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TESIS DOCTORAL

The cognitive control of emotional distraction in working memory

From behaviour to functional connectivity

MEMORIA PARA OPTAR AL GRADO DE DOCTOR

PRESENTADA POR

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The cognitive control of emotional distraction in working memory: from behavior to functional connectivity

Thesis submitted by Javier García Pacios to obtain the PhD Degree by Universidad Complutense de Madrid, in accordance with the requirements for the European PhD diploma

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*porque de él aprendí la curiosidad científica y el
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Glossary of abbreviations

ACC	Anterior cingulate cortex
ANOVA	Analysis of variance
AAL	Automated Anatomical Labeling
BDI	Beck Depression Inventory
CVLT	California Verbal Learning Test
DLPFC	Dorsolateral prefrontal cortex
ERF	Event related field
fT	femtoTesla
FDR	False Discovery Rate
fMRI	Magnetic Resonance Imaging
IAPS	International Affective Picture System
IFC	Inferior frontal cortex
ITI	Intertrial interval
LCMV Beamformer	Linearly Constrained Minimum Variance Beamformer
LPC	Lateral parietal cortex
LTL	Lateral temporal cortex
MEG	Magnetoencephalography
MI	Mutual Information
MNI	Montreal Neurological Institute

MPFC	Medial prefrontal cortex
MTC	Medial temporal cortex
ms	Milisecond
WM	Working Memory
OC	occipital cortex
OTC	Occipitotemporal cortex
OFC	Orbitofrontal cortex
PC	Parietal cortex
pT	picoTesla
PosFC	Posterior frontal cortex
Rs	Spearman's Rho
SAM	Self-Assessment Manikin
STAI	Spielberger State-Trait Anxiety Inventory for Adults
STAI-T	Spielberger State-Trait Anxiety Inventory for Adults - Trait score
STAI-S	Spielberger State-Trait Anxiety Inventory for Adults - State score
STC	Superior temporal cortex
TAVEC	España-Complutense Verbal Learning Test
VTC	Ventral temporal cortex
VLPFC	Ventrolateral prefrontal cortex

Contents

List of Tables

List of Figures

SPANISH SUMMARY

1.   INTRODUCCIÓN GENERAL

La emoción y la cognición son dos aspectos fundamentales en la vida mental que, aunque se entienden como distintos, están profusamente relacionados entre sí (Dalgleish & Power, 1999; Paul Ekman & Davidson, 1994; Martin & Clore, 2001). Estas abundantes interacciones han generado tradicionalmente un vivo interés en el campo de la psicología cognitiva, de tal manera que áreas específicas de estudio como los vínculos entre la memoria y la emoción, han sido objeto de intensa investigación (e.g. Banich et al., 2009; Christianson, 1992; LeDoux, 1994; Reisberg & Hertel, 2004).

Las interacciones entre memoria y emoción son especialmente interesantes, ya que dan lugar a diferentes consecuencias dependiendo de si la emoción es o no relevante para la tarea en curso. Siguiendo el concepto de "atención motivada" propuesto por Peter J. Lang y colaboradores (Lang, Bradley, & Cuthbert, 1998; Lang, Greenwald, Bradley, & Hamm, 1993), los estímulos emocionales representarían información intensamente ligada a la supervivencia del organismo, como la comida o los depredadores (Anderson & Phelps, 2001; LeDoux, 1996; Ohman, Flykt, & Ludqvist, 2000). Por esta razón, la información emocional tiene un acceso preferente a nuestro

sistema cognitivo y recluta recursos atencionales que mejoran nuestra preparación para procesar dicha información biológicamente relevante (Armony & Dolan, 2002; Bradley et al., 2003; Lang, Bradley, Fitzsimmons, et al., 1998; Mogg, Bradley, de Bono, & Painter, 1997; Morris, Ohman, & Dolan, 1998; Ohman et al., 2000; Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005). En lo que concierne a la memoria, este fenómeno tiende a hacer la información emocional más resistente al olvido, ya que es extremadamente adaptativo recordar dónde crecen los frutos más grandes o qué animales son los más peligrosos. La investigación de laboratorio en Psicología ha demostrado que la información emocional se recuerda mejor que la información no emocional (Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Dietrich et al., 2001; E. B. Jones, O'Gorman, & Byrne, 1987; Kensinger, 2007; Ochsner, Krou, Dobbins, & Lazzara, 2000; Schmidt & Williams, 2001) pero, ¿qué sucede cuando la información emocional no es relevante para la tarea en la que uno está involucrado? En tales circunstancias, nuestra predisposición natural a procesar profundamente la información emocional convierte estos elementos en fuertes interferencias que compiten con la información relevante, provocando un deterioro en el desempeño de la tarea (Anticevic, Repovs, & Barch, 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos, Diaz-Granados, Wang, & McCarthy, 2008; Dolcos & McCarthy, 2006).

No existen muchos estudios que hayan explorado el efecto perjudicial de los estímulos emocionales en el mantenimiento de la información no emocional en memoria a corto plazo. El método más habitual ha recurrido a paradigmas de reconocimiento demorado en memoria operativa (MO), en los que los participantes tienen que memorizar diferentes tipos de material no emocional y mantenerlo en memoria mientras se presentan estímulos emocionales (Anticevic et al., 2010; Chuah et

al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013a, 2008; Dolcos, Kragel, Wang, & McCarthy, 2006; Iordan, Dolcos, Denkova, & Dolcos, 2013; Oei et al., 2011). En general, los resultados muestran que los distractores emocionales desagradables pueden afectar el mantenimiento de elementos no emocionales en MO (Anticevic et al., 2010; Chuah et al., 2010; Dolcos & McCarthy, 2006; Oei et al., 2011), de acuerdo con la idea introducida anteriormente: si un estímulo para el que estamos biológicamente predeterminados a no ignorar (es decir, los estímulos emocionales) se presenta en el contexto de una tarea de MO, funcionará como una potente interferencia y perjudicará la recuperación de la información relevante más que otras interferencias no emocionales. Sin embargo, otros estudios no han encontrado este efecto perjudicial a nivel global, sino sólo en subgrupos de participantes (Dolcos et al., 2008; Iordan, Dolcos, & Dolcos, 2013) o en los ensayos en los que los voluntarios estaban más seguros de su respuesta (Denkova et al., 2010). Estas discrepancias se han atribuido a diferencias individuales en impulsividad atencional (Dolcos et al., 2008) y en procesamiento emocional (Denkova et al., 2010), si bien las posibles diferencias en mecanismos generales de control cognitivo que podrían explicar dichas diferencias, no han sido aún evaluadas.

Siguiendo la lógica que postula que los estímulos emocionales funcionan como poderosas interferencias, ya que representan información biológicamente relevante, los estímulos emocionalmente agradables también producirían niveles equivalentes de interferencia en MO. De hecho, algunos autores han sugerido que los estímulos altamente activantes, independientemente de si son agradables o desagradables, pueden reclutar más recursos atencionales (de Oca, Villa, Cervantes, & Welbourne, 2012; Lang, Bradley, Fitzsimmons, et al., 1998) que elementos neutros. Sin embargo, el

efecto real de los distractores emocionales con valencia positiva en el mantenimiento en MO no se ha abordado todavía.

