

# INVESTIGATING THE MECHANISMS OF NEGATIVE PRIMING: FROM THE EPISODIC MEMORY MODEL TO THE BRAIN'S FUNCTIONAL PLEOMORPHISM

*D. CÎRNECI\**, *DELIA GHEORGHE \**, *S. CONSTANTINESCU\*\**, *MONICA BERCEA\*\*\**

\*Synergion Consulting, 4–10 Munții Tatra st, 011022 Bucharest, Romania,  
e-mail: dragos.cirnei@brainperform.ro,

\*\*“Victor Babeș” Center for Diagnostic and Treatment, 281 Mihai Bravu st, 030303 Bucharest,  
Romania \*\*\*Department of Marketing, Economy and Business Administration Faculty,  
“Alexandru Ioan Cuza” University, 22 Copou Blvd, Iași, Romania

*Abstract.* Negative priming tasks evaluate the ability to maintain an active attention on a task while inhibiting other irrelevant information. Although it is traditionally viewed as an attention task, growing evidence has shown that negative priming obeys memory retrieval principles. In this study, 12 healthy male participants (mean age 35) were investigated using fMRI whilst performing a memory retrieval task referring to the content of four short movies. Subsequently, participants completed a spatial negative priming task. We found that performance in a negative priming task positively correlated with performance in the memory retrieval task and also with the BOLD signal in the anterior dorsomedial prefrontal cortex (aMPFC) during the memory retrieval task. In agreement with recent literature, we believe that performance in a spatial negative priming task is a reflection of the brain's pleomorphism, indicating towards the brain network responsible for the generation of virtual future states by combining pieces of information from episodic memory.

*Key words:* spatial negative priming task, episodic memory, functional pleomorphism, negative priming, prospective brain theory.

## INTRODUCTION

People can be described in terms of development and pathology by their ability to inhibit informational distracters. Negative priming tasks evaluate the ability to maintain an active attention on a task at hand while inhibiting other irrelevant information. The first experimental evidence linked to negative priming (although the name was not used at that time) was established by Dalrymple-Alford and Budayr in 1966 [as cited in 34], by using the Stroop task. The task requires fast

---

Received: October 2014;  
in final form November 2014.

naming of the word's colour. Naming the colour requires a greater reaction time, should the word match an incompatible colour (e.g., GREEN written in red). This is the well-known "stroop effect". The above mentioned authors discovered that the naming of the colour determines greater reaction times when using a list of words in which each word designated the subsequent colour in the list (e.g., GREEN written in red, followed by YELLOW written in green, followed by BLUE written in yellow, etc.). The authors hypothesized that participants need to inhibit the response for each word in order to be able to name the colour; if the inhibited response was necessary for the subsequent colour, then the response was slower [as cited in 34].

In 1985, Tipper introduces the concept of negative priming to describe the inhibitory effect produced by the ignored stimuli, as opposed to the facilitation effect (or priming effect), naturally produced by the stimuli for which previous attention was employed. The slowed response to a stimulus that is the same as, or shares characteristics with a previously ignored stimulus, has since been termed the *Negative Priming Effect* [40]. Negative priming experiments typically involve presentation of two displays. First a "prime" display is presented followed by a "probe" display, both of these containing a target that requires a response and a distractor that simply needs to be ignored. When the probe target is the same or similar to the prime distractor, probe responses are slowed compared to when the probe target is a completely new item, not related to the preceding prime display. Negative priming includes the term "prime", thus conveying the first step of a procedure. This concept implies the processing of a certain target characteristic (colour, positioning, significance, semantics, shape, etc.) whilst disregarding other distractor indicatives. The term "probe" refers to the second step of a procedure in which the ignored elements from the prime phase become processing targets.

This behavioral response bias has been extensively covered by the literature over the past three decades to provide strong evidence of an inhibitory component of selective attention [see 41 for reviews]. The negative priming effect has been found when the probe target and prime distractor share the same spatial location [43], color [44], shape [13], size, [45], semantic meaning [26, 32, 42], or the same semantic category [1, 40]. Additionally, the effect has been found to be triggered when allowing various response alternatives: verbal naming, pressing response keys on a keyboard or pointing [34]. But more importantly, negative priming occurs when performing different types of cognitive operations: identification, categorization, comparison, counting and localization. One can conclude that negative priming is a highly generalized phenomenon [30].

In line with the above conclusion suggesting a common inhibitory cognitive mechanism, some studies have found a positive relationship between the negative priming effect and working memory load. For instance, if between the prime and

probe phases, the participant has to maintain information in working memory (e.g., by counting backwards), the effect fails to be triggered. With the enhancement of demand on working memory, the processing of distracter information to be inhibited becomes greater [12]. Furthermore, other studies revealed that people with a greater working memory capacity elicit stronger priming effects as opposed to those with a more limited competence [10]. This aspect becomes apparent with regard to the neural activity as well, working memory processes being found to involve the activation of the structures responsible for perceptive processing of distracter information [15, 16]. In support of these results, imaging studies conducted in the early 2000's concluded that the same neuronal system considered relevant for working memory processes is important for sustained attention too. Additionally, the inter-individual differences in terms of working memory correspond to the differences with regard to sustained attention [14]. Hence, concentrating for a matter of seconds on a piece of information stored in memory can be considered sustained attention just as well as working memory. Furthermore, the same brain systems that help us concentrate our attention on an external stimulus, whilst ignoring others, are also believed to aid the sustenance of active information in working memory. Given the connections found between working memory, attention, and negative priming, it is no surprise that negative priming was believed to play a critical role both in attention and memory retrieval.

