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RESEARCH ARTICLE

Interaction between attentional systems and episodic memory encoding: the impact of conflict on binding of information

Marco Sperduti[1,2] · **Allan Armougum**[1,2] · **Dominique Makowski**[1,2] · **Philippe Blondé**[1,2] · **Pascale Piolino**[1,2,3]

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Abstract Episodic memory (EM) is defined as a long-term memory system that stores information that can be retrieved along with details of the context of the original events (binding). Several studies have shown that manipulation of attention during encoding can impact subsequent memory performance. An influential model of attention distinguishes between three partially independent attentional networks: the alerting, the orienting and the executive or conflict resolution component. To date, the impact of the engagement of these sub-systems during encoding on item and relational context binding has not been investigated. Here, we developed a new task combining the Attentional Network Test and an incidental episodic memory encoding task to study this issue. We reported that when the alerting network was not solicited, resolving conflict hindered item encoding. Moreover, resolving conflict, independently of the cueing condition, had a negative impact on context binding. These novel findings could have a potential impact in the understanding EM formation, and memory disorders in different populations, including healthy elderly people.

Keywords Episodic memory · Encoding · Attention · Source memory · Binding

Introduction

Episodic memory (EM) is defined as the long-term memory system storing information that can be retrieved along with details of the spatio-temporal context and the circumstances of the original events (source memory), and with a subjective feeling of remembering (Tulving 2002). Thus, EM concerns the recollection of factual information (what), along with its association with specific contextual features (e.g., spatial and temporal). The process of creating a unified event linking these different features is known as binding. We will employ throughout the manuscript the term binding to refer to the process of linking an item with its contextual information, and not to the binding of different features (e.g., colour, shape) of the item. Moreover, we will use the term of multiple binding for the association of factual information with multiple contextual sources, and that of source memory for the association of factual information with a unique contextual source.

While binding represents a core feature of EM, and is even considered a distinctive feature of the feeling of remembering (Meiser et al. 2008), the crucial question of what determines the bound of information during encoding is still unsolved. This process has been classically attributed to the hippocampus and other medial temporal structures (Davachi 2006; Ranganath 2010; Staresina and Davachi 2008; van den Honert et al. 2017). Nevertheless, converging lines of evidence suggest a pivotal role of frontal lobe based

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✉ Marco Sperduti
marcosperduti@yahoo.it

[1] Paris Descartes University, Sorbonne Paris Cité, Institute of Psychology, Memory and Cognition Laboratory, Boulogne Billancourt, France

[2] INSERM, UMR S894, Center for Psychiatry and Neurosciences, Paris, France

[3] Institut Universitaire de France (IUF), Paris, France

cognitive functions, such as executive functions and attention, in efficiently formed novel items-context associations (Dulas and Duarte 2014; Janowsky et al. 1989; Ranganath 2010).

The contribution of attentional process to EM encoding is not a novel idea, and can be traced back to the depth of processing theory proposed by Craik and Lockhart (1972) stating that the quality of the memory trace depends on the depth of the elaboration of the information at encoding. Deeper elaborative processes at encoding would require adequate attentional resources. This proposal has been sustained by studies showing that divided attention at encoding produces a decline of memory performance (e.g., Anderson et al. 2000; Naveh-Benjamin et al. 2003).

An influential model of attention proposes a distinction between three sub-systems: the alerting, orienting and conflict resolution (Posner and Petersen 1990). These networks can be characterized at the behavioural, neuronal and neurochemical level (Fan et al. 2002, 2005). The alerting system correspond to the ability to increase vigilance toward an incoming stimulus, the orienting to the capacity of selecting information among multiple sensory inputs and spatial locations, and the conflict resolution or executive component to the ability to resolve conflict or allocate limited attentional resources between competing stimuli. Fan et al. (2002) proposed a single task, the Attentional Network Test (ANT), allowing testing the efficiency of these three systems. They reported that these attentional sub-components are partially independent, but that they also interact in some circumstances (Fan et al. 2009). These results have been further supported by neuroimaging studies reporting separated, but also overlapping, brain activations (Fan et al. 2005).