Durante la última década, varios estudios de neuroimagen han utilizado la Imagen por Resonancia Magnética funcional (fMRI) para estudiar los mecanismos neurales que subyacen al control cognitivo de la distracción emocional. Una parte importante de estos experimentos ha identificado un patrón de actividad diferenciado entre la superficie más dorsal del cerebro, incluyendo la corteza prefrontal dorsolateral (DLPFC) y la corteza parietal lateral (LPC), que tradicionalmente se han relacionado con el funcionamiento ejecutivo y la MO (Berryhill & Olson, 2008; D'Esposito, Postle, & Rypma, 2000; Derrfuss, Brass, & von Cramon, 2004; Koenigs, Barbey, Postle, & Grafman, 2009; Nee et al., 2013; Smith & Jonides, 1999), y las áreas ventrales del cerebro, incluyendo la corteza orbitofrontal (OFC), la corteza prefrontal ventrolateral (VLPFC) , la corteza occipitotemporal (OTC) y la amígdala , que tradicionalmente se han relacionado con el procesamiento emocional y la regulación de las emociones (Davidson & Irwin, 1999; Kober et al., 2008; Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012; Phan, Wager, Taylor, & Liberzon, 2002). Los distractores desagradables parecen disminuir la actividad cerebral de áreas dorsales/ejecutivas del cerebro mientras que simultáneamente, aumentan la actividad en regiones ventrales/emocionales. En resumen, los distractores desagradables parecen incrementar las influencias ascendentes de las regiones ventrales/emocionales sobre las áreas dorsales/ejecutivas del cerebro, reasignando recursos atencionales hacia los estímulos emocionales y afectando negativamente el rendimiento en MO (ver Dolcos et al., 2011 para una revisión).

Sin embargo, nuestro sistema cognitivo y más específicamente nuestra MO, no se afecta constantemente cada una de las veces que nos enfrentamos a un distractor emocional, de tal manera que nuestro sistema cognitivo debe contar con mecanismos de control eficaces para anular la interferencia emocional. De hecho, regiones específicas parte de estos sistemas dorsal/ejecutivo y ventral/emocional, a saber, la VLPFC y la DLPFC se han encontrado involucradas en el control efectivo de la distracción emocional en MO (Anticevic et al., 2010; Denkova et al., 2010; Dolcos et al., 2013a, 2006).

Mientras que la literatura neurocientífica en este campo ha proporcionado información sustancial sobre las regiones particulares del cerebro implicadas en el control cognitivo de distracción emocional en MO, la dinámica temporal de dicha actividad neural no ha sido explorada, aun cuando este enfoque proporcionaría información muy valiosa acerca de la naturaleza exacta de este proceso cognitivo.

Por otra parte, hoy en día existe un amplio consenso en la idea de que el cerebro humano no funciona como un sistema modular, en el que cada función está relativamente localizada en un sector específico. En su lugar, nuestro comportamiento emerge del funcionamiento integral de redes complejas y dinámicas ampliamente distribuidas en el cerebro (ver Sporns, 2011 para un intoductión al concepto de las redes del cerebro).

El mantenimiento activo de información se ha descrito como el resultado de la actividad sincronizada y sostenida de grupos locales de neuronas, así como de redes funcionales ampliamente distribuidas en el cerebro (Fuster & Alexander, 1971; Goldman-Rakic, 1990; Miller, 1996). En particular, estudios recientes han señalado que

el acoplamiento funcional a larga distancia entre áreas frontales y posteriores sería un mecanismo clave en el mantenimiento de información en MO (Gazzaley, Rissman, & D'Esposito, 2004; Palva, Monto, Kulashekhar, & Palva, 2010; Rissman, Gazzaley, & D'Esposito, 2004, 2008; Sarnthein, 1998; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005).

Varios estudios han explorado el efecto de la distracción no emocional en las redes cerebrales funcionales de la MO, centrándose en la corteza prefrontal y las áreas posteriores del cerebro. Este enfoque se basa en la extensa literatura que vincula la corteza fronto-parietal a los procesos de mantenimiento activo en MO (e.g. Curtis & D'Esposito, 2003; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000) y las áreas occipito-temporales a la formación de la representación sensorial del estímulo en la MO visual (e.g. Desimone, 1998; Fuster, 1990; Miyashita, 2000). Mediante este procedimiento, estudios recientes han descrito alteraciones en el grado de conectividad funcional entre la corteza prefrontal y la corteza sensorial posterior debidas a la aparición de elementos distractores, y que dichas alteraciones pueden restaurarse tras la presentación del distractor para conseguir un desempeño correcto en MO (Clapp, Rubens, & Gazzaley, 2010; Clapp, Rubens, Sabharwal, & Gazzaley, 2011; Yoon, Curtis, & D'Esposito, 2006).

A pesar de estas evidencias, muy pocos trabajos han utilizado medidas de conectividad funcional en el estudio de las dinámicas cerebrales implicadas en el control de la distracción emocional, y todos ellos han limitado sus análisis a las conexiones concretas entre la amígdala y la corteza prefrontal (Chuah et al., 2010; Clarke & Johnstone, 2013; Dolcos et al., 2006), sin explorar las redes posteriors relacionadas con

el mantenimiento de información en MO (e.g. Corbetta, Kincade, & Shulman, 2002; Todd & Marois, 2004).

La motivación de la presente serie de estudios es la de contribuir a llenar los vacíos de la literatura existente en relación con el control cognitivo de distracción emocional en MO. Para lograr este objetivo, se comenzó con dos experimentos conductuales con la intención de replicar resultados previos, explorar el efecto de los estímulos agradables como distractores y aclarar el papel de las diferencias individuales en los mecanismos de control cognitivo que limitan la distracción emocional en MO. En el siguiente estudio, recurrimos a la magnetoencefalografía (MEG) para investigar la dinámica espacio-temporal de los mecanismos cerebrales que nos permiten controlar la distracción emocional agradable y desagradable. Por último, utilizamos medidas de conectividad funcional para analizar la dinámica de las redes funcionales cerebrales que sostienen los procesos cognitivos de mantenimiento activo en MO, durante la distracción emocional.

2.   OBJETIVOS E HIPÓTESIS GENERALES

2.1.   Primer estudio

En este estudio se diseñó una tarea de MO en la que los elementos relevantes para la tarea fueron caras neutrales, mientras que los distractores fueron imágenes emocionales y no emocionales irrelevantes para la tarea, con el fin de explorar el efecto de los distractores tanto agradables como desagradables en el mantenimiento en MO. Si los efectos perjudiciales de la distracción desagradable se deben a la relevancia biológica de estos estímulos y a nuestra predisposición natural para procesarlos

profundamente, otro tipo de estímulos biológicamente relevantes, como los eventos agradables, debería afectar el rendimiento de forma similar. También se estudió el efecto potencial de la distracción emocional y no emocional, en comparación con un mantenimiento de información sin interferencia, añadiendo una cuarta condición al diseño original, en la que no se presentó ningún estímulo distractor. Por último, se evaluó la capacidad individual de control inhibitorio en memoria, mediante el uso de una prueba neuropsicológica estandarizada. Si la inhibición cognitiva y la capacidad de resolución de interferencia son los procesos clave implicados en el control de la distracción, los participantes con las puntuaciones más altas en esta capacidad mostrarían una mayor precisión y unos tiempos de reacción más cortos en la fase de reconocimiento.

2.2.   Segundo estudio

En el segundo estudio se utilizó una tarea de MO muy similar a la empleada en el primer estudio, y la implementamos en un experimento de MEG. El objetivo principal de este estudio fue desvelar los perfiles espaciotemporales de la actividad cerebral que subyace a los mecanismos de control cognitivo involucrados en la resistencia a la distracción emocional. En base a la evidencia previa que muestra procesamiento temprano de los estímulos emocionales (Batty & Taylor, 2003; Bradley et al., 2003; Carretié, Hinojosa, Martín-Loeches, Mercado, & Tapia, 2004; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005), postulamos que los estímulos emocionales aumentarán la respuesta cerebral en las latencias tempranas del procesamiento de la distracción. Dado que dicha activación temprana se ha descrito en tareas perceptuales, en las que los estímulos emocionales no tienen que ser controlados, postulamos también que el

control efectivo de los distractores emocionales ocurrirá más tarde en el procesamiento, y que dicho control cognitivo estará relacionado con una mayor activación de las cortezas prefrontales. Por último, y basándonos en los resultados obtenidos en el primer estudio sugerimos que las diferencias entre el control cognitivo de distracción agradable y la desagradable serán también evidentes a nivel de la actividad cerebral.