Although the negative priming effect has been traditionally investigated in the area of selective attention, some theories conceptualize negative priming as a memory phenomenon. Neill and Valdes (1991) [as cited in 34] have proposed the episodic retrieval model of negative priming, which claims that the inhibition of distracters appears during the *probe* step. They ascertained the negative priming effect as a “backwards retrieval” mechanism or a blocking process of the *prime* step. In the following years Neill [33] claimed that his experimental results strongly support episodic retrieval theories while very recent studies suggest the involvement of episodic retrieval processes in negative priming in younger and older adults [27]. Also, in a review involving 20 years of negative priming research, Mary and Buchner [28] concluded that evidence has increased with regard to negative priming clearly obeying memory retrieval principles.

Data from cognitive neuroscience also provides evidence on the relationship between attention and memory. Among the cognitive abilities, memory is one of the most extensively studied since the beginning of cognitive neuroscience. Hence, many studies have focused on the brain networks involved in information retrieval, identifying in detail the entire circuit used for the above mentioned process. As a consequence, today we know that consciously remembering episodic memories is a process that initiates in the dorsal hippocampus [17, 48], more specifically the perirhinal cortex [21]. From here, the information reaches the mammillary bodies

(part of the diencephalon) that are connected to the hippocampus, transferring the information to the anterior thalamic nuclei [47]. From the thalamus, the information reaches the retrosplenial and the posterior cingulate cortex, the intraparietal region and the lateral inferior parietal cortex. At this point, the information is projected to the medial prefrontal area, the anterior insular cortex, the ventro-lateral prefrontal region, the dorsolateral prefrontal cortex, the frontopolar cortex and the medial frontal cortex [7, 8, 9, 22, 24, 35]. So, if we want to study the neural common bases of attention and memory retrieval processes we should investigate the above mentioned networks.

Some authors have proposed that memory can be regarded as an instrument used by the “prospective brain” to generate simulations of possible future events. In order to function, these simulations need a system that can flexibly recombine the details of past events. Encoding requires a constructive process of combining pieces of information from episodic memory, generating the construction of future events through the extraction and recombination of the encoded information, thus simulating a new event [38]. The brain can be seen as a prediction machine that creates virtual future states. This ability to generate expectancies related to the occurrence of sensory information or to consequences of previous actions is traditionally named “attention”. Through the activation of attention, the brain generates predictions and synchronizes the ongoing action with changes in the environment, thus leading to better performances and successful target-oriented behaviors [20]. Specifically, one part of the brain, *the dorsomedial prefrontal cortex*, is involved in the representation and continuous updating of the appraisal linked to a possible future action, targeted toward behavior regulation [2].

With respect to the episodic retrieval model, the aim of the current study is to investigate the correlation between performance in an episodic retrieval task and a spatial negative priming task. In addition, we studied the relationship between the brain activations during the episodic memory retrieval task and the performance in the spatial negative priming task. Our hypothesis is that performance in a spatial negative priming task positively correlates with performance in an episodic memory retrieval task. The second hypothesis is that performance in the episodic memory retrieval task positively correlates with activation within the brain areas previously associated with negative priming tasks.

## METHODOLOGY

### PARTICIPANTS

Twelve male participants were included in the study and their ages ranged from 18 to 54 ( $M = 35$ ,  $SD = 12.53$ ). All of them were right-handed and had

graduated minimum 12 years of education, i.e. having passed the Romanian baccalaureate exam. None of the participants had any psychiatric or neurologic history, and they were all native Romanian speakers of white ethnicity. Recruitment was done via voluntary sampling. All participants gave written informed consent for taking part in the study. Involvement in the experiment was optional and participants retained the right to withdraw at any time. Importantly, information specific to fMRI experiments were considered and participants were made aware of all the relevant particularities. In addition, a selection questionnaire was issued before the start of the experiment to establish relevant parameters, such as the absence of claustrophobia, epilepsy, metals within the body etc.

#### MATERIALS AND METHODS

The current study used a memory retrieval task to assess episodic memory. The task involved viewing four short consecutive movies with amusing content, on a tablet computer screen. Consequently, participants were asked to recall the content of the movies both internally, whilst being scanned, and verbally, after scanning. This method generated data regarding brain activation and episodic memory, respectively.

fMRI scanning used a Siemens Magnetom Avanto 1.5 Tesla and brain activation was established using Neuro3D Software systems from Siemens. As a consequence, assessment of significant brain activation was established against an activation map comprising of t-test images with significance levels set at  $\alpha < 0.05$ , one-tailed. *P* values were adjusted for family-wise errors within each region of interest, using the Bonferroni correction.

Finally, the study used a spatial negative priming task to identify the negative priming effect, as previously described (Fig. 1). Two images were shown on a black background on the screen of a computer, being displayed one under the other at approximately 7 cm distance. The images were 3×4 cm big and exemplified animals, trees, cars and other common objects (books, etc.). The participants had to fix their gaze on the upper image, while ignoring the bottom image. One second later, one of the images was replaced with a yellow star. The participants were instructed to press a key on the keypad immediately after seeing the star, disregarding the location of the image that replaced it. After pressing the key, the screen became black and the participants were required to fix their gaze on the upper image appearing 0.5 sec later, in the same display as previously seen. The first 10 trials were practice exercises, then the following 30 sequences were experimental trials and the participants' results were recorded. The software used recorded reaction times measured from the appearance of the star to the moment a key was pressed, as well as the location in which the star appeared (replacing the

upper or lower image). The location of the star was randomly generated, equally appearing either in the upper or in the lower part of the screen. Performance in the spatial negative priming task was measured as follows: arithmetic means of reaction times were calculated for each participant and for each of the two appearance instances: upper and lower parts of the screen. Subsequently, the difference between mean reaction times for the lower image and mean reaction times for the upper image was calculated.