Existing studies suggest that the engagement of the alerting or the orienting network modulate EM encoding. For example, it has been shown that predictable items at encoding, likely representing a form of alerting mechanism, were better remembered than unpredictable ones (Summerfield and Mangels 2006). Concerning the orienting system, it has been shown that items preceded by a valid spatial cue are better remembered compared to items preceded by an invalid one (Turk-Browne et al. 2013; Uncapher et al. 2011). Findings concerning the executive or conflict resolution component of attention are more controversial. Rosner et al. (2015) reported a better memory for items presented in a conflict condition. These data are coherent with a previous neuroimaging study employing a modified Stroop task in which, during encoding, subjects had to indicate the sex of faces in a congruent (the sex of the presented face and the superimposed word indicating the sex were congruent), an incongruent condition (the sex of the presented face and the superimposed word indicating the sex were incongruent), or a neutral condition (the face were accompanied be the word "house"). At the behavioural level, the authors reported a classic Stroop effect, that is slower reaction times for incongruent versus congruent trials, that was, nevertheless, accompanied by a higher rate of recognition for stimuli presented in the incongruent condition. Nevertheless, two recent studies reported opposite results (Chiu and Egner 2015a, b). Chiu and Egner (2015a) presented pictures of faces in a go/no-go protocol. Briefly, participants were instructed to press a button (go) when they saw a male face, and to avoid responding (no-go) when a female face was presented (or vice versa). They reported that pictures presented in the no-go condition were less recognised in a subsequent surprise memory test. The authors interpreted these results as a competition of resources between response inhibition and memory encoding. Moreover, they tried to reconcile their results with the aforementioned findings (Krebs et al. 2013; Rosner et al. 2015) suggesting that conflict resolution in the Stroop-like task could boost the allocation of attentional resources toward the stimulus, thus, enhancing encoding. On the other hand, response inhibition in the no-go condition would draw attentional resources, resulting in an opposite effect on memory encoding.

The role of attentional processes in the fostering the relational aspect of EM encoding (binding) has deserved less interest. Some studies reported that divided attention affects more source than item memory (Troyer et al. 1999), while others found that item and source memory (Kilb and Naveh-Benjamin 2007) were equally hindered. In a previous cited work (Uncapher et al. 2011), the authors reported that memory for spatial location of items was more accurate for items presented in the valid cued condition. In another study, Uncapher and Rugg (2008) selectively directed the attentional focus of attention toward two alternative contextual features (location or colour of presented images). They found that source memory was increased for the feature that was attended during encoding. Their neuroimaging findings showed a subsequent source memory effect (greater activity for correct versus incorrect source memory) in the hippocampus, independently of the type of source. Additionally, feature-specific subsequent source memory effect was found in the striate cortex for colour and superior parietal cortex for location. These data are coherent with the hypothesis that selective attention could bias the cortical processing of a sub-set of contextual information in specific cortical structures that can then be bound by the hippocampus.

To date, there is no study directly assessing the interplay between each attentional sub-system and the encoding of different features of EM in the same task. Moreover, given the central role of binding in EM, it is surprising the paucity of research investigating the contribution of attention to this process. The aim of our study was to fill this gap. Based on the aforementioned findings, we made the hypothesis that alerting and orienting should improve item memory encoding due to a top–down attentional recruitment, compared to condition in which there is no warning signals. Concerning conflict resolution, two alternative hypotheses could be made. On the one hand, according to Krebs et al. (2013) and Rosner et al. 2015, we could expect that item presented in the incongruent condition would be better remembered. On the other hand, in line with the inhibition-induced forgetting hypothesis proposed by Chiu and Egner (2015a, b), the opposite prediction can be made. A possible interaction between top–down attentional allocation and the executive component could be observed. Indeed, Fan et al. (2009) showed that alert elicited a greater conflict effect, while orienting facilitated conflict resolution. We could, thus, expect that alerting and orienting cues could magnify or attenuate, respectively, the effect of the executive component on memory encoding. For the source memory and multiple binding we made the hypothesis that both processes would be facilitated by conditions eliciting top–down attentional engagement as alerting and orienting (Uncapher et al. 2011). Concerning the effect of the executive component on source memory and multiple binding, our study is more exploratory, since there is no other work investigating this aspect.

To test our hypothesis, we developed a new task, the Attentional Network Episodic encoding Task (ANET), that consists of an incidental memory task (using pictures of everyday life objects) in which the activation of the three attentional networks is elicited by the experimental manipulation similar to those employed in the Attentional Network Test (Fan et al. 2002).

Materials and methods

Subjects

Thirty young healthy participants (17 women, mean age 22.8 ± 3.4 years) were recruited at the Institute of Psychology of the University Paris Descartes. All participants preliminary signed an informed written consent in accordance with the declaration of Helsinki.

Protocol

General organization of the task

The present task is a combination of the ANT (Fan et al. 2002) with an episodic memory incidental encoding task. Visual stimuli were presented in three attentional Cuing conditions: no cue (NC), double cue (DC), and a spatial cue (SC); and could be either congruent (CON) or incongruent (INC). Cuing condition and congruency were orthogonally manipulated, giving rise to six experimental conditions: NC_ CON, NC_ INC, DC_ CON, DC_ INC, SC_CON, SC_ INC. In each trial, the stimulus consisted of the same pictures repeated five times, with one central target and four lateral distractors (two on each side). In the congruent condition all pictures composing the stimulus pointed in the same direction (left or right), while in the incongruent condition the lateral distractors pointed in the opposite direction with respect to the central target. We selected 72 pictures from the Behavioural Pattern Separation—Object Version (BPS-O) database (Stark et al. 2013). Pictures were selected for having a non-ambiguous orientation. 48 pictures were presented during the encoding phase, and the remaining 24 pictures were presented, along with the 48 old pictures, during the recognition test. The assignment of pictures to each experimental condition during the encoding phase was counterbalanced across subjects.