2.3.   Tercer estudio

En el tercer estudio se recurrió al análisis de la conectividad funcional en los datos obtenidos en el segundo estudio para determinar el efecto potencial de la distracción emocional en las dinámicas de conectividad funcional que han sido observadas en el mantenimiento en MO. En base a la literatura existente que muestra que la interrupción no emocional puede alterar transitoriamente las conexiones fronto-posteriores (Clapp et al., 2010, 2011; Yoon et al., 2006) esperamos que dicha red se afecte más debido a la distracción emocionales que debido a la distracción neutra. De acuerdo con la extensa literatura que vincula la VLPFC con el éxito en el control de la distracción emocional (Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013, 2006; Iordan et al., 2013) esperamos también que esta región prefrontal esté fuertemente conectada con regiones posteriores.

3.   DISCUSIÓN GENERAL

En la Introducción general revisamos la literatura existente en relación con el control cognitivo de la distracción emocional en MO, desde el nivel conductual hasta los enfoques más avanzados consistentes en la aplicación de métodos de conectividad funcional en el estudio de las redes dinámicas que sustentan dicho proceso cognitivo. Nuestra revisión identificó varias lagunas en el conocimiento actual acerca de cómo

nuestro sistema cognitivo se ve afectado por los distractores emocionales, y cómo es capaz de anular este efecto, con el fin de llevar a cabo distintas tareas en el día a día.

A nivel conductual, parece estar claro que los distractores desagradables pueden comportarse como potentes interferencias en la MO debido a su relevancia biológica, aunque el efecto de otro tipo de estímulos ligados a la supervivencia no se ha abordado todavía. En nuestro Primer Estudio replicamos resultados previos que muestran que la distracción desagradable afecta al mantenimiento de elementos no emocionales en MO (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008; Dolcos & McCarthy, 2006). Sin embargo, los distractores agradables no produjeron mayores tasas de olvido que los neutros, como cabría esperar, ya que también representan una información muy importante para nuestra supervivencia (e.g. alimentos). Por tanto, si tanto los estímulos agradables como los desagradables son relevantes para la supervivencia y tienden a ser procesado de forma preferente (Armony & Dolan, 2002; Mogg et al., 1997; Ohman, Flykt, & Esteves, 2001), ¿por qué sólo los distractores desagradables funcionan como potentes interferencias en el mantenimiento de otros elementos en la memoria a corto plazo, mientras que los distractores agradables comportan como los neutros? En la sección de Discusión y conclusiones de ese Estudio argumentamos que la razón por la que estamos preparados para prestar atención y procesar profundamente los estímulos emocionales está relacionada probablemente con las posibles consecuencias de ignorar esos estímulos. Así, si no prestamos atención a un animal peligroso nuestra supervivencia se pone en peligro de forma inmediata. Sin embargo, si ignoramos los alimentos o los estímulos relacionados con la reproducción, nuestra supervivencia se verá comprometida en el medio o largo plazo. Por tanto, es razonable pensar que nuestro control ejecutivo puede

controlar por un momento la respuesta atencional provocada por los estímulos agradables, si estamos realizando otra tarea relevante, ya que nuestra supervivencia no se pone inmediatamente en riesgo (Ekman, 1992; Ohman, 1992). De esta manera, podemos beneficiarnos del resultado de realizar con éxito la tarea actual, sin comprometer nuestra supervivencia. Por el contrario, también es lógico que nuestro control inhibitorio sea bloqueado y no pueda controlar las respuestas atencionales provocadas por los estímulos desagradables, ya que esto podría poner en peligro inmediato nuestra supervivencia sólo por un beneficio secundario potencial. Los análisis posteriores confirmaron esta idea, ya que la capacidad individual de resistencia a la interferencia en MO correlacionó positivamente con el rendimiento después de la distracción neutra y agradable, pero no después de la distracción desagradable.

En lo que respecta a la actividad cerebral, varios estudios han proporcionado información sustancial sobre las regiones particulares del cerebro implicadas en el control cognitivo de la distracción emocional en MO (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013b, 2008, 2006; Iordan, Dolcos, Denkova, et al., 2013), mostrando que la distracción emocional desagradable puede producir una disminución de actividad en áreas del cerebro dorsales/ejecutivas mientras que aumenta la actividad en las regiones ventrales/emocionales corticales y subcorticales. Esta disociación se ha interpretado como un incremento de las influencias ascendentes desde las áreas ventrales/emocionales del cerebro hasta las regiones dorsales/ejecutivas, que reasigna los recursos atencionales perjudicando el rendimiento en MO (ver Dolcos et al., 2011 para una revisión). Además, estos estudios han puesto de relieve las regiones específicas tanto en el sistema dorsal/ejecutivo como en el ventral/emocional, a saber,

la VLPFC y la DLPFC , que estarían críticamente involucradas en el control efectivo de la distracción emocional en MO (Anticevic et al., 2010; Denkova et al., 2010; Dolcos et al., 2013a, 2006).

En el Segundo Estudio exploramos la dinámica temporal de la actividad neuronal que sustenta nuestra capacidad de hacer frente a la distracción emocional, con el fin de comprender la naturaleza exacta de este proceso cognitivo altamente adaptativo. Nuestros resultados revelaron que mecanismos prefrontales se reclutan a latencias muy tempranas del procesamiento distractor, permitiendo la rápida detección de la distracción emocional agradable y desagradable. En etapas posteriores del procesamiento, los distractores desagradables iniciaban un mecanismo específico de control cognitivo dependiente de la actividad de la DLPFC, la MPFC y la OFC, para un control efectivo de la distracción. La especificidad de este mecanismo en la distracción desagradable coincide con los resultados conductuales de nuestro primer estudio, ya que en aquél se obtuvieron mayores tasas de olvido para la distracción desagradable que para la distracción tanto neutra como agradable. Por lo tanto, es razonable pensar que necesitaríamos un mecanismo específico de control cognitivo de alto orden para anular la potente interferencia que supone la distracción desagradable.

A pesar de la creciente evidencia sobre los mecanismos cerebrales que nos permiten hacer frente a la distracción emocional, muy pocos experimentos han investigado el efecto de este tipo de distracción en las redes cerebrales funcionales de la MO, a pesar de la reciente evidencia que sugiere que las conexiones funcionales de largo alcance entre la corteza frontal y las áreas posteriores son un mecanismo clave para el mantenimiento de la información en MO (Gazzaley, Rissman, & D'Esposito, 2004;

Palva, Monto, Kulashekhar, & Palva, 2010; Rissman, Gazzaley, & D'Esposito, 2004, 2008; Sarnthein, 1998; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005). De hecho , sólo tres trabajos han aplicado métodos de conectividad funcional en este campo y todos ellos han limitado su análisis a las conexiones particulares entre la amígdala y la corteza prefrontal (Chuah et al., 2010; Clarke & Johnstone, 2013; Dolcos et al., 2006), dejando a un lado las redes corticales posteriores que sabemos participan en el mantenimiento en MO (e.g. Corbetta, Kincade, & Shulman, 2002; Todd & Marois, 2004).