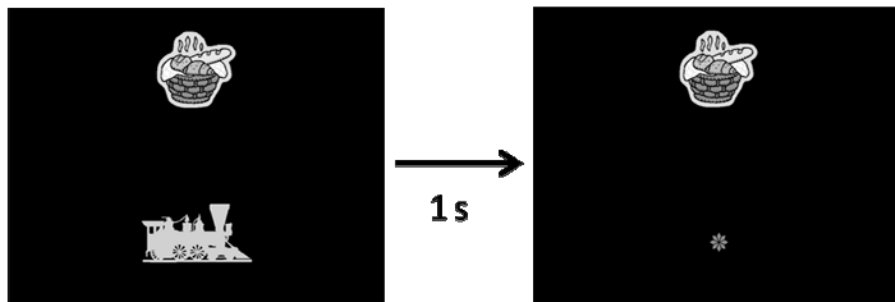


Fig. 1. The figure depicts a sequence of the spatial negative priming task. The image on the left shows two stimuli (images) displayed in opposite sides of the computer screen (top and bottom).

Subsequently, the bottom stimulus (image on the right) is replaced by the yellow star, which cues the participant's response.

#### PROCEDURE

In the first phase of the study participants were asked to watch in a separate room four short consecutive movies with amusing content. All the movies were displayed on a tablet computer screen and their duration added up to four minutes and 41 seconds. None of the participants reported being familiar with the movies presented.

In the second phase of the experiment, the participants were investigated using an fMRI scanner, 30 minutes after having watched the movies. During scanning, participants were asked to passively recall the content of each movie with their eyes shut. As a result, brain activation of passive recollection was established whilst participants recalled the content of each movie in the scanner. The baseline condition during scanning was established while participants were asked to look at a fixation point that was projected on a screen situated on a wall in front of the MRI machine. The subjects were able to see the screen through the optical helmet part of the MRI scanner. Each condition (activation and baseline) lasted 30 seconds. The former included three recollection sequences whereas the latter involved three sequences that served as baseline corrections before each recollection phase.

After the six sequences, participants verbally reported their recollection of the content of each movie. During this phase, the participants were not scanned, but their responses were recorded. Transcripts of participant reports were rated on a scale from one to five, depending on the amount of details remembered from the four videos (Table 1). Consequently, analysis measured the degree of agreement between ratings. Assessment of inter-rater reliability was established based on ratings obtained from two trained raters, using Cohen's Kappa. Results showed substantial agreement between raters,  $k = 0.75$ ,  $p < 0.001$ . The day after the memory retrieval task, all participants completed the spatial negative priming task.

*Table 1*

Coding table

Score 1 point	Remembers sporadically only a few elements from the recently viewed material
Score 2 points	Remembers one material in detail whereas the other materials only sporadically or not at all
Score 3 points	Remembers two materials in detail whereas the other materials only sporadically or not at all
Score 4 points	Remembers three materials in detail whereas the fourth material only sporadically or not at all
Score 5 points	Remembers all four materials in detail

#### STATISTICAL ANALYSIS

Statistical analyses were performed to identify significant correlations between performances in the spatial negative priming task, brain activation and remembering scores corresponding to the video material. Taking into account the limitations imposed by the small sample size ( $N = 12$ ) and the dichotomous and ordinal variables involved, the analysis performed point-biserial correlations as well as Kendall's tau non-parametric correlations on ranked data. Additionally, significance levels were set at  $\alpha < 0.05$  and  $\alpha < 0.01$ , wherever appropriate, one-tailed. Analyses are discussed further to shed light on the type of operations employed.

Firstly, analysis of brain activation and performance in the negative priming task was performed on binary and interval level data. This analysis involved a point-biserial correlation conducted with one-tailed significance levels set at  $\alpha < 0.01$ . The results assume a directional statistical decision, inferred from previous research linking BOLD responses in prefrontal brain regions to better performance in attention tasks. Within this category of tasks, good performers show strong activations in particular brain regions that include the frontal structures, while poor performers show the opposite effect [25].

Secondly, remembering scores were analysed in relation to the activation in the cerebral regions of interest. Analysis involved a directional statistical approach, which relied on previous research demonstrating that good performers in memory tasks involving episodic retrieval show greater activation in particular brain structures, including the frontal cortex [5]. Significance was thus set at  $\alpha < 0.05$  and datasets were binary and ordinal level. Analysis used simple ranks transformation for the remembering scores dataset to counterbalance the small sample limitations. Additionally, Kendall's tau test was used to depict the association between a dichotomy and a ranking, considering that the formula for rank biserial tests has been shown to be equivalent to the non-parametric equivalents of Pearson's  $r$  [11].

Finally, results on the negative priming task and the memory retrieval task were correlated. Analysis used Kendall's tau correlation with significance levels set at  $\alpha < 0.05$ , one-tailed, involving ordinal and interval level data. The ordinal data was ranked by the interval level scores obtained from the negative priming task, using savage score ranks, considering the limitations imposed by the small sample size. Naturally, the unidirectional approach assumes that better remembering scores are apparent with enhanced attention performances in the spatial negative priming task.

