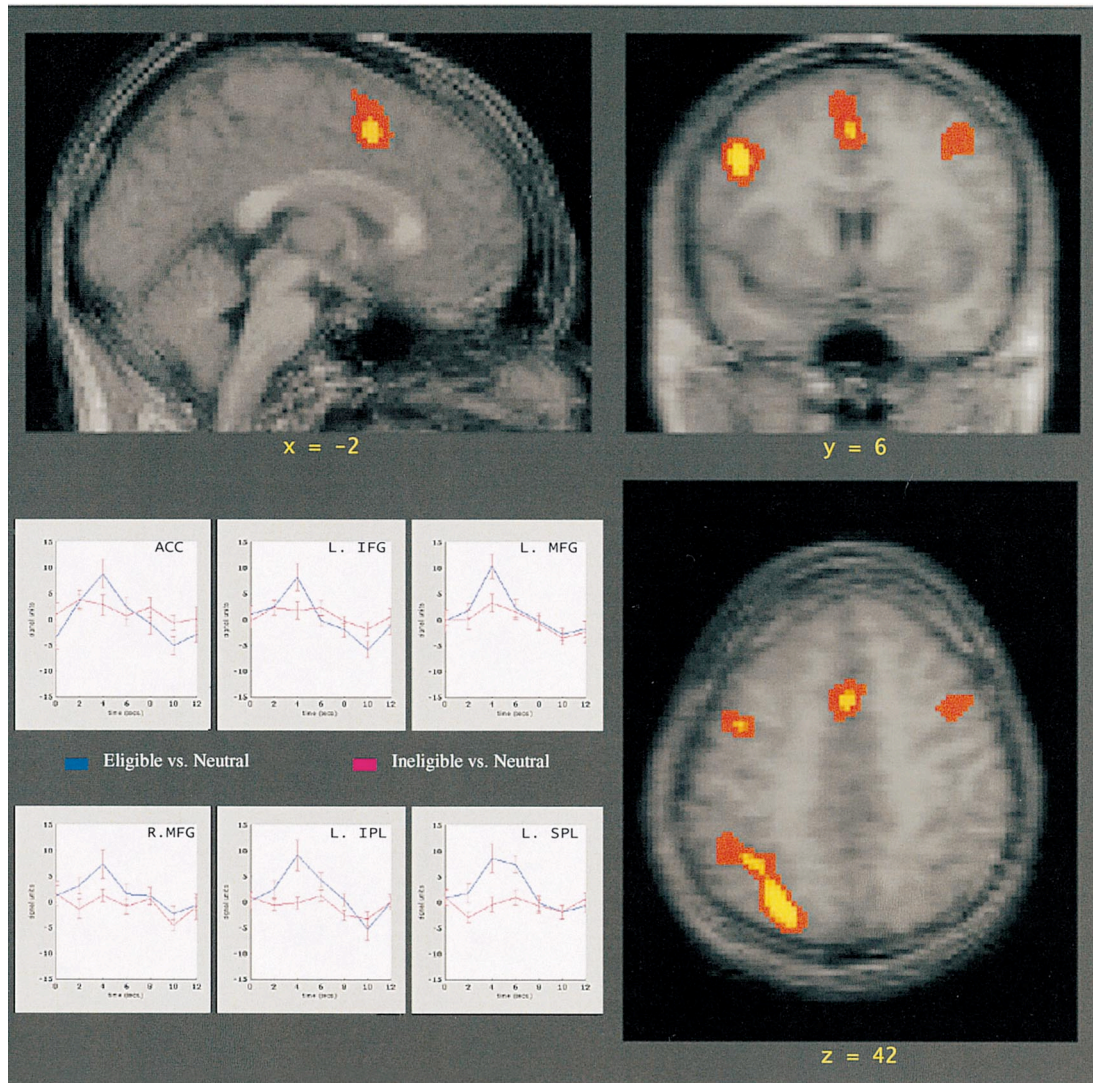
INCONGRUENT > NEUTRAL

Fig. 1. Incongruent vs. neutral. Incongruent trials produced increases in activity throughout the attentional network, including regions of anterior cingulate, prefrontal and parietal cortex. While increases in activity within anterior cingulate cortex were limited to incongruent-eligible trials, significant responses were detected within regions of left prefrontal cortex for both incongruent trial types.

LMFG: $F(6, 90)=6.622$, $P<2.7\times 10^{-6}$; ACC: $F(6, 90)=5.224$, $P<1.1\times 10^{-4}$; ineligible vs. neutral: LMFG: $F(6, 90)=2.432$, $P<0.032$; ACC: $F(6, 90)=0.643$, $P<0.432$].