Encoding phase

At the beginning of each trial, a screen with a central fixation cross and two empty rectangular box positioned over and above the fixation cross was presented. After a random variable interval ranging between 2000 and 5000 ms (in steps of 250 ms) a cue was presented for 100 ms. The cue consisted in a change of the colour (red) of the boxes. In the DC condition both boxes turned to red, in the SC condition only one of the boxes changed to red, and in the NC none of the boxes changed to red. After a fixed interval of 400 ms, a stimulus, either congruent or incongruent, appeared in one of the boxes and remained visible for a fixed duration of 1000 ms. After the SC condition the stimulus always appeared in the cued position. The presentation of the experimental conditions as well the position of stimuli (half of the stimuli appeared in the upper box and half in the lower box) was randomised within subjects.

The task of the participants was to indicate, as fast as possible, the direction (left or right) of the central picture (target), trying to be as accurate as possible. The maximum time allowed to give a response was fixed to 1500 ms. After this interval, or after the subjects' response (not before the fixed 1 s duration of items presentation), a new trial started. For a schematic representation of the experimental protocol see Fig. 1.

Recognition test

Following a brief distracting task, counting backward by 7 starting form 100 for 30 s, a surprise recognition test was presented. During the recognition phase, the 48 previously presented pictures, along with 24 new pictures, were presented at the centre of the screen. Subjects were asked to indicate if they were sure to have seen the pictures during the encoding phase (SURE), if they were not sure having seen the picture (MAYBE), or if the picture had not been

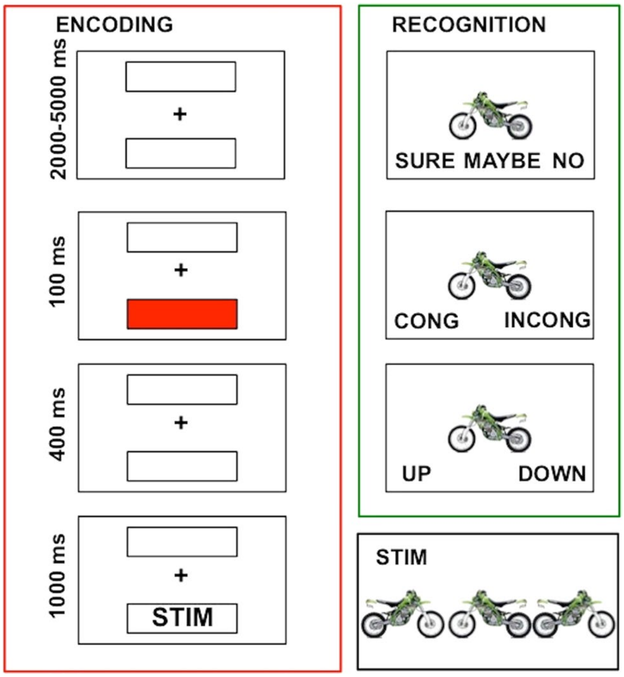

Fig. 1 Schematic representation of the protocol. In the red box, the time course of the events in one trial during the encoding phase. Here is represented a trial with a spatial cue. In the *black* box, an example of an incongruent stimulus is presented. For clarity of representation, only two lateral distractors are shown, the real stimulus comprised four distractors. In the *green* box, the sequence of events during the recognition phase is illustrated. If the subjects responded SURE at the question "Did you see this object?", they were prompted to indicate the condition source, and the spatial source

presented (NO). If participants answered SURE, two source memory questions were presented: (1) in which position (spatial source) the picture was presented (top or bottom box) and (2) in which condition (condition source) the picture was presented (congruent or incongruent) (Fig. 1). The presentation of the pictures was randomised, and the timing of presentation was self-paced, depending on the subjects' responses.

Presentation of the stimuli and recording of data were automatically accomplished using PsychoPy© (Peirce 2007).

Data analysis

Encoding reaction times

Reaction times (RTs) inferior to 100 ms and for incorrect responses were removed from further analyses. RTs were then log transformed to approach a normal distribution. We then computed, for each subject, the mean of RTs for each experimental condition. These scores were submitted to a 3 Cue × 2 Congruency rANOVA. We also computed the efficiency of the three Attentional Networks as described in previous studies (e.g., Sperduti et al. 2016). For the alerting network (ALE) we subtracted reaction time in the DC from that in the NC condition. For the orienting network (ORI) we subtracted reaction time in the SC from that in the DC condition. For the executive network (EXE) we subtracted reaction time in the CON from that in the INC condition. These scores were separately submitted to one-sample *t* test comparing the score against 0. This analysis was run as a control measure to verify that our task actually elicited behavioural costs and benefits expected in the different attentional conditions. Moreover, we run, across subjects, correlations between the scores of the three networks to confirm their independence.