## RESULTS

Analysis focused on five regions of interest, i.e., anterior dorsomedial prefrontal cortex, ventromedial prefrontal cortex, subgenual anterior cingulate cortex, posterior cingulate cortex and precuneus. Associations involving results on the episodic memory retrieval task were performed relative to the aforementioned regions of interest, as specified by the literature [18, 23, 29, 39]. Results were found to be significant with regard to the hemodynamic changes of the amPFC (Fig. 2). Correlations between the remaining four regions under analysis and performance on the spatial negative priming task and the memory retrieval task were found to be non-significant (Table 2).

Performance in the memory retrieval task ( $M = 3.58$ ,  $SD = 1.44$ ) showed that 6 out of 12 participants scored four, thus remembering minimum three materials in detail (Table 1). In the spatial negative priming task ( $M = -18.61$ ,  $SD = 44.183$ ) 5 out of 12 participants obtained positive scores and 7 out of 12 scored negatively, which equaled to lower and higher accuracy, respectively.



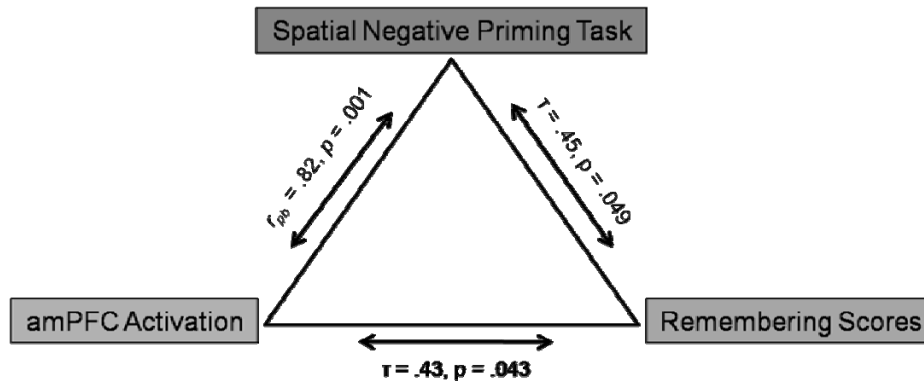


Fig. 2. Statistical analysis found significant associations between the Spatial negative priming task and remembering scores on the one hand, and brain activation in the anterior dorsomedial prefrontal cortex on the other hand. All correlations were performed one-tailed.

Table 2

Correlations

Anterior dorsomedial prefrontal cortex ( $M = 0.67, SD = 0.49$ )	Ventromedial prefrontal cortex ( $M = 0.83, SD = 0.39$ )	Subgenual anterior cingulate cortex ( $M = 0.75, SD = 0.45$ )	Posterior cingulate cortex ( $M = 0.25, SD = 0.45$ )	Precuneus ( $M = 0.25, SD = 0.45$ )	
$r_{pb} = 0.82, p = 0.001^*$	$r_{pb} = -0.23, p = 0.237$	$r_{pb} = 0.29, p = 0.182$	$r_{pb} = 0.03, p = 0.467$	$r_{pb} = 0.30, p = 0.168$	Spatial negative priming task
$\tau = 0.45, p = 0.049$	$\tau = 0.18, p = 0.255$	$\tau = 0.02, p = 0.462$	$\tau = 0.10, p = 0.353$	$\tau = 0.25, p = 0.172$	Memory retrieval task

Hemodynamic changes in the amPFC were found to be positively and significantly correlated with performance in the negative priming task,  $r_{pb} = 0.82$ ,  $p$  (one-tailed) = 0.001 (Fig 3). Particularly, more brain activation in the aforementioned structure was found to be related to better performance in the negative priming task. Furthermore, there was a moderate significant correlation between cerebral activations in the anterior dorsomedial prefrontal cortex and remembering scores resulting from the four video materials,  $\tau = 0.45$ ,  $p$  (one-tailed) = 0.049 (Fig 4). Finally, analysis found that greater remembering scores were associated with better performance in the spatial negative priming task. Specifically, there was a moderate positive correlation between the amount of details remembered from the four videos and performance in the negative priming task,  $\tau = 0.43$ ,  $p$  (one-tailed) = 0.043 (Fig. 5).

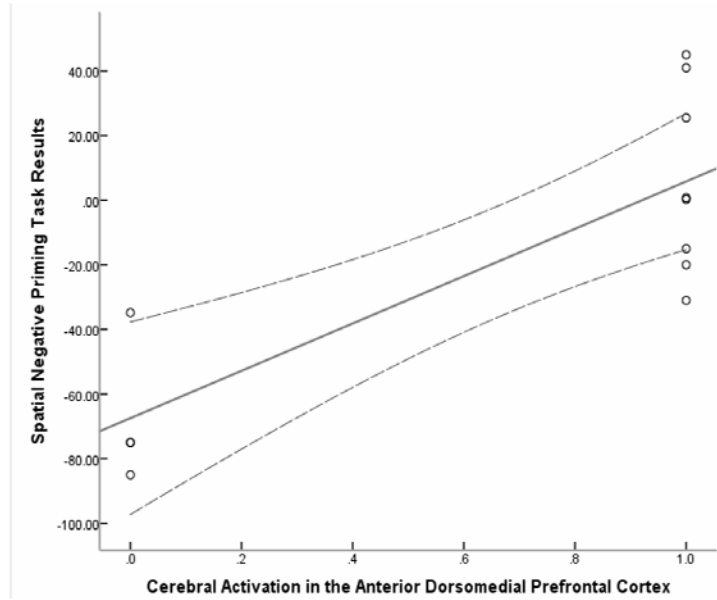


Fig. 3. The figure depicts correlations between spatial negative priming task results and anterior dorsomedial prefrontal cortex activation and ranks corresponding to remembering scores. The regression lines summarize the associations between variables; the external curved lines represent the mean confidence intervals of the significant correlations, and the circles represent data points.

