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The effects of negative emotion on encoding-related neural activity predicting item and source recognition

Yee Ying Yick [a,b,*], Luciano Grüdtner Buratto [a,c], Alexandre Schaefer [a,d]

[a] University of Durham, UK
[b] Nanyang Technological University, Singapore
[c] University of Brasília, Brazil
[d] Monash University, Malaysia

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ABSTRACT

We report here a study that obtained reliable effects of emotional modulation of a well-known index of memory encoding – the electrophysiological "Dm" effect – using a recognition memory paradigm followed by a source memory task. In this study, participants performed an old–new recognition test of emotionally negative and neutral pictures encoded 1 day before the test, and a source memory task involving the retrieval of the temporal context in which pictures had been encoded. Our results showed that Dm activity was enhanced for all emotional items on a late positivity starting at ~400 ms post-stimulus onset, although Dm activity for high arousal items was also enhanced at an earlier stage (200–400 ms). Our results also showed that emotion enhanced Dm activity for items that were both recognised with or without correct source information. Further, when only high arousal items were considered, larger Dm amplitudes were observed if source memory was accurate. Three main conclusions are drawn from these findings. First, negative emotion can enhance encoding processes predicting the subsequent recognition of central item information. Second, if emotion reaches high levels of arousal, the encoding of contextual details can also be enhanced over and above the effects of emotion on central item encoding. Third, the morphology of our ERPs is consistent with a hybrid model of the role of attention in emotion-enhanced memory (Pottage and Schaefer, 2012).

1. Introduction

It is well-known that emotional memories are richer in details than neutral memories (Grider and Malmberg, 2008; Kensinger and Corkin, 2003; Kensinger and Schacter, 2008b; Ochsner, 2000; Rimmele et al., 2012; Schaefer and Philippot, 2005; Sharot et al., 2007a; Weymar et al., 2009). Existing theoretical models suggest that this effect might be caused by a facilitating effect of emotions on encoding processes, that is, neural processes that create memory traces for novel information (Conway and Pleydell-Pearce, 2000; LeDoux, 1996; Schaefer and Philippot, 2005; Watts et al., 2014). A useful method to examine whether emotional effects on memory depend on encoding processes is provided by the subsequent memory effect, or "Dm" effect ("Differential neural activity based on memory"; Paller and Wagner, 2002). In the classic version of the Dm paradigm, neural activity recorded while participants are studying items is separated according to whether items were remembered or forgotten on a subsequent memory test. The contrast between these two types of brain activity forms the Dm effect, which is generally considered as a neural index of memory encoding (Otten et al., 2006; Paller et al., 1987,1988; Paller and Wagner, 2002; Shimamura and Squire, 1987). Several studies using functional magnetic resonance imaging (fMRI) have used the Dm effect to show that a number of structures (amygdala, hippocampus and prefrontal cortex) are involved in the formation of emotional memories at the encoding stage (Dolcos et al., 2005; Erk et al., 2003; Fenker et al., 2005; Richardson et al., 2004).

Beyond fMRI, the Dm effect has also been studied using the event-related potentials (ERP) technique. These studies have consistently shown that ERPs were more positive for subsequently remembered compared to forgotten pictures (Friedman and Johnson, 2000; Friedman, 1990; Paller et al., 1988; Righi et al., 2012). In addition, results from these studies suggest that different spatio-temporal properties of Dm activity reflect distinct encoding processes. For instance, a commonly observed subtype of the Dm

* Corresponding author at: Division of Psychology, School of Humanities and Social Sciences, Nanyang Technological University, 14 Nanyang Drive, 637332 Singapore, Singapore. Fax: +65 65148393.
E-mail address: belleyick@gmail.com (Y.Y. Yick).

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effect has a frontal topography and an onset around 400 ms. This effect has often been interpreted as reflecting an overt attentional engagement aimed at enhancing the processing of the semantic meaning of information (Paller and Wagner, 2002; Friedman and Trott, 2000; Friedman et al., 1996; Otten and Rugg, 2001; Otten et al., 2007). In the same time window, Dm effects with a centro-parietal distribution have been interpreted as the manifestation of overt attentional processes aimed at the maintenance and processing of visual information in working memory (Otten et al., 2007). In contrast, early Dm effects have also been linked to early perceptual and attentional processes that facilitate memory encoding (Duarte et al., 2004; Mangels et al., 2001; Otten et al., 2007). Finally, late Dm effects (occurring at or after ~800 ms) have also been linked to temporally sustained attentional and cognitive control processes likely to involve working memory (Caplan et al., 2009; Kim et al., 2009; Mangels, et al., 2001; Otten and Rugg, 2001), as well as encoding processes predicting subsequent retrieval demands (Bridger and Wilding, 2010).