Memory performances

We first computed signal detection theory indexes to assess the global recognition performances of our participants, separately for the two confidence responses (SURE and MAYBE). In particular we calculated the non-parametric index of discriminability (A'). This index was preferred since it is not dependent on assumptions about the distribution of signal and noise, and is not sensitive to extreme values of Hit and False alarms rates [Stanislaw and Todorov (1999); for the R code employed for computing this index see Pallier (2002)]. These scores were submitted to separate one-sample *t* tests comparing them against 0.5 (chance level for recognition performance using the A' index). Then the A' was compared between the two confidence responses employing a two-tailed paired *t* test. Since we were interested in correct episodic responses and we asked source memory questions only after SURE answers, we further analysed only high-confidence responses (SURE) associated to correct recognition. Moreover, only items corresponding to correct responses during the encoding phase were considered in computing memory scores. Error rates for each experimental condition are reported in Supplementary Table 1. For each experimental condition, we computed the following scores: (1) the ratio of correct recognition (Hit) as the proportion of SURE responses given the item was old and the subject gave a correct response during encoding; (2) the ratio of correct spatial source (Spatial) as the number of items followed by a correct spatial source response divided by the number of Hit; (3) the ratio of correct condition source (Condition) as the number of items followed by a correct condition source response divided by the number of Hit; (4) the ratio of multiple binding (binding) as the number of items followed by a correct spatial source and a correct condition source divided by the number of Hit. These scores were submitted to a 3 Cue × 2 Congruency rANOVA. We exploratory run correlation analyses, across subjects, between the scores of the three attentional networks and the different memory scores (Hit, Spatial, Condition and Binding) in each experimental condition. This analysis did not reveal any significant correlation. Thus, we only reported results in supplementary material (Supplementary Table 2). Finally, to exclude the possibility that any differences in memory performances could be linked to prolonged processing time as expressed in longer RTs, we computed a logistic regression to predict the probability for an item to be remembered or forgotten (coded as a binary factor). We only run this analysis on the Hit, Condition and Binding scores, since we did not report any significant effect on the Spatial score (see "Results" section). We entered RT as continuous predictor, and participants and items as random factors. Effect sizes are reported with partial eta squared (η^2_P). All statistical analyses were performed using R (R Development Core Team 2008). Logistic regression was run using the lm4 package (Bates et al. 2014).

Results

Encoding reaction times

The 3 Cue × 2 Congruency rANOVA revealed a significant main effect of Cue [$F(2, 58) = 28.92$, $p < .001$, $\eta^2_P = .16$). Post hoc comparisons (Tukey adjusted p values) showed that all differences were significant. In particular, NC was associated with slower RTs compared to DC et SC ($p = .04$ and $p < .001$, respectively), and DC with slower RTs compared to SC ($p < .001$). We also found a significant main effect of Congruency [$F(1, 29) = 19.45$, $p < .001$, $\eta^2_P = .06$], with INC condition associated with slower RTs compared to CON. The interaction between the two factors was not significant [$F(2, 58) = .87$, $p = .42$, $\eta^2_P = .004$]. A graphical representation of the results is reported in Fig. 2.

The t tests showed that the scores for each attentional network were significantly different from 0: ALE (mean .03 ± .06, $t(29) = 2.94$, $p = .006$); ORI (mean .07 ± .07, $t(29) = 5.48$, $p < .001$); EXE (mean .05 ± .07, $t(29) = 4.41$, $p < .001$). These results confirm that our attentional manipulation was efficient. Moreover, the analysis of correlation demonstrates no significant correlation between the three networks: ALE-ORI ($r = -0.21$, $p = .98$); ALE-EXE ($r = -0.14$, $p = .46$); ORI-EXE ($r = 0.21$, $p = 0.25$). These results support the independence of the three attentional networks.

Memory performances

One-sample t test on the A' showed that participants' recognition responses significantly differed from chance level when they gave SURE answers [mean .84 ± .08, $t(29) = 23.29$, $p < .001$], but not when they gave MAYBE answer [mean .47 ± .16, $t(29) = -.93$, $p = .36$]. Moreover, the A' was significantly greater for SURE compared to MAYBE responses [$t(29) = 10.04$, $p < .001$].

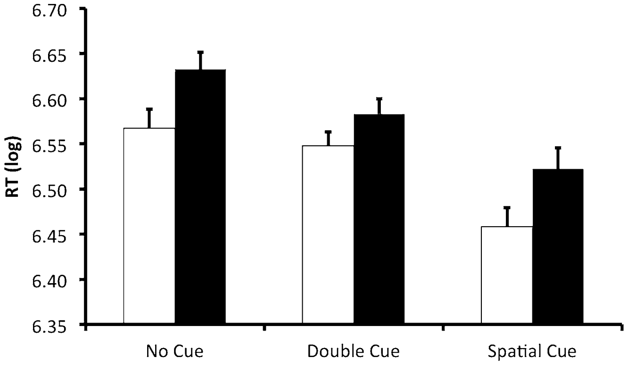

Fig. 2 Reaction times in each of the six difference experimental conditions. *White* and *black* bars represent the congruent and the incongruent condition, respectively. Error bars represent standard error mean (SEM)