4. Behavioral results

A repeated-measures ANOVA with the factors of BLOCK (response-eligible, response-ineligible) and TRIAL TYPE (incongruent, neutral) yielded a main effect of TRIAL TYPE [$F(1, 15)=14.65$], as responses were slower to incongruent than neutral trials, and a main effect of BLOCK [$F(1,15)=9.98$, $P<0.006$] with slower responses to response-eligible than response-ineligible

blocks. However, the interaction between block and trial type was not significant, indicating no greater interference for the response-eligible than response-ineligible block (mean RT for eligible blocks: neutral=658 ms and incongruent=701 ms; mean RT for ineligible blocks: neutral=620 ms and incongruent=657 ms). The lack of an interaction appears to occur because responses to neutral trials in the eligible block were slowed relative to the ineligible block, a finding that is not unique to our study [6]. This pattern suggests some general strategic slowing or inhibition of responding across all trials in the incongruent-eligible block relative to the incongruent-ineligible block. Supporting such an idea, we found a decreased response to incongruent-eligible blocks relative to incon-

Table 2

Talairach coordinates and results of event-related analysis for regions identified in exploratory comparison of incongruent-response eligible > incongruent-response ineligible

Significant activations							
Location	BA	X	Y	Z	% Subjects passing	Eligible vs. neutral –log (Prob)	Ineligible vs. neutral –log (Prob)
<i>Areas exhibiting response-related activity</i>							
Anterior cingulate cortex	32/6	8	20	42	75	1.564	n.s.
R. inferior frontal gyrus	44	56	14	16	69	1.491	n.s.
R. inferior frontal gyrus	46/10	44	46	10	75	2.921	n.s.
R. superior frontal gyrus	8/9	28	50	38	69	1.476	n.s.
R. middle frontal gyrus	8/9	52	20	38	69	1.351	n.s.
R. superior parietal lobule	7	34	–66	48	81	3.154	n.s.
<i>Areas exhibiting non-response-related activity</i>							
L. middle frontal gyrus	9/6	–40	6	34	69	2.244	1.551
L. precuneus	7	–6	–60	52	89	2.659	1.268
L. superior parietal lobule	7	–26	–66	48	81	3.522	1.519

Note: $-\log(0.050)=1.301$, $-\log(0.005)=2.301$, $-\log(0.001)=3.000$.

gruent-ineligible blocks in the left pre-central (BA 6; 69% subjects passing), post-central gyrus (BA 3 and BA 4; 81% subjects passing for each) and the superior temporal gyrus (BA 22; 81% subjects passing). Furthermore, our event-related analyses for these regions did not detect significant differences between the responses to incongruent and neutral trials within either block type. Hence, we believe these deactivations reflect a tonic suppression across all trials within the incongruent-eligible block.

5. Discussion

We found that anterior cingulate and prefrontal cortices, two regions previously implicated in the support of attentional control [1,3,6,17,22,24,20,14], differ with respect to the conditions under which they are involved. Our data suggest that the ACC's involvement in attentional control is primarily limited to situations in which competition is present at the response level, while the PFC's involvement is sensitive to the presence of competition at non-response levels as well. These findings also suggest that the classic debate as to whether Stroop interference arises at a response or pre-response level [15] is a false dichotomy, as our neuroimaging data provides evidence for the occurrence of interference at both levels.

The findings of the present study have implications for newly emerging theories of anterior cingulate and prefrontal cortex function. Some researchers [7] have suggested that ACC is involved in detecting the potential for error and/or monitoring for conflict [3]. Our data suggest ACC involvement in such evaluatory processes is limited to the response level. Thus, we propose that cingulate cortex monitors for the presence of competing or conflicting actions only at the response level in an effort to prevent the execution of erroneous motor actions and responses. On

the other hand, dorsolateral and posterior inferior prefrontal cortices are involved in attentional control at the non-response level as well, consistent with our proposal [1,2] that prefrontal regions are responsible for maintaining an attentional set that biases the selection of information from the task-relevant processing system. Hence, prefrontal cortex facilitates selection when discriminating between task-relevant and task-irrelevant information (e.g., semantic representations, phonological representations) is difficult. Our data are more consistent with suggestions that prefrontal regions are important for attentional control because they help to represent task demands [8] rather than being involved in action monitoring [10].

Our data also suggest hemispheric differences in attentional control. While homologous regions of prefrontal and parietal cortex were found to be involved (e.g., right and left middle frontal gyrus, right and left superior parietal lobule), they differed with respect to the situations that invoked their involvement. Regions within the right hemisphere appear to be more involved in control when conflict arises at the response level, while regions within the left hemisphere appear to be involved in attentional control when it arises at non-response levels. These findings are consistent with others [13], who have found that right prefrontal activity occurs when shifting motor sets in a Go/No-Go task, whereas shifting cognitive sets, as in a Wisconsin Card-Sorting Task, produces bilateral activity. The involvement of left posterior inferior frontal gyrus in attentional control at the non-response level is consistent with prior findings of its role in accessing and manipulating phonological representations [12,26]. Thus, while homologous prefrontal regions may support similar attentional functions, their involvement may differ depending on the level at which conflict arises. Although our study focused on the role of the ACC and PFC in attentional control, this does not preclude contributions of other

regions (e.g. posterior parietal cortex) to attentional regulation in response to conflict.

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