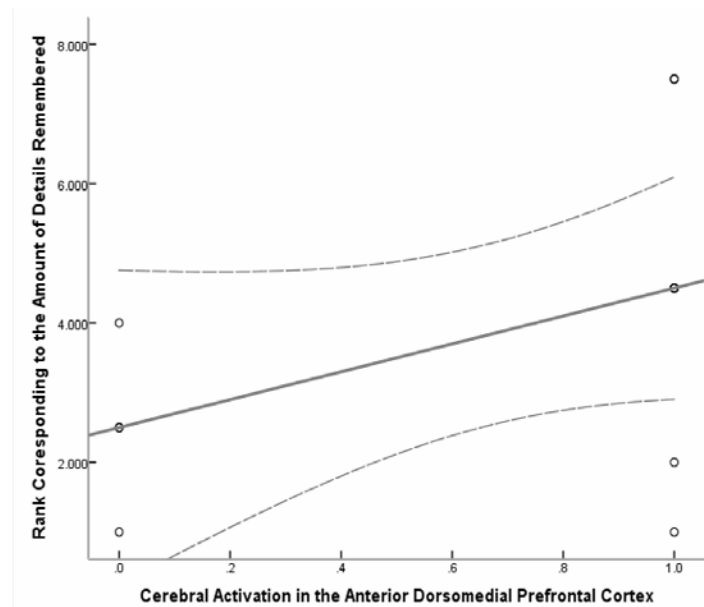


Fig. 4. The figure depicts correlations between spatial negative priming task results, anterior dorsomedial prefrontal cortex activation and ranks corresponding to remembering scores.

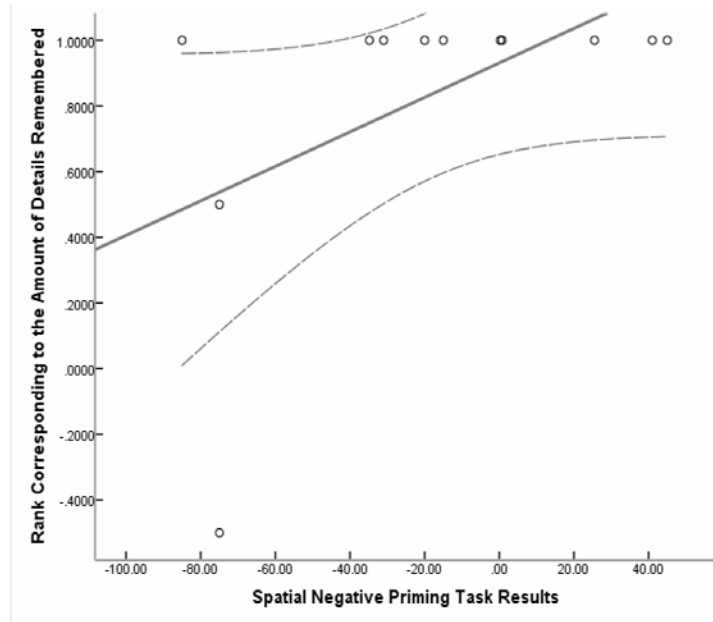


Fig. 5. The figure depicts correlations between spatial negative priming task results and ranks corresponding to remembering scores.

## DISCUSSION

In this study we found that performance in a spatial negative priming task positively correlated with performance in an episodic memory retrieval task and with the activation of the dorsomedial prefrontal cortex during the memory retrieval task (Fig. 6). As mentioned in the introduction of this paper, although the negative priming effect has been traditionally investigated in the area of selective attention, more recent theories conceptualize negative priming as a memory phenomenon. Given that in our study performance in the spatial negative priming task correlated with performance in an episodic memory task and the brain activations observed in the last one point towards the brain areas associated with negative priming in other studies, we suggest that our results seem to be congruent with the conclusions drawn by previous reviews suggesting that negative priming obeys memory retrieval principles [27, 28]. According with the episodic retrieval approach, the brain maintains mental representations of processing *episodes* and these episodic representations contain information about the identity and location of objects, their status as “relevant” or “irrelevant”, and the responses they require (“Respond” vs. “Do not respond”). If there is a conflict in the retrieval episode in which an item previously encoded as “irrelevant” on the prime is coded as “relevant” on the probe, slower reaction times occur as a result of the mismatch

between processing episodes and not as a consequence of the inhibition applied during the prime. Hence the episodic retrieval model can explain the negative priming effect without the need for any inhibitory mechanism in selective attention [19]. Note, however, that the results obtained from our study are not pointing toward a black and white explanation, but rather to a more complex one.

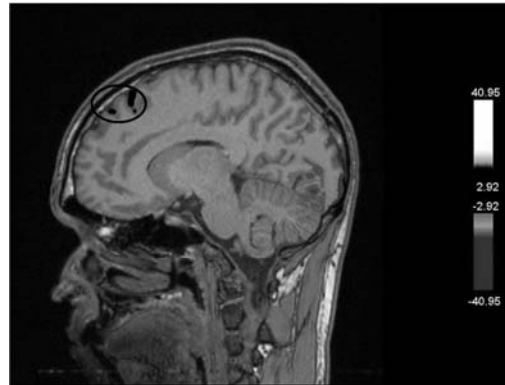


Fig. 6. Activation in the anterior dorsomedial prefrontal cortex (BA 9 and BA 8) was correlated both with performance in a memory retrieval task and with performance in a spatial negative priming task.