The ANOVA on Hit revealed a trend toward a significant effect of the Congruency [$F(1,29) = 3.90$, $p = .05$, $\eta^2_P = 0.015$] that was further characterised by a significant interaction between Cue and Congruency [$F(2,58) = 3.66$, $p = .028$, $\eta^2_P = 0.027$]. Post hoc comparisons (Tukey adjusted p values) showed that the only significant difference was between the CON (.70 ± .23) and the INC (.55 ± .29) conditions in the NC condition ($p = .04$). The main effect of the Cue [$F(2,58) = .18$, $p = .83$, $\eta^2_P = 0.001$] was not significant (Fig. 3a).

The ANOVA on the Spatial score did not reveal any significant effect: main effect of the Congruency [$F(1,29) = 1.03$, $p = .31$, $\eta^2_P = 0.004$], main effect of the Cue [$F(2,58) = .17$, $p = .83$, $\eta^2_P = 0.002$], interaction between Cue and Congruency [$F(2,58) = .16$, $p = .85$, $\eta^2_P = 0.002$]. See Fig. 3b.

The same analysis on the Condition score revealed a significant main effect of Congruency [$F(1, 29) = 9.74$, $p = .002$, $\eta^2_P = .05$]. The Condition score was higher for item in the CON (.68 ± .28) compared to the INC (.54 ± .33) condition. The main effect of Cue [$F(2, 58) = 1.03$, $p = .36$, $\eta^2_P = .01$] and the interaction [$F(2, 58) = .11$, $p = .90$, $\eta^2_P = .001$] between Congruency and Cue were not significant (Fig. 3c).

The same analysis on the Binding score revealed a significant main effect of Congruency [$F(1, 29) = 11.22$, $p = .001$, $\eta^2_P = .05$]. The Binding score was higher for item in the CON (.48 ± .29) compared to the INC (.34 ± .31) condition. The main effect of Cue [$F(2, 58) = .61$, $p = .54$, $\eta^2_P = .005$] and the interaction [$F(2,58) = .45$, $p = .64$, $\eta^2_P = .005$] between Congruency and Cue were not significant (Fig. 3d).

The logistic regression showed that RTs were not a significant predictor for Hit [$\beta = .28$, 95% CI (−.51, 1.07),

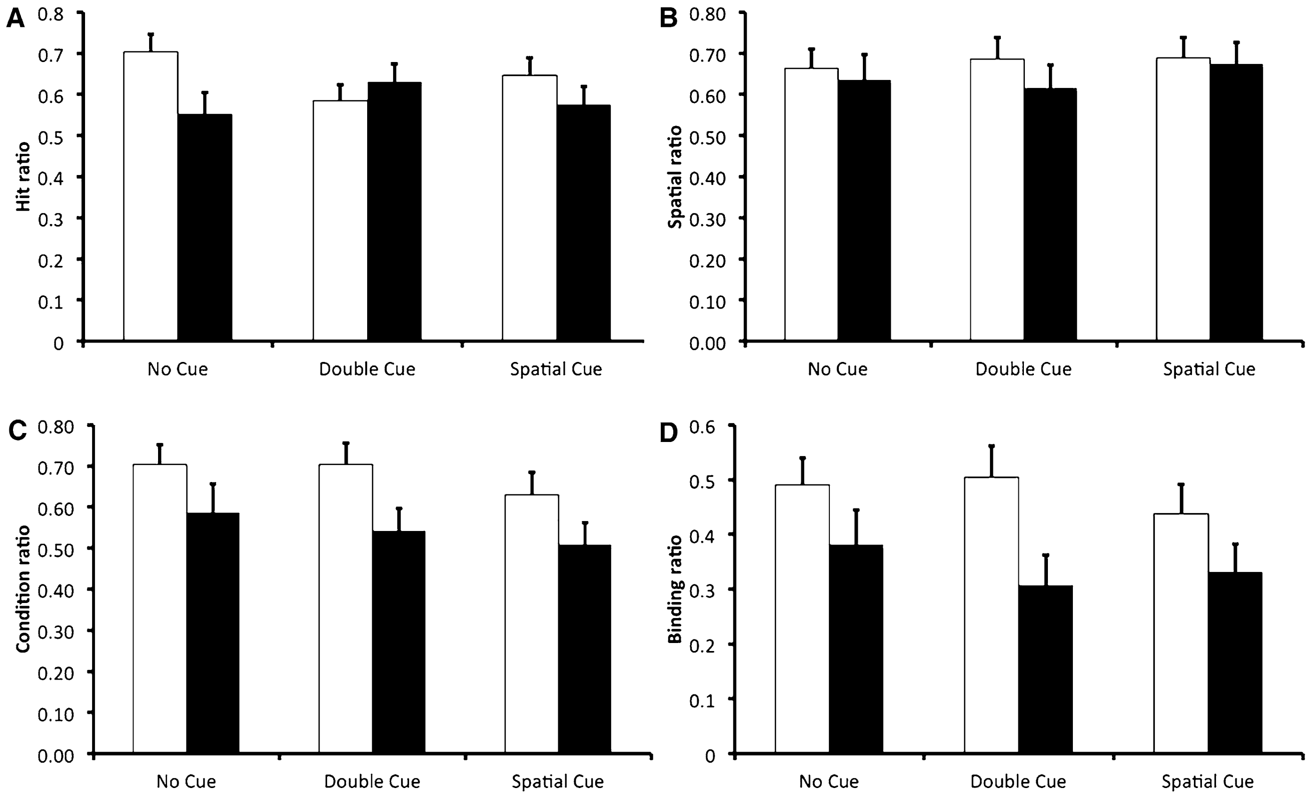

Fig. 3 Memory performances. **a** Interaction between the cuing condition and the congruency on the correct responses (Hit ratio); **b** Spatial source ratio in the difference experimental conditions; **c** Condition source ratio in the difference experimental conditions; **d** Binding ratio in the different experimental conditions. White and black bars represent the congruent and the incongruent condition, respectively. Error bars represent standard error mean (SEM)

$p = .49$], Condition [$\beta = -.38$, 95% CI (-1.23, .46), $p = .37$] or Binding [$\beta = -.08$, 95% CI ($-.92$, .77), $p = .86$].

Discussion

In the present work we developed a new task to investigate the interaction between the recruitment of different attentional networks and the encoding of items and their context (source memory and multiple binding), a core feature of episodic memory. We manipulated the engagement of each network during encoding of pictures using the experimental design inspired by the Attentional Network Test (Fan et al. 2002). The analysis of reaction times confirmed that our experimental manipulation was effective in producing the expected costs and benefits in the speed of responses according to the different cueing conditions and type of stimuli (congruent or incongruent). These findings suggest that our task effectively recruited different attentional components previously described in the literature (Fan et al. 2002, 2005).

Contrary to our hypothesis, and to previous reports (Summerfield and Mangels 2006; Uncapher et al. 2011), we did not find a memory benefit for items encoded in the cued conditions, which were expected to engage top–down attentional processes, compared with items encoded in the absence of cue, and that were expected to engage more bottom–up attentional capture. Nevertheless, while we used an incidental encoding task, Summerfield and Mangels (2006) employed a voluntary encoding. Moreover, they used verbal material, while we employed pictures. These methodological differences could, thus, account for the divergent results. Moreover, subjects in our study were actively engaged in a speed reaction time task that could had induced a high tonic state of vigilance that possibly overrun the effect of phasic alerting and could be sufficient in promoting items encoding. This interpretation is sustained by studies showing a partial overlap between brain regions engaged in tonic and phasic alerting (for a review see Posner 2008).

Concerning Uncapher et al. (2011)'s study, they reported that encoding pictures in a spatial invalid cued condition (producing a bottom–up attentional reorienting) negatively impact later recognition, compared to items encoded in a valid cue condition. Their results are more likely due to a cost of attentional reorienting in the invalid cue condition. It should be noted that in our study attentional reorienting processes were never at stake, and that our no cue condition, that was thought to elicit bottom–up attentional processes, is substantially different from Uncapher et al. (2011)'s study. These findings are coherent with the frequent observation that the benefits, in terms of stimulus processing, of valid cues are smaller than the cost of invalid cues (Fan et al. 2009). Thus, it is possible that the benefit of stimulus processing elicited by the valid cue in our task were not effective in producing a memory improvement. On the contrary, the cost of invalid cues in the Uncapher et al. (2011)'s work succeeded in hindering memory formation. Thus, our results are not necessarily incompatible with this previous work and aid in disentangling the role of different sub-components of attentional orienting in memory encoding.

We found that incongruent items that were not preceded by a cue in the encoding phase had a lower probability of being recognised. These results seem coherent with the hypothesis of the inhibition-induced forgetting recently proposed by Chiu and Egner (2015a, b), and contradict the encoding advantage for items presented in a conflict condition reported in some previous studies (Krebs et al. 2013; Rosner et al. 2015). It has to be noted that the latter two studies employed a conflict condition (Stroop-like) that was quite different from the present research (flanker). While the Stroop and the Flanker tasks are both thought to elicit conflict resolution, they could engage different processes, namely inhibition of prepotent responses and inhibition of irrelevant distractors, respectively. The two processes are underpinned by overlapping, but partially separable, cortical networks (Nee et al. 2007), they are differently affected by experimental manipulation (Chajut et al. 2009), and they can independently be altered in pathological conditions (Adams and Jarrold 2012; Sanderson and Allen 2013). Moreover, there are other lines of evidence suggesting that congruent information (Staresina et al. 2009), or stimuli presented with no distractors (Park et al. 2014), could enhance memory encoding. The novel finding is that the modulation on memory encoding of conflict resolution seems evident only when top–down attentional resources could not be recruited. It is possible that preparatory engagement of attentional resources by a warning signal could lighten the cognitive effort to inhibit the processing of irrelevant distractors, and, in turn, leave more attentional resources available for memory encoding. This interpretation is obviously difficult to sustain with only behavioural results. Thus, further neuroimaging studies could shed light on this issue.