En el tercer estudio aplicamos un análisis de conectividad funcional a los datos recogidos en el segundo estudio con el fin de estudiar los posibles efectos de la distracción emocional en las redes corticales fronto-posteriores que han sido relacionadas con el mantenimiento activo de información en MO. Nuestros resultados mostraron que los estímulos emocionales producen una interrupción temprana y transitoria del componente parieto-temporal de la red fronto-posterior descrito anteriormente. Dicha interrupción se encontró en la misma latencia en el que se detectan los distractores emocionales, como se observó en el segundo estudio, lo que indica que esta detección temprana provoca inmediatamente una perturbación de la red fronto-posterior en Mo. Sin embargo, y de acuerdo con la literatura anterior (Clapp et al., 2010, 2011), dicha interrupción se restablecía para obtener un rendimiento conductual adecuado. Por otra parte, ambos distractores emocionales incrementaron el grado de acoplamiento funcional entre la VLPFC-OFC derecha y la corteza parieto-temporal, a una latencia de procesamiento relativamente temprana. En el caso de la condición de distracción emocional desagradable, este acoplamiento también fue crucial para un buen rendimiento en MO y se acompañó de un mayor grado de acoplamiento entre el DLPFC y el PC. Este resultado en concreto, se observó

exclusivamente en la condición desagradable, siendo consistente con los resultados conductuales de nuestro primer estudio y la actividad cerebral obtenida en nuestro segundo estudio. De forma interesante, los resultados de este tercer estudio sugieren que el control cognitivo efectivo de la distracción emocional puede comenzar incluso antes de lo reportado en el segundo estudio, y que este mecanismo rápido y sutil podría basarse en el acoplamiento funcional de largo alcance.

En resumen, la presente serie de estudios ha investigado por primera vez los mecanismos cognitivos de control de la distracción emocional, comenzando a un nivel conductual, explorando los perfiles espacio-temporales de la actividad cerebral y, finalmente, investigando los cambios dinámicos de las redes cerebrales funcionales que los sustentan.

4.   CONCLUSIONES GENERALES

La presente serie de estudios demuestra que los estímulos desagradables afectan al mantenimiento de la información no-emocional cuando no son relevantes para la tarea en curso. Al mismo tiempo, estos estudios muestran por primera vez que la interferencia agradable no afecta necesariamente la MO, como lo hace la interferencia desagradable. Estos resultados indican que no todos los eventos emocionales pueden distraernos cuando estamos inmersos en una tarea relevante, ya que nuestro sistema cognitivo parece ser capaz de resistir los distractores agradables tan bien como los eventos no-emocionales.

La relación entre el rendimiento en la tarea y la capacidad individual de resolución de interferencia en MO sugiere que la inmediatez de las consecuencias de

ignorar la información emocional irrelevante es el aspecto clave que permite o no a nuestro control ejecutivo anular la respuesta de atencional. En otras palabras, nuestro control cognitivo es capaz de inhibir nuestra tendencia a prestar atención a los acontecimientos agradables, ya que nuestra supervivencia no se verá comprometida inmediatamente. Sin embargo, no somos capaces de resistir la captura atencional provocada por eventos aversivos, ya que al hacerlo, pondremos en peligro nuestra supervivencia a muy corto plazo.

Nuestra exploración de los mecanismos cerebrales implicados en el procesamiento de eventos emocionales irrelevantes muestra que la corteza prefrontal se activa a latencias muy tempranas del procesamiento del distractor, lo que permite la detección rápida de las distracciones emocionalmente agradables y desagradables. Sin embargo, estas áreas prefrontales están también involucradas en el control cognitivo de la distracción emocional, más tarde en el procesamiento. Curiosamente, el control de los eventos desagradables requiere de una mayor actividad en la DLPFC, la MPFC y la OFC, en concordancia con la mayor dificultad en el control de dichos eventos a nivel conductual.

Hoy en día sabemos que el mantenimiento activo de información no es sólo el resultado de la actividad neuronal en regiones cerebrales concretas, sino que está sostenido por la actividad sincronizada de redes funcionales, ampliamente distribuidas por todo el cerebro. Nuestro análisis de conectividad funcional muestra que la detección temprana de la distracción emocional produce una interrupción transitoria de un importante centro de la red fronto-posterior que contribuye a sostener el mantenimiento de información en MO. A pesar de ello, la conectividad funcional entre

la corteza prefrontal y el OC se intensifica durante la detección temprana de distractores desagradables, ya que éstos contienen información potencialmente amenazante.

En consonancia con nuestro análisis de la actividad regional, el control cognitivo de la distracción emocional se produce más tarde en el procesamiento. En este punto, la red fronto-posterior se restablece para lograr una ejecución adecuada, mientras que la CPFVL-OFC derecha y las cortezas posteriores se vuelven conectan fuertemente como mecanismo de control de la distracción emocional.

En contra de la idea popular sobre el efecto de la emoción en la cognición, este trabajo revela por primera vez que cualquier tipo de información emocional no es capaz de afectar nuestra capacidad para mantenernos focalizados en asuntos importantes. Aunque la mayor parte de las veces podemos hacer frente a la mayoría de los distractores emocionales, los acontecimientos desagradables son más difíciles de controlar y afectan a nuestro rendimiento cognitivo con más frecuencia que los agradables o neutras. Nuestros resultados también ponen de manifiesto dos mecanismos diferentes que son la base de nuestra capacidad para resistir el efecto negativo de la distracción emocional. En primer lugar, tenemos que detectar la potencial importancia biológica de los eventos distractores, ya que estar preparado para procesarlos es altamente adaptativo. Este mecanismo se sustenta en la corteza prefrontal, aunque dicha detección temprana induce también una interrupción de la red cerebral funcional que sustenta la información relevante para la tarea en curso. Una vez detectada, la corteza prefrontal contribuye a controlar dicha distracción emocional por medio de una mayor actividad local, así como por medio de intensas conexiones funcionales con cortezas posteriores del cerebro.

5.   LIMITACIONES Y LÍNEAS FUTURAS DE INVESTIGACIÓN

En esta serie de estudios hemos explorado nuestra capacidad de hacer frente a los eventos emocionales que pueden distraernos mientras estamos manteniendo en mente información relevante, partiendo del nivel conductual hasta llegar a las bases neurales de dicha capacidad, ya sea usando un enfoque tradicional basado en activaciones cerebrales regionales o una metodología más innovadora que permite estudiar cómo áreas distantes del cerebro trabajan juntas. A pesar de los resultados obtenidos en los diferentes niveles de análisis, todavía hay algunas cuestiones relevantes que la investigación futura debería abordar.

Nuestro primer estudio se basó en el concepto de atención motivada, y por lo tanto, asumimos que ambos tipos de estímulos emocionales reclutarían recursos atencionales en un mismo grado. Sin embargo, es posible que las diferencias entre los distractores agradables y desagradables se debieran a diferencias en la captura atencional que producen. Esta hipótesis podría ser sometida a prueba si los voluntarios procesaran cada tipo de distractor con la misma profundidad. Para lograr este objetivo, podría pedirse a los participantes que evalúen algunos aspectos de los distractores, por ejemplo, si la escena representada en la imagen se lleva a cabo en interiores o al aire libre. Si los voluntarios llevan a cabo esta tarea secundaria igualmente bien en todos los tipos de distracción, podríamos estar seguros de que están prestando atención por igual a todos los distractores y por tanto, las diferencias entre condiciones no podrían atribuirse a las diferencias en captura atencional.