Our study has also found that performance in the spatial negative priming task positively correlated with the activation of the dorsomedial prefrontal cortex during the memory retrieval task (Fig. 6). In order to discuss our imaging findings and to present our point of view regarding the episodic retrieval model, we will first summarize the data from cognitive neuroscience concerning the brain correlates of negative priming. One early study published in 1999 found that right frontal and posterior damage resulted in a virtual loss of negative priming at all levels of complexity in a location-based (“select-what, respond-where”) priming task, while bifrontal damage resulted in a virtual loss of negative priming only related to increase in the complexity selection [39]. In another lesion study, Metzler and Parkin [29] found that uni- and bilateral frontal lobe damage disrupt distractor inhibition in an identity negative priming task involving letter naming.

In one of our previous studies, investigating with the use of ERPs (Event Related Potentials) the brain correlates of the same spatial negative priming task, we found that the P300 late potential in the right dorsomedial prefrontal area is associated with performance in this task [23]. These findings are consistent with the imaging data obtained from healthy individuals, where the “filtering” of locations to be ignored occurred in the prefrontal cortex [18]. One fMRI study using colour Stroop negative priming task revealed significant greater activation in medial frontal gyrus/anterior cingulate gyrus and right middle frontal gyrus [46]. It is known that the superior area of the right prefrontal cortex allocates attentional resources to solve the competition between target and distracters [3], and the

dorsomedial prefrontal cortex is coupled with the dorsolateral prefrontal area, this circuit implementing the attentional control [4]. Cognitive control is generally involved in tasks requiring the sheltering of information in working memory or sustained attention against distracters and interferences [6, 37].

As we mentioned in the introduction of this paper, given the connections found between working memory, attention, and negative priming, negative priming was believed to play a critical role both in attention and memory retrieval. Our results confirmed this hypothesis, and link this role with one specific brain region – the dorsomedial prefrontal cortex. How can we interpret these findings? Here we introduce the concept of functional pleomorphism. Functional pleomorphism refers to the ability of a brain region to activate different functions in different circumstances [31]. In our study we can infer that the brain areas involved in focused attention overlap with the brain areas involved in working memory, both of them being part of the brain’s “simulation machine” which builds representations of future events and possible behavioral responses to them, as we have shown in the introductory part.

From the very beginning, psychology and cognitive sciences have investigated memory, dividing it into various components: sensory, short and long term, declarative and procedural, implicit and explicit, episodic and semantic. All these paradigms are based on the same definition of memory: the ability to encode, store and recall information. One fundamental aspect in this definition is that information is initially stored and subsequently revealed, in the same way a “refrigerator” assumes that a certain temperature prevents food from going bad. Nonetheless, experimental data from neuroscience has revealed that the ability to recall information is not independent from perception, imagination or attention, but rather shares an intimate relation with them [36]. Some scholars believe that we should detach ourselves from the idea that the brain possesses hierarchical separate modules, but rather investigates how similar information tends to be processed in contiguous locations [31]. Consequently, we should understand the actual functions of different brain structures, the representations they entail and the processes they employ. The use of these concepts extracted from traditional psychology hinders the understanding of brain functions corresponding to actual physiological activity.

With respect to our study, we believe that instead of explaining the performance in an “attention” task by referring to the principles of “memory retrieval”, we should reconcile our understanding of brain functions, thus stepping outside the traditional psychological constructs. Performance in a negative priming task probably points towards the brain mechanism responsible for the generation of virtual future representations by combining pieces of information from episodic memory. This is an effortful process which necessitates the allocation of resources – or what we traditionally call sustained attention – in order to be implemented.

#### LIMITATIONS OF THE STUDY

One of the main limitations of this study is the small number of participants, the wide age spread and the exclusion of female participants from the sample. This latter aspect considered, our data cannot be extrapolated to women, and results, as well as our interpretation and forwarded theory should be interpreted with caution.

In our procedure of course we were not able to directly check if the subjects were actively tried to remember the content of the movies during the recollection phase inside the MRI. However, this is not an issue, because studies showed that every time we try to retrieve some information from memory, the brain is involved in a scene construction. Scene construction is an excellent candidate for a common core process that underpins a host of related cognitive functions including imagination, navigation and episodic future thinking [49]. Hence the actual content of the material our subjects recollect is not necessary an issue.

In addition, we were not able to directly assess brain activation during the spatial negative priming task, mainly because of technical difficulties related to using the response box inside the fMRI machine.

#### CONCLUSIONS

Negative priming tasks evaluate the ability to maintain an active attention on a task at hand while inhibiting other irrelevant information. A large number of studies derived from attentional paradigms of facilitation *versus* inhibition have shown that people performed slower and less accurately when asked to respond to the stimuli that were related to the previously ignored items. Although negative priming effects have been traditionally investigated in the area of selective attention, more recent theories conceptualize negative priming as a memory phenomenon. Additionally, recent reviews point towards the hypothesis that negative priming obeys memory retrieval principles. The current study found that performance in a spatial negative priming task positively correlated with performance in an episodic memory retrieval task and also with the activation of the dorsomedial prefrontal cortex during the memory retrieval task. The results were similar to other experimental data from neuroscience studies showing that the ability to recall information is not independent from perception, imagination or attention, but rather shares an intimate relation with these functions? In the last years several authors claimed that the module-oriented approach of the brain should be reconsidered and instead of viewing psychological processes as having specific neural components-based functions, we should rather try to understand its functioning under the functional pleomorphism principles. In agreement with the “prospective brain theory”, we believe that performance in a spatial negative priming task probably points towards the brain mechanisms responsible for the generation of virtual future states by combining pieces of information from

episodic memory. This reconstruction of information is an effortful process which necessitates the allocation of resources in order to be implemented, and here the episodic retrieval and the sustained attention combined.