The mapping between different Dm subtypes and distinct encoding processes can be particularly useful to disentangle models trying to account for "emotion-enhanced memory" (EEM), that is, the fact that emotional contents are better remembered than neutral contents. There are two main competing models regarding the role of attention in EEM: the first model suggests that emotion modulates encoding through quick, automatic processes largely independent of attention, whereas the other model suggests that overt attention plays a predominant role in the formation of emotional memories (Christianson, 1992; Kern et al., 2005; Pottage and Schaefer, 2012; Talmi et al., 2013). Empirical evidence in favour of the latter comes mainly from eyewitness memory studies in which memory for the details of an emotional scene are impaired if they are distant from the main focus of attention (Christianson and Loftus, 1987; Christianson, 1992; Steblay, 1992). Evidence for the former comes from studies showing that the EEM effect can be observed even when attention resources are depleted at encoding (Kensinger and Corkin, 2004; Kern et al., 2005; Pottage and Schaefer, 2012; Buratto et al., 2014). More recently, hybrid models have been proposed. Pottage and Schaefer (2012) found that an index of overt attention partially mediated the EEM effect, which could suggest that both overt attention and pre-attentive processes may play a role in EEM. These models can lead to specific predictions regarding the Dm effect. Effects of emotion on pre-400 ms Dm activity would be consistent with pre-attentive models, whereas an emotional modulation of post-400 ms Dm effects would support models emphasising the role of overt attention in EEM. If a hybrid model is true, both early and late Dm effects should be affected by emotion. These predictions are also consistent with a vast literature on ERPs to emotional stimuli in which early ERPs (approximately pre-400 ms) are often thought to reflect stimulus-driven automatic attention to emotional stimuli, whereas later ERPs (such as the "Late Positive Potential", LPP) are seen as reflecting overt attentional processes (Codispoti et al., 2007; Olofsson et al., 2008; Schupp et al., 2006; Walker et al., 2011; Watts et al., 2014). A few studies have investigated the effects of emotion on the electrophysiological Dm effects using recall tasks (Dolcos and Cabeza, 2002; Watts et al., 2014). Overall, these studies indicate that EEM in recall is mainly associated with post-400 ms Dm effects that can also extend beyond 800 ms (Watts et al., 2014), thus suggesting that overt attentional and working memory processes are involved in EEM formation for recall tasks (see also Palomba et al. (1997)). In addition, these recall studies have found that effects of emotion on the Dm effect are mainly due to emotional arousal, as no clear effect of valence (negative vs. positive emotions) has been consistently reported.

However, these recall studies could not answer the question of whether emotions can selectively modulate encoding processes leading to distinct sub-processes of retrieval such as recollection (when an item is retrieved with information about the context in which it was encoded) and familiarity (defined as the retrieval of a studied item without recollection of any information about the context in which it was encoded). These subprocesses are often thought to be the core components of recognition memory (Aggleton and Brown, 1999; Düzel et al., 1999; Mandler, 1980; Mecklinger, 2000; Rugg and Curran, 2007; Yonelinas, 1994; Yonelinas and Parks, 2007) and the question whether emotions can differentially modulate them is not fully settled (Schaefer et al., 2011). Some studies have found that emotion can enhance "source memory" performance (Croucher et al., 2011; D'Argembeau and Van der Linden, 2005; Doerksen and Shimamura, 2001; Murray and Kensinger, 2013). These results suggest that emotion can modulate recollection processes, given that source memory tasks require participants to retrieve information belonging to the context in which a central item has been encoded (Koenig and Mecklinger, 2008; Wilding and Rugg, 1996, 1997; Yick and Wilding, 2014). In addition, studies using subjective indices of recollection (e.g. the "Remember-Know" task; Gardiner and Java, 1993) also tend to show that emotion increases the number of "Remember" judgements in recognition, whereas "Know" judgments are typically unaffected (Ochsner, 2000; Kensinger and Corkin, 2003; Sharot et al., 2004; Dolcos et al., 2005; Rimmele et al., 2011; Schaefer et al., 2011). Contrary to the view that emotions modulate recollection processes at encoding, there are models suggesting that emotion might enhance the encoding strength of central items rather than the encoding of contextual information (e.g. Phelps and Sharot, 2008). This view is supported by data showing that the effects of emotion on memory may cause a trade-off between item and context memory. For instance, results from the field of eyewitness memory research show that the central aspects of an emotional scene tend to be better remembered, whereas memory for more peripheral aspects of the scene are poorer compared to neutral scenes (Christianson, 1992; Easterbrook, 1959). However, it has to be noted that recent research indicates that the effects of emotion on item-context trade-offs are complex and can vary according to multiple factors (Waring et al., 2010).

These questions could be examined through the investigation of the effects of emotion on Dm activity using a recognition task that separates items according to whether they were accompanied or not by the retrieval of the encoding context (i.e. a source memory paradigm). However, the few ERP studies that have tested the effects of emotion on the Dm effect using recognition tasks have yielded contradictory results. For instance, Righi et al., (2012) used an old/new recognition task involving emotional and neutral faces. They found that the Dm effect for fearful faces was larger compared to happy and neutral faces in the 350–600 ms time window. Another study has used realistic emotional scenes (Galli et al., 2011), similar to most of the recall studies mentioned above. However, these authors did not find an emotional enhancement of recognition memory performance, nor did they find an effect of emotion on post-stimulus Dm measures. However, they did report interesting facilitating effects of emotion on pre-stimulus Dm activity. Notably, these two studies did not separate items according to whether they had been retrieved with or without the recollection of contextual information. A previous study investigated ERPs recorded at encoding using a recognition task followed by a source memory procedure (Koenig and Mecklinger, 2008). However, these authors reported an absence of enhancement effects of emotion on source memory performance.

There are multiple potential explanations for the contradictions between Righi et al. (2012) and the two other studies (Galli et al., 2011; Koenig and Mecklinger, 2008). First, an important difference between these studies is that the face stimuli used in Righi et al.