En el segundo estudio, utilizamos un análisis de correlación para explorar la relación entre la actividad cerebral y la conducta. Aunque se trata de una estrategia

común, la manera más robusta de abordar este problema habría consistido en comparar la actividad cerebral durante los aciertos y los fallos. Sin embargo, el número limitado de ensayos de error en nuestro experimento nos impidió la reconstrucción de fuentes para los datos correspondientes. Investigaciones futuras deberían aumentar el número total de ensayos para tratar de obtener datos suficientes a partir de los errores.

Por último, en nuestro Tercer Estudio, exploramos la conectividad funcional a larga distancia en una banda de frecuencias ancha. Dado que éste es el primer estudio que explora las dinámicas de conectividad funcional que sustentan nuestra capacidad para hacer frente a la distracción emocional, decidimos centrarnos en las tres ventanas temporales en las que surgieron diferencias significativas entre los distintos tipos de distractores, a nivel de la actividad cerebral. Así pues, decidimos también usar el mismo rango de frecuencias que en el Segundo Estudio, con el fin de mantener consistentes ambos análisis. Sin embargo, cada vez más evidencia sugiere que bandas de frecuencia específicas, p.e. la banda alfa, pueden estar fuertemente relacionadas con los procesos inhibitorios que se suponen involucrados en nuestra capacidad para hacer frente a cualquier tipo de evento distractor. Estudios futuros deberían analizar las diferentes bandas de frecuencia para desvelar la contribución potencial de cada ritmo a nuestra capacidad de controlar la distracción emocional.

GENERAL INTRODUCTION

Emotion and cognition are two primary concepts in human mental life that are understood as distinct though profusely interrelated (Dalgleish & Power, 1999; Paul Ekman & Davidson, 1994; Martin & Clore, 2001). These rich interactions have traditionally brought about a vivid interest in cognitive psychology, in such a way that specific areas of study such as bonds between memory and emotion, have been object of an intense research (e.g. Banich et al., 2009; Christianson, 1992; LeDoux, 1994; Reisberg & Hertel, 2004).

Interactions between memory and emotion are especially intriguing, as they give rise to different consequences depending on whether the emotion is relevant for the ongoing task or not. Under the concept of "motivated attention" proposed by Peter J. Lang and colleagues (Lang, Bradley, & Cuthbert, 1998; Lang et al., 1993), emotional stimuli represent information that is intensely linked to the survival of the organism, like food or predators (Anderson & Phelps, 2001; LeDoux, 1996; Ohman et al., 2000). For this reason, emotional information have preferential access to our cognitive system and recruit attentional resources that improve our preparation to process such biologically relevant information (Armony & Dolan, 2002; Bradley et al., 2003; Lang, Bradley,

Fitzsimmons, et al., 1998; Mogg et al., 1997; Morris et al., 1998; Ohman et al., 2000; Sabatinelli et al., 2005). When talking about memory, this phenomenon tends to make emotional information more resistant to forgetting, since it is highly adaptive to remember where the biggest fruits grow up and what animals are the most dangerous. In the laboratory, much psychological research has demonstrated that emotional information is better remembered that non-emotional information (Canli et al., 2000; Dietrich et al., 2001; E. B. Jones et al., 1987; Kensinger, 2007; Ochsner et al., 2000; Schmidt & Williams, 2001) but, what happens when the emotional information is not relevant for the particular business in which you are involved? In such circumstances, our natural predisposition to deeply process the emotional information turns these elements into strong interferences that compete with the actual relevant information and provoke a worsening in the performance of the current task (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008; Dolcos & McCarthy, 2006).

To our knowledge, not many studies have explored the detrimental effect of emotional stimuli on the maintenance of non-emotional information in short-term memory. The most usual approach has leant on delayed-recognition working memory (WM) paradigms, in which participants have to memorize different types of non-emotional materials and maintain them in memory while emotional stimuli are presented (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013a, 2008, 2006; Iordan, Dolcos, Denkova, et al., 2013; Oei et al., 2011). The general finding shows that unpleasant emotional distractors may affect the maintenance of non-emotional elements in WM (Anticevic et al., 2010; Chuah et al., 2010; Dolcos & McCarthy, 2006; Oei et al., 2011), which would be in accordance with the idea previously introduced: if a stimulus for which we are biologically

predetermined to not ignore (i.e. emotional stimuli) is presented within a WM task, it will work as a powerful interference and will impair the recovery of relevant information more than other non-emotional interferences. However, some other studies have not showed such a detrimental effect in their whole samples, but only in subsets of participants (Dolcos et al., 2008; Iordan, Dolcos, & Dolcos, 2013) or in trials in which their volunteers were more confident about their response (Denkova et al., 2010). These discrepancies have been ascribed to individual differences in attentional impulsiveness (Dolcos et al., 2008) and in emotional processing (Denkova et al., 2010), although potential differences in general cognitive control mechanisms that might account for such differences has not been assessed yet.

Following the rationale that posit that emotional stimuli work as powerful interferences because they represent biologically relevant information, pleasant emotional stimuli would also produce equivalent levels of interference in WM. Indeed, some authors have suggested that higher levels of arousal in the stimulus, regardless of whether it is pleasant or unpleasant, can recruit more attentional resources (de Oca et al., 2012; Lang, Bradley, Fitzsimmons, et al., 1998) than neutral elements. However, the actual effect of positively valenced emotional distractors in WM maintenance has not been addressed and it remains unexplored.

Over the last decade, several neuroimaging studies have used functional Magnetic Resonance (fMRI) to explore the neural mechanisms that underlie the cognitive control of emotional distraction. A significant part of these experiments have identified a dissociable pattern of activity between the dorsal surface of the brain, including the dorsolateral prefrontal cortex (DLPFC) and the lateral parietal cortex (LPC),

traditionally been related to executive functioning and WM (Berryhill & Olson, 2008; D'Esposito et al., 2000; Derrfuss et al., 2004; Koenigs et al., 2009; Nee et al., 2013; Smith & Jonides, 1999), and ventral brain areas, including the orbitofrontal cortex (OFC), the ventrolateral prefrontal cortex (VLPFC), the occipitotemporal cortex (OTC) and the amygdala, traditionally involved in emotional processing and emotional regulation (Davidson & Irwin, 1999; Kober et al., 2008; Lindquist et al., 2012; Phan et al., 2002). Unpleasant distractors seems to decrease the brain activity over dorsal/executive brain areas while, simultaneously, increases activity in ventral/emotional regions. In short, unpleasant distractors seem to enhance bottom-up influences from ventral/emotional to dorsal/executive brain areas, reallocating attentional processes in favor of emotional stimuli and deploying WM performance (see Dolcos et al., 2011 for a review).

Nevertheless, cognition and more specifically WM, is not consistently depleted by every single emotional distractor, in such a way that our cognitive system must have control mechanisms for overriding emotional the interference. Indeed, specific regions over both the ventral/emotional and the dorsal/executive dissociable systems, i.e. the VLPFC and DLPFC have been found critically involved in successful coping with emotional distraction in WM (Anticevic et al., 2010; Denkova et al., 2010; Dolcos et al., 2013a, 2006).

Whereas the neuroscientific literature in this field has provided substantial information about the particular brain regions involved in the cognitive control of emotional distraction in WM, the temporal dynamics of such neural activity has not been explored, though this approach would surely provide valuable information about the exact nature of cognitive process.

On the other hand, nowadays it is widely accepted that the human brain does not work as a modular system, in which every single function is relatively well located in a specific sector. Furthermore, the our complex behavior emerges from the integrative functioning of complex and dynamic networks widely distributed across the brain (see Sporns, 2011 for a comprehensive intoduction to the concept of brain networks).