*Acknowledgements.* This study was supported by the Beer, Health, and Nutrition Research Centre, Bucharest, Romania. The funders had no role in the design of the study or in the preparation of the manuscript.

#### REFERENCES

1. ALLPORT, D.A., S.P. TIPPER, N. CHMIEL, Perceptual integration and post-categorical filtering, in: *Attention and performance XI*, Hillsdale, NJ, Lawrence Erlbaum Associates, Inc., 1985, pp. 107–132.
2. AMODIO, D.M., C.D. FRITH, Meeting of minds: The medial frontal cortex and social cognition, *Nature Reviews Neuroscience*, 2006, **7**, 268–277.
3. BLEADOWSKI, C., D. PRVULOVIC, KARSTEN HOECHSTETTER, M. SCHREG, M. WIBRAL, R. GOEBEL, D.E.J. LINDEN, Localizing P300 generators in visual target and distractor processing: a combined event-related potential and functional magnetic resonance imaging study, *The Journal of Neuroscience*, 2004, **24**, 9353–9360.
4. BOTVINIK, M.M., J.D. COHEN, C.S. CARTER, Conflict monitoring and anterior cingulate cortex: an update, *Trends in Cognitive Science*, 2004, **8**, 539–546.
5. BRANCUCCI, A., Neural correlates of cognitive ability, *Journal of Neuroscience Research*, 2012, **90**, 1299–1309.
6. BUNGE, SILVIA, K.N. OCHSNER, J.E. DESMOND, G.H. GLOVER, J.D.E. GABRIELI, Prefrontal regions involved in keeping information in and out of mind, *Brain*, 2001, **124**, 2074–2086.
7. CABEZA, R., ELISA CIARAMELLI, INGRID OLSON, M. MOSCOVITCH, The parietal cortex and episodic memory: An attentional account, *Nature Reviews Neuroscience*, 2008, **9**, 613–625.
8. CANLI, T., J.E. DESMOND, Z. ZHAO, J.D.E. GABRIELI, Sex differences in the neural basis of emotional memories, *PNAS*, 2002, **99**, 10789–10794.
9. CAVANNA, ANDREA, M.R. TRIMBLE, The precuneus: A review of its functional anatomy and behavioural correlates, *Brain*, 2006, **129**, 564–583.
10. CONWAY, A.R.A., S.W. TUHOLSKI, REBECCA SHISLER, R.W. ENGLE, The effect of memory load on negative priming: an individual differences investigation, *Psychological Review*, 1999, **27**, 1042–1050.
11. CURETON, E.E., Rank-biserial correlation, *Psychometrika*, 1956, **21**, 287–290.
12. DE FOCKERT, J., G. REES, C.D. FRITH, NILLI LAVIE, The role of working memory in visual selective attention, *Science*, 2001, **291**, 1803–1806.
13. DESCHEPPER, B., ANNE TREISMAN, Visual memory for novel shapes: Implicit coding without attention, *Journal of Experimental Psychology: Learning, Memory and Cognition*, 1999, **22**, 27–47.
14. DIAMOND, A., Attention-deficit disorder (attention-deficit/hyperactivity disorder without hyperactivity): A neurobiologically and behaviorally distinct disorder from attention-deficit/hyperactivity disorder (with hyperactivity), *Development and Psychopathology*, 2005, **17**, 807–825.
15. DOWNING, P., JIA LIU, NANCY KANWISHER, Testing cognitive models of visual attention with fMRI and MEG, *Neuropsychologia*, 2001, **39**, 1329–1342.
16. DRUZGAL, T.J., M. D'ESPOSITO, Activity in fusiform face area modulated as a function of working memory load, *Cognitive Brain Research*, 2001, **10**, 355–364.