Concerning source memory, the previously cited studies (Park et al. 2014; Staresina et al. 2009) showed an advantage of the congruent condition, not only for items memory, but also for source memory. This is in line with our results. Indeed, we showed that source memory was better for pictures presented in the congruent, compared to the incongruent condition. This was true for the condition source, but not for the spatial source. One possible explanation could be that the condition (congruent, incongruent), contrary to the spatial position (up, down), was a behaviourally salient feature of the task. This proposal would be in accordance with Uncapher and Rugg (2008)'s results showing that source memory is selectively modulated for stimulus' features that are attended during encoding. Moreover, we showed that multiple binding (association between spatial and condition sources) was better for pictures presented in the congruent, compared to the incongruent condition. These data suggest, according to Staresina et al. (2009), that congruency could elicit multiple binding encoding. Neuroimaging studies have reported greater activity during the incongruent condition in the flanker task in several regions including the anterior cingulate cortex (ACC), the dorsolateral prefrontal cortex (DLPFC), the superior parietal cortex, and the cerebellum (e.g., Casey et al. 2000). Interestingly, some of these regions are thought to be the source of top–down control signals that would modulate activity of sensory areas responsible for processing different pieces of information during associative encoding (Summerfield et al. 2006). Thus, our results are probably due to a competition of these top–down control resources, between inhibiting the processing of irrelevant information (the distractors in our task), and selecting the relevant features to bind together to form a new episodic trace. This hypothesis could be further explored employing neuroimaging techniques.

Conclusion

We proposed here a new task to investigate the interaction between attentional processes and episodic memory encoding. Our data suggest that, when full attentional resources are available, a tonic alerting state could be sufficient in promoting item encoding processes, but that conflict resolution could hinder item encoding when anticipatory top–down attentional processes, due to the lack of a warning signal, are not at stake. Moreover, we showed that resolving conflict could hinder contextual encoding, especially multiple binding. This result is apparently in contrast with some previous reports showing that conflict resolution has a negative impact on the task at hand, but a positive one on subsequent memory. Nevertheless, tasks that differently manipulate interference, such as Stroop-like and flanker-like tasks, could possibly have dissociable effects on memory encoding. This topic merits further investigations. Our data are of potential interest in explaining episodic memory encoding difficulties in different populations, in particular in elderly, in which the ability to effectively ignore irrelevant information has been shown to be directly linked with memory impairment (Gazzaley and D'Esposito 2007).

References

Adams NC, Jarrold C (2012) Inhibition in autism: children with autism have difficulty inhibiting irrelevant distractors but not prepotent responses. J Autism Dev Disord 42(6):1052–1063

Anderson ND, Iidaka T, Cabeza R, Kapur S, McIntosh AR, Craik FI (2000) The effects of divided attention on encoding-and retrieval-related brain activity: a PET study of younger and older adults. J Cogn Neurosci 12(5):775–792

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B (2014) lme4: linear mixed-effects models using Eigen and S4 (version 1.1-7). http://cran.r-project.org/web/packages/lme4/index.html

Casey BJ, Thomas KM, Welsh TF, Badgaiyan RD, Eccard CH, Jennings JR, Crone EA (2000) Dissociation of response conflict, attentional selection, and expectancy with functional magnetic resonance imaging. Proc Natl Acad Sci 97(15):8728–8733

Chajut E, Schupak A, Algom D (2009) Are spatial and dimensional attention separate? Evidence from Posner, Stroop, and Eriksen tasks. Mem Cognit 37(6):924–934

Chiu YC, Egner T (2015a) Inhibition-induced forgetting when more control leads to less memory. Psychol Sci 26(1):27–38

Chiu YC, Egner T (2015b) Inhibition-induced forgetting results from resource competition between response inhibition and memory encoding processes. J Neurosci 35(34):11936–11945

Craik FI, Lockhart RS (1972) Levels of processing: a framework for memory research. J Verbal Learn Verbal Behav 11(6):671–684

Davachi L (2006) Item, context and relational episodic encoding in humans. Curr Opin Neurobiol 16(6):693–700

Dulas MR, Duarte A (2014) Aging affects the interaction between attentional control and source memory: an fMRI study. J Cognit Neurosci 26(12):2653–2669

Fan J, McCandliss BD, Sommer T, Raz A, Posner MI (2002) Testing the efficiency and independence of attentional networks. J Cognit Neurosci 14(3):340–347

Fan J, McCandliss BD, Fossella J, Flombaum JI, Posner MI (2005) The activation of attentional networks. Neuroimage 26(2):471–479

Fan J, Gu X, Guise KG, Liu X, Fossella J, Wang H, Posner MI (2009) Testing the behavioral interaction and integration of attentional networks. Brain Cogn 70(2):209–220

Gazzaley A, D'Esposito MARK (2007) Top–down modulation and normal aging. Ann N Y Acad Sci 1097(1):67–83

Janowsky JS, Shimamura AP, Squire LR (1989) Source memory impairment in patients with frontal lobe lesions. Neuropsychologia 27(8):1043–1056

Kilb A, Naveh-Benjamin M (2007) Paying attention to binding: further studies assessing the role of reduced attentional resources in the associative deficit of older adults. Mem Cognit 35(5):1162–1174

Krebs RM, Boehler CN, De Belder M, Egner T (2013) Neural conflict–control mechanisms improve memory for target stimuli. Cereb Cortex 25(3):833–843

Meiser T, Sattler C, Weißer K (2008) Binding of multidimensional context information as a distinctive characteristic of remember judgments. J Exp Psychol Learn Mem Cogn 34(1):32

Naveh-Benjamin M, Guez J, Marom M (2003) The effects of divided attention at encoding on item and associative memory. Mem Cogn 31(7):1021–1035

Nee DE, Wager TD, Jonides J (2007) Interference resolution: insights from a meta-analysis of neuroimaging tasks. Cogn Affect Behav Neurosci 7(1):1–17

Pallier C (2002) Computing discriminability and bias with the R software. http://www.pallier.org/ressources/aprime/aprime. Accessed 12 June 2015

Park H, Leal F, Abellanoza C, Schaeffer JD (2014) The formation of source memory under distraction. Behav Brain Funct 10(1):40

Peirce JW (2007) Psychopy–psychophysics software in Python. J Neurosci Methods 162(1):8–13

Posner MI (2008) Measuring alertness. Ann N Y Acad Sci 1129(1):193–199

Posner MI, Petersen SE (1990) The attention system of the human brain. Annu Rev Neurosci 13:25–42

Ranganath C (2010) Binding items and contexts the cognitive neuroscience of episodic memory. Curr Dir Psychol Sci 19(3):131–137

R Development Core Team (2008) R: a language and environment for statistical computing. Manual. Vienna, Austria. http://www.r-project.org

Rosner TM, D'Angelo MC, MacLellan E, Milliken B (2015) Selective attention and recognition: effects of congruency on episodic learning. Psychol Res 79(3):411–424

Sanderson C, Allen ML (2013) The specificity of inhibitory impairments in autism and their relation to ADHD-type symptoms. J Autism Dev Disord 43(5):1065–1079

Sperduti M, Makowski D, Piolino P (2016) The protective role of long-term meditation on the decline of the executive component of attention in aging: a preliminary cross-sectional study. Aging Neuropsychol Cogn 23(6):691–702

Stanislaw H, Todorov N (1999) Calculation of signal detection theory measures. Behav Res Methods Instrum Comput 31(1):137–149

Staresina BP, Davachi L (2008) Selective and shared contributions of the hippocampus and perirhinal cortex to episodic item and associative encoding. J Cogn Neurosci 20(8):1478–1489

Staresina BP, Gray JC, Davachi L (2009) Event congruency enhances episodic memory encoding through semantic elaboration and relational binding. Cereb Cortex 19(5):1198–1207

Stark SM, Yassa MA, Lacy JW, Stark CE (2013) A task to assess behavioral pattern separation (BPS) in humans: data from healthy aging and mild cognitive impairment. Neuropsychologia 51(12):2442–2449

Summerfield C, Mangels JA (2006) Dissociable neural mechanisms for encoding predictable and unpredictable events. J Cogn Neurosci 18(7):1120–1132

Summerfield C, Greene M, Wager T, Egner T, Hirsch J, Mangels J (2006) Neocortical connectivity during episodic memory formation. PLoS Biol 4(5):e128

Troyer AK, Winocur G, Craik FI, Moscovitch M (1999) Source memory and divided attention: reciprocal costs to primary and secondary tasks. Neuropsychology 13(4):467

Tulving E (2002) Episodic memory: from mind to brain. Annu Rev Psychol 53(1):1–25

Turk-Browne NB, Golomb JD, Chun MM (2013) Complementary attentional components of successful memory encoding. NeuroImage 66:553–562

Uncapher M, Rugg M (2008) Fractionation of the component processes underlying successful episodic encoding: a combined fMRI and divided-attention study. J Cogn Neurosci 20(2):240–254

Uncapher MR, Hutchinson JB, Wagner AD (2011) Dissociable effects of top–down and bottom–up attention during episodic encoding. J Neurosci 31(35):12613–12628

van den Honert RN, McCarthy G, Johnson MK (2017) Holistic versus feature-based binding in the medial temporal lobe. Cortex 91:56–66