Active maintenance of information has been described as a result of synchronized and sustained activity within local groups of neurons and over functional networks widely distributed across the brain (Fuster & Alexander, 1971; Goldman-Rakic, 1990; Miller, 1996). In particular, recent studies have pointed out to long-range functional coupling between frontal and posterior areas as the key mechanism for maintaining information in WM (Gazzaley et al., 2004; Palva et al., 2010; Rissman et al., 2004, 2008; Sarnthein, 1998; Sauseng et al., 2005).

Several studies have explored the effect of non-emotional distraction on functional brain networks of WM by focusing on the prefrontal cortex and the posterior areas of the brain. Such approach is based on extensive literature that links the fronto-parietal cortex to active maintenance processes in WM (e.g. Curtis & D'Esposito, 2003; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000), and occipito-temporal areas to the formation of sensory representation in visual WM (e.g. Desimone, 1998; Fuster, 1990; Miyashita, 2000). Following this procedure, recent studies have described interference-based disturbances in the functional coupling between the prefrontal cortex and the posterior sensory cortex, and that such disturbances can be restored after the presentation of the

interfering stimulus for a successful WM performance (Clapp et al., 2010, 2011; Yoon et al., 2006).

Despite of these evidences, very few papers have applied functional connectivity measures to the study of the brain dynamics involved in overriding emotional distraction, and all of them have limited their analysis to the particular connections between the amygdala and the prefrontal cortex (Chuah et al., 2010; Clarke & Johnstone, 2013; Dolcos et al., 2006), leaving aside posterior cortical networks known to be engaged in WM maintenance (e.g. Corbetta, Kincade, & Shulman, 2002; Todd & Marois, 2004).

The aim of the present series of studies is to contribute to fill in the gaps of the existent literature in regard with the cognitive control of emotional distraction in WM. To accomplish such objective we first proceeded with two behavioral experiments with the intention of replicate previous results, explore the effect of the pleasant stimuli as distractors and clarify the role of individual differences in cognitive control mechanisms of overriding emotional distraction in WM. In a further study, we used Magnetoencephalography (MEG) to investigate the spatio-temporal dynamics of the brain mechanisms that allow us to cope with both pleasant and unpleasant emotional distraction. Finally, we applied functional connectivity measures to analyze the dynamics of the functional brain networks that support the cognitive processes that actively maintain information in WM, in the context of emotional distraction.

GENERAL OBJECTIVES AND HYPOTHESIS

1.   FIRST STUDY

In this study we designed a WM task in which neutral faces were task-relevant items and emotional and non-emotional pictures were task-irrelevant distractors, in order to explore the effect of both pleasant and unpleasant distractors in WM maintenance. If detrimental effects of unpleasant distraction were due to the biological relevance of emotional stimuli and our natural predisposition to deeply process them, other kind of biologically relevant stimuli such as pleasant ones, should affect performance in a similar way. We also studied the potential effect of emotional and non-emotional distraction in comparison with a non-interference scenario, by adding a fourth condition to the original design, in which no stimulus was presented during the maintenance of task-relevant information. Finally, we measured the individual capacity of inhibitory control in memory, by using a standardized neuropsychological test. If cognitive inhibition and interference resolution are the key processes involved in control of distraction, participants with higher scores in this capacity will show higher accuracy and faster reaction times at the recognition stage.

2.   SECOND STUDY

In the Second Study we used a very similar WM task to that employed in the First Study, and implemented it in a MEG experiment. The principal objective of this study was to unravel the spatio-temporal profiles of the brain activity that underlies the cognitive control mechanisms involved in coping with emotional distraction. Based on previous evidence showing an early processing of emotional stimuli (Batty & Taylor, 2003; Bradley et al., 2003; Carretié et al., 2004; Pourtois et al., 2005), we predict that emotional stimuli would increase the brain response at early latencies of distraction processing. Since such an early activation have been reported in perceptual task, in which the emotional stimuli do not have to be controlled, we also hypothesize that the effective overriding of emotional distractors would occur later in the processing, and that such cognitive control would be mediated by higher activation prefrontal cortices. Finally, and based on results from the First Study we posit that differences between the cognitive control of unpleasant and pleasant distraction would appear at the brain activity level.

3.   THIRD STUDY

In the Third Study we applied a functional connectivity analysis to the data collected in the Second Study in order to determine the potential effect of the emotional distraction on the dynamics of functional connectivity that have been observed in WM maintenance. Based on the existent literature showing that non-emotional disruption can transiently disrupt fronto-posterior connections (Clapp et al., 2010, 2011; Yoon et al., 2006) we expect that such network would be more disrupted by emotional distractors than by neutral ones. According with the extensive literature that

links the VLPFC to the successful coping with emotional distraction (Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013, 2006; Iordan et al., 2013) we also hypothesize that this prefrontal region would be highly coupled with posterior areas.

FIRST STUDY

Emotional interference-based forgetting in short-term memory. Cognitive inhibition of pleasant but not unpleasant biologically relevant distractors

1.   INTRODUCTION

Do you remember any situation in which you felt that your memory was disrupted by an emotional event while trying to keep in mind some relevant information? Imagine for example, that you are in a cafe with a friend, having a conversation. At some point, a car collides with a traffic light out in the street. Right after the initial fright you would probably say: "What were we talking about?" That is, you would have forgotten necessary information to pick the talk up.

The effect of emotion on our cognition and behavior is an issue widely addressed by the psychological literature. The wealthy interactions between these "hot" and "cold" systems have attracted widespread attention. In particular, interactions between memory and emotion are especially interesting because of the opposed consequences resulting from emotional information being a relevant part of the current activity (Canli et al., 2000), contrary to when emotional facts are irrelevant for the ongoing task. Emotional stimuli automatically fall into the focus of our attention (Armony & Dolan, 2002; Mogg et al., 1997; Ohman et al., 2001). Such an effect is explained by the biological relevance of emotional stimuli, since they contain information that is

important for survival (e.g. food or predators) (Anderson & Phelps, 2001; LeDoux, 1996; Ohman et al., 2000). The concept of "motivated attention" (Lang, Bradley, & Cuthbert, 1998; Lang et al., 1993) proposes that emotional information seems to have a privileged access to our cognitive system, recruiting attentional resources automatically and improving our preparation to process them (Bradley et al., 2003; Lang, Bradley, Fitzsimmons, et al., 1998; Morris et al., 1998; Sabatinelli et al., 2005). This phenomenon usually brings about more adaptive responses since we can easily and accurately remember crucial information for survival. Many laboratory studies have reported enhanced memory for emotional pictures (Canli et al., 2000), emotional word-lists (Dietrich et al., 2001; E. B. Jones et al., 1987) or memory for humor (Schmidt & Williams, 2001). However, there are other situations in which the most adaptive behavior consists precisely in ignoring emotional information, for example to accomplish a more immediate goal. It is in these circumstances when the biological salience of emotional stimuli and our natural predisposition to deeply process them turn them into powerful interferences that compete with relevant information for cognitive resources (Ellis & Ashbrook, 1988). This finally results in a worsening of performance of the current task (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008; Dolcos & McCarthy, 2006).

Detrimental effects of emotional interference on working memory (WM) for non-emotional materials provide an opportunity to explore limits of cognitive inhibition in memory control. The impact of non-emotional interference in WM has been largely explored, leading to several interpretations about the interference-based forgetting in short-term memory, such as process-based interference (Barrouillet, Bernardin, & Camos, 2004; Jolicoeur & Dell'Acqua, 1998), interference by superposition (Farrell &

Lewandowsky, 2002), interference by feature overwriting (Nairne, 1990; Oberauer & Kliegl, 2006) and interference by retrieval confusion (Wixted, 2004). However, there is no much information about how cognitive inhibition helps us to ignore stimuli for which evolution has prepared us to pay attention to, in the context of WM.

To our knowledge, few studies have addressed the issue of interference-based forgetting in short-term memory due to the appearance of emotional distractors during the maintenance of non-emotional information. Dolcos and colleagues have conducted a series of studies using several modifications of the same WM task, developed for fMRI experiments. In an early study (Dolcos & McCarthy, 2006), they used a delayed-recognition WM task with sets of three human faces as items to be memorized and pictures depicting unpleasant emotional scenes, pictures depicting neutral scenes and digitally scrambled versions of these pictures as distractors presented during the delay interval. The worst recognition scores were associated with the appearance of unpleasant distractors. Accuracy was also lower for neutral than for scrambled distractors. These results seem to be in accordance with interference-based forgetting theories (Berman, Jonides, & Lewis, 2009) since the introduction of both emotional and non-emotional irrelevant information during the maintenance stage of a WM memory task impaired the recovery of relevant information in comparison with introduction of a colored picture without any meaning, which could be considered a non-interference condition. In addition, these results seem to confirm the idea previously introduced: if a stimulus for which we are biologically predetermined to not ignore (i.e. emotional stimuli) is presented within a WM task, it will work as a powerful interference impairing the recovery of relevant information more than other non-emotional interference. However, in a later study using a similar task (Dolcos et al., 2008), they did not find any

behavioral effect. Further exploration identified a subgroup of participants who seem to profit from emotional interference.   Dolcos and cols. ascribed this opposing behavioral effect to individual differences. Nevertheless, the effect of both emotional and non-emotional distractions compared with non-interference scenario, was not addressed since they did not include a non-interference condition. Other studies from this group developed to investigate the effect of sleep deprivation (Chuah et al., 2010) and the effect of anxiety-induced distraction (Denkova et al., 2010) have replicated the main effect of impaired WM after unpleasant distraction. However, they did not find differences in performance after neutral distraction and no distraction.

Anticevic and cols. (2010) addressed this issue in a delayed-recognition WM task using complex geometric shapes as relevant items to memorize and recognize. During the maintenance stage, three types of distractors were presented: unpleasant emotional pictures, neutral pictures and task related geometric shapes. A fourth condition was added as non-interference, in which no distractor was introduced. The authors also manipulated the difficulty of the task by including low WM load trials and high WM load trials, in which two or four geometric shapes were presented at the encoding stage, respectively. Consistent with previous work (Chuah et al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006), unpleasant distractors were associated with worsening of accuracy compared with neutral distraction in low WM load trials. Surprisingly, no differences appeared in high WM load and accuracy for non-interference condition was lower than for all distraction conditions. The authors explained this unexpected pattern as an artifact of their experimental design. All the conditions were pseudo-randomly presented so that no experimental condition appeared during more than three consecutive trials. This made distraction trials much

more common than free-distraction trials and therefore volunteers may have been surprised by the recognition stimulus on the non-interference trials. This hypothesis was supported by additional data using the same task but in which free-distraction trials were presented in a separate block, instead of intermixed with distraction trials (Anticevic et al., 2010). Using this blocked design, performance after non-interference was substantially better than after distraction conditions which is consistent with previous findings (Dolcos & McCarthy, 2006).

Hence, results from different studies from several groups suggest that unpleasant emotional irrelevant stimuli seems to worsen the maintenance of neutral relevant information in WM (Anticevic et al., 2010; Chuah et al., 2010; Dolcos & McCarthy, 2006), although this effect might be not very consistent as in some other studies it has been found only in a subset of participants (Dolcos et al., 2008) or only within the most confident responses (Denkova et al., 2010). However, the effect of pleasant emotional interference in WM is still an open issue. Some authors have pointed out that stimuli with higher levels of arousal could recruit more attentional resources (Lang, Bradley, Fitzsimmons, et al., 1998), leading to worsening of performance when those stimuli are not relevant for the ongoing task. But, has the affective valence of those high arousing stimuli any influence on their power as distractors? Exploring the effect of both, pleasant and unpleasant interference in comparison with neutral interference might provide us with valuable information about the mechanisms that turn this type of stimuli out into powerful sources of interference.

Apart from that, the extent to which emotionally neutral stimuli disrupt WM maintenance, in comparison to a non-interference scenario, has not been completely

clarified. In other words, might subjects be able to completely ignore neutral distractors? Dolcos and McCarthy 2006) and Anticevic et al. (2010) found poorer performance during neutral distraction compared with non-interference, while other studies failed to replicate this difference (Chuah et al., 2010; Denkova et al., 2010). This inconsistency might be explained by individual differences in executive control of distraction. Thus, people with higher capacity of interference resolution could perform WM tasks with neutral interference as well as without any interference, while performance of people with lower capacity of interference resolution might be affected by the appearance of neutral distractors. Considering individual differences in the ability to control interference might probably help to clarify the effect of neutral distraction with respect to non-interference scenario.

In two experiments we tried to address these open questions using a WM task in which neutral faces were task-relevant items and emotional and non-emotional pictures were task-irrelevant distractors. In the first experiment we explored the mechanisms that turn emotional stimuli out into powerful sources of interference. To do this, we included three experimental conditions in which pleasant, neutral and unpleasant pictures were displayed as interference during the maintenance stage of the WM task. We aimed to verify whether pleasant interference has any detrimental effect. Thus, contributions of both valence and arousal dimensions were investigated. In the second experiment, we further explored potential differences in the effect of emotional and non-emotional interference in comparison to non-interference scenario, by adding a fourth condition to the original design, in which no stimulus was presented during the maintenance of task-relevant information. Moreover, we measured the individual capacity of inhibitory control over memory using a standardized neuropsychological test

in both experiments. These data served to examine whether individual differences in this ability influence coping with emotional interference in WM.

2.   EXPERIMENT 1

In the first experiment, we explored the effect of two valence emotional distractors, pleasant, unpleasant, as well as the effect of neutral distraction in WM maintenance. If detrimental effects of unpleasant distraction were due to the biological relevance of emotional stimuli and our natural predisposition to deeply process them, other kind of biologically relevant stimuli such as pleasant ones, should affect performance in a similar way. If this was the case, the worsening of performance by emotional distraction would seem to be mainly arousal-driven. Indeed, taking into account that pleasant stimuli are usually more arousing than neutral ones, but less arousing than unpleasant stimuli, performance after pleasant distraction should be better than after unpleasant distraction, but worse than after neutral distraction.

We also tried to relate individual cognitive inhibition capacities to performance in each experimental condition. If cognitive inhibition and interference resolution are the key processes involved in control of distraction, participants with higher scores in this capacity will show higher accuracy and faster reaction times at the recognition stage.

2.1.   METHOD

2.1.1. Participants

Participants were 30 students from the Complutense University of Madrid and the Camilo José Cela University of Madrid (mean age 21 year and a range between 18 and 35 years). They had normal or corrected-to-normal vision. Half of the participants

were females (18-35 years old and a mean age of 19.46 years) and half of them were

males (18-34 years old and a mean age of 22.66 years).

	Age	STAI-S	STAI-T	BDI	TAVEC List A	TAVEC List B	TAVEC Short term	Interference Resolution
Exp. 1								
Mean	21,06	16,50	17,33	5,40	13,4	6,03	12,10	1,30
SD	5,00	8,26	8,50	4,28	1,92	1,71	2,50	1,39
Exp. 2								
Mean	21,69	15,41	16,86	6,81	7,25	6,06	5,18	-2,06
SD	4,48	6,07	8,76	5,66	1,66	1,72	2,08	1,35

Table 1. Volunteer's demographic information in Experiment 1 and Experiment 2. STAI-S: Spielberger State-Trait Anxiety Inventory for Adults - State score; STAI-S: Spielberger State-Trait Anxiety Inventory for Adults - Trait score; BDI: Beck Depression Inventory; TAVEC List A: Number of items successfully recalled at the first immediate recall of List A; TAVEC List B: Number of items successfully recalled at the first immediate recall of Interference list or List B; TAVEC Short term: Number of items successfully recalled at the short delay free recall of List A; Interference Resolution: Score at TAVEC Short term minus score at TAVEC List A. Scores below zero represent loss of information due to interference, or low interference resolution in WM, while scores equal-to or over zero represent no loss of information after the interference, or high interference resolution in WM.

They all completed the Spanish version of the Spielberger State-Trait Anxiety

Inventory for Adults (Spielberger, Gorsuch, & Lushene, 2002), the Beck Depression

Inventory (Beck, Steer, & Brown, 2006) and the España-Complutense Verbal Learning

Test (TAVEC), a Spanish version of the California Verbal Learning Test (CVLT) (Benedet &

Alexandre, 1998) (see Table 1 for demographic information). Participants received

course credits for their time.

2.1.2. Materials

Items at encoding and recognition stages consisted of colored images of neutral

faces. An oval mask was applied along the contours of the faces to remove ears and hair

and avoid any potential non-face specific cues. A pair of faces was presented at the encoding stage while just one face was displayed at the recognition stage. Faces were counterbalanced across experimental conditions. For the interfering items presented at the maintenance period, 90 pictures from the International Affective Picture System (IAPS) (Lang, Bradley, & Cuthbert, 2005) were selected and matched in luminance, contrast, color and figure-ground relationships.

Condition	IAPS Valence	IAPS Arousal	Subjective Valence	Subjective Arousal
Experiment 1				
Pleasant	7,33 (0,33)	5,84 (0,33)	7,14 (0,52)	5,35 (1,20)
Neutral	4,91 (0,35)	2,77 (0,35)	5,09 (0,52)	2,27 (0,50)
Unpleasant	2,29 (0,70)	6,54 (0,70)	2,23 (0,82)	6,48 (0,48)
Experiment 2				
Pleasant	7,34 (0,32)	6,23 (0,53)	7,09 (0,46)	5,40 (1,01)
Neutral	4,91 (0,35)	2,77 (0,38)	5,09 (0,55)	1,92 (0,66)
Unpleasant	2,39 (0,67)	6,23 (0,56)	2,37 (0,97)	6,71 (0,91)

Table 2. Mean normative values of pictures used in Experiment 1 and Experiment 2 and mean subjective ratings of those pictures by our volunteers. Standard deviations are shown in parenthesis.

They were divided in tree experimental sets according to their normative valence and arousal ratings: pleasant, neutral and unpleasant pictures (see Table 2 for mean normative values).

2.1.3. Procedure

A delayed-recognition WM paradigm with three experimental conditions, pleasant, neutral and unpleasant interference was used. Each condition comprised 30 trials. Each trial began with a 1000 ms intertrial interval (ITI), followed by the presentation of a pair of faces for 2000 ms (encoding phase). After a 1000 ms blank

screen, an interfering stimulus was displayed for 2000 ms, followed by another 1000 ms

blank screen (maintenance phase). Next, just one face appeared on the screen for 1500

ms, followed by a 500 ms blank screen (recognition stage). Participants had to decide

whether the face at the recognition stage has been one of the two previously encoded

or not, by pressing one of two keys (Figure 1).
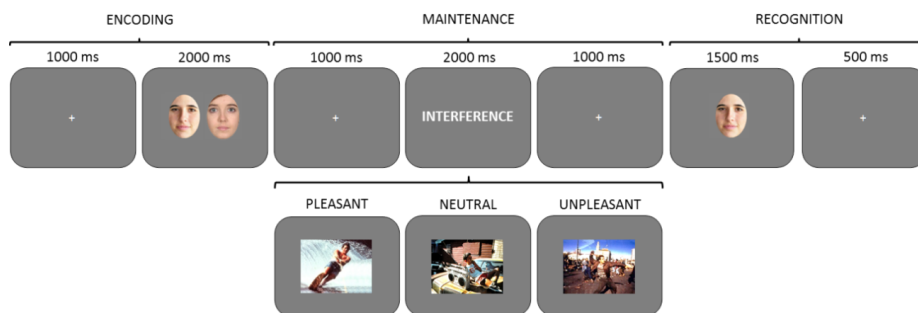
Figure 1. Diagram of the delayed-recognition WM paradigm in Experiment 1 and the Second Study. Three types of distractors (pleasant, neutral and unpleasant) were pseudorandomly presented during the maintenance stage. Volunteers were trained to learn and maintain the pair of faces into WM, look at the distracter, and then decide whether the face at the recognition stage is one of the two previously encoded or not, by pressing one of two keys.

Before the experiment, all the volunteers underwent four training trials in order

to ensure that they completely understood the task. To avoid inducing long-lasting

mood states, the order of trials were constrained so that no more than three trials of

the same condition were consecutively presented. Once the WM paradigm was

completed, all the pictures used as interference were presented to the participants and

they were asked to rate them regarding emotional valence and arousal, using the Self-

Assessment Manikin (SAM) self-report scale (Lang, 1980). Participants were allowed to

see each picture as long as they wanted, and the order of presentation of the pictures

was also constrained in the same way, but in a different sequence, than for the WM task.

2.2.   RESULTS

2.2.1. Accuracy

Figure 2a plots the mean accuracy (hits and correct rejections) for each condition averaged across subjects. A one-way repeated-measures analysis of variance (ANOVA) revealed a significant main effect of condition [$F(2, 28)=14.32$, $p<.0001$, eta squared=.50]. Pairwise comparisons using the Bonferroni correction revealed a lower performance during unpleasant interference compared to pleasant ($p<.001$) and neutral interference ($p<.0001$). There was no differences between pleasant and neutral interference ($p>0.1$).

2.2.2. Reaction times

Figure 2b shows the mean reaction times for correctly recognized items for each condition. Results from one-way repeated-measures ANOVA yielded a main effect of condition [$F(2, 28)=11.87$, $p<.0001$, eta squared=.45]. Pairwise comparisons using the Bonferroni correction revealed slower performance during unpleasant interference compared to pleasant ($p<.0001$) and neutral interference ($p<.007$). No differences were found between pleasant and neutral interference ($p=1.00$).

2.2.3. Subjective emotional ratings

As expected, subjective valence ratings differed as a function of affective category [$F(2,28)=284.85$, $p<.0001$, eta squared=.95], with pleasant pictures rated as most pleasant followed by neutral pictures, and unpleasant pictures rated as least pleasant [mean valence ratings: 7.14, sd=0.52 (pleasant), 5.09, sd=0.52 (neutral), 2.23,

sd=0.82 (unpleasant), *p*<.0001 for all comparisons]. Arousal ratings also varied as a function of affective category [F(2,28)=139.47, *p*<.0001, eta squared=.90], with pleasant and unpleasant pictures rated as more arousing than neutral pictures [mean arousal ratings: 5.35, sd=1.20 (pleasant), 2.27, sd=0.5 (neutral), 6.48, sd=0.48 (unpleasant), *p*<.0001 for both comparisons]. Unpleasant pictures were rated as more arousing than pleasant pictures (*p*<.001) (see Table 2 for mean subjective values).