17. ELDRIDGE, LAURA, S.A. ENGEL, M.M. ZEINEH, SUSAN BOOKHEIMER, BARBARA KNOWLTON, A dissociation of encoding and retrieval processes in the human hippocampus, *The Journal of Neuroscience*, 2005, **25**, 3280–3286.
18. EVERLING, S., C.J. TINSLEY, D. GAFFAN, J. DUNCAN, Filtering of neural signals by focused attention in the monkey prefrontal cortex, *Nature Neuroscience*, 2002, **5**, 671–676.
19. FOX, ELAINE, J. DE FOCKERT, Negative priming depends on prime-probe similarity: Evidence for episodic retrieval, *Psychonomic Bulletin & Review*, 1998, **5**, 107–113.
20. GHAJAR, JAMSHID, R.B. IVRY, The predictive brain state: asynchrony in disorders of attention, *The Neuroscientist*, 2009, **20**, 1–10.
21. HANNESSON, D.K., J.G. HOWLAND, A.G. PHILLIPS, Interaction between perirhinal and medial prefrontal cortex is required for temporal order but not for recognition memory for objects in rats, *The Journal of Neuroscience*, 2004, **24**, 4596–4604.
22. HENSON, R.N.A., M.D. RUGG, T. SHALLICE, Confidence in recognition memory for words: dissociating right prefrontal roles in episodic retrieval, *Journal for Cognitive Neuroscience*, 2001, **12**, 913–923.
23. JAGLA, F., M. JERGELOVA, D. CÎRNECI, P. KUKUMBERG, Oculomotor and evoked potential changes in panic and depressive patients, *Homeostasis*, 2003, **42**, 145–147.
24. KONISHI, S., IDAI UCHIDA, T. OKUAKI, T. MACHIDA, I. SHIROUZU, Y. MIYASHITA, Neural correlates of recency judgement, *The Journal of Neuroscience*, 2002, **22**, 9549–9555.
25. LABRENZ, FRANZISKA, MARIA THEMANN, E. WASCHER, C. BESTE, BETTINA PFLEIDERER, Neural correlates of individual performance differences in resolving perceptual conflict, *Plos One*, 2012, **7**, e42849.
26. LOWE, D.G., Strategies, context, and the mechanisms of response inhibition, *Memory & Cognition*, 1979, **7**, 382–389.
27. MAYR, SUSANNE, A. BUCHNER, Negative priming as a memory phenomenon: A review of 20 years of negative priming research, *Zeitschrift für Psychologie/Journal of Psychology*, 2007, **215**, 35–51.
28. MAYR, SUSANNE, A. BUCHNER, Intact episodic retrieval in older adults: evidence from an auditory negative priming task, *Experimental Aging Research*, 2014, **40**, 13–39.
29. METZLER, CLAUDIA, A.J. PARKIN, Reversed negative priming following frontal lobe lesions, *Neuropsychologia*, 2000, **38**, 363–379.
30. MILLIKEN, B., S. JOORDENS, P.M. MERIKLE, A.E. SEIFFERT, Selective attention: A reevaluation of the implications of negative priming, *Psychological Review*, 1998, **105**, 203–229.
31. NACHEV, P., C. KENNARD, M. HUSAIN, Functional role of the supplementary and pre-supplementary motor areas, *Nature Reviews Neuroscience*, 2008, **9**, 856–869.
32. NEILL, W.T., Inhibition and facilitation processes in selective attention, *Journal of Experimental Psychology: Human Perception and Performance*, 1977, **3**, 444–450.
33. NEILL, W.T., Episodic retrieval in negative priming and repetition priming, *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 1997, **23**, 1291–13105.
34. NEILL, W.T., L.A. VALDES, K.M. TERRY, Selective attention and the inhibitory control of cognition, in: *Interference and inhibition in cognition*, San Diego, Academic Press, 1995.
35. RANGANATH, C., MARCIA JOHNSON, M. D'ESPOSITO, Left anterior prefrontal activation increases with demands to recall specific perceptual information, *The Journal of Neuroscience*, 2000, **20**, 1–5.
36. RIEGLER, A., Constructive memory, *Kybernetes*, 2005, **34**, 89–104.
37. SAKAI, K., J.B. ROWE, R.E. PASSINGHAM, Active maintenance in prefrontal area 46 creates distractor-resistant memory, *Nature Neuroscience*, 2002, **5**, 479–484.
38. SCHACTER, D.L., DONNA ADDIS, R.L. BUCKNER, Remembering the past to imagine the future: The prospective brain, *Nature Reviews Neuroscience*, 2007, **8**, 657–661.
39. STUSS, D.T., J. P. TOOTH, DINA FRANCHI, M. P. ALEXANDER, S. TIPPER, F.I.M. CRAIK, Dissociation of attentional processes in patients with focal frontal and posterior lesions, *Neuropsychologia*, 1999, **37**, 1005–1027.



40. TIPPER, S.P., The negative priming effect: Inhibitory priming by ignored objects, *Quarterly Journal of Experimental Psychology: Human Experimental Psychology*, 1985, **37A**, 571–590.
41. TIPPER, S.P., Does negative priming reflect inhibitory mechanisms? A review and integration of conflicting views, *The Quarterly Journal of Experimental Psychology*, 2001, **54A**, 321–343.
42. TIPPER, S.P., J. DRIVER, Negative priming between pictures and words in a selective attention task: Evidence for semantic processing of ignored stimuli, *Memory and Cognition*, 1988, **16**, 64–70.
43. TIPPER, S. P., J. C. BREHAUT, J. DRIVER, Selection of moving and static objects for the control of spatially directed action, *Journal of Experimental Psychology: Human Perception & Performance*, 1990, **16**, 492–504.
44. TIPPER, S.P., B. WEAVER, G. HOUGHTON, Behavioral goals determine inhibitory mechanisms of selective attention, *Quarterly Journal of Experimental Psychology*, 1994, **47A**, 809–840.
45. TIPPER, S.P., B. WEAVER, B. MILLIKEN, Spatial negative priming without mismatching: Comment on Park and Kanwisher, *Journal of Experimental Psychology: Human Perception and Performance*, 1995, **21**, 1220–1229.
46. UNGAR, LIDA, P.G. NESTOR, MARGARET NIZNIKIEWICZ, CYNTHIA WIBLE, M. KUBICKI, Color Stroop and negative priming in schizophrenia: An fMRI study, *Psychiatry Research*, 2010, **181**, 24–29.
47. VANN, SERALYNNE, J.P. AGGLETON, The mammillary bodies: two memory systems in one? *Nature Reviews Neuroscience*, 2004, **5**, 35–44.
48. VARGHA-KHADEM, F., D.G. GADIAN, K.E. WATKINS, A. CONNELLY, W. VAN PAESSCHEN, M. MISHKIN, Differential effects of early hippocampal pathology on episodic and semantic memory, *Science*, 2002, **277**, 376–380.
49. HASSABIS, D., ELEANOR, A. MAGUIRE, Deconstructing episodic memory with construction, *Trends in Cognitive Science*, 2007, **11**, 299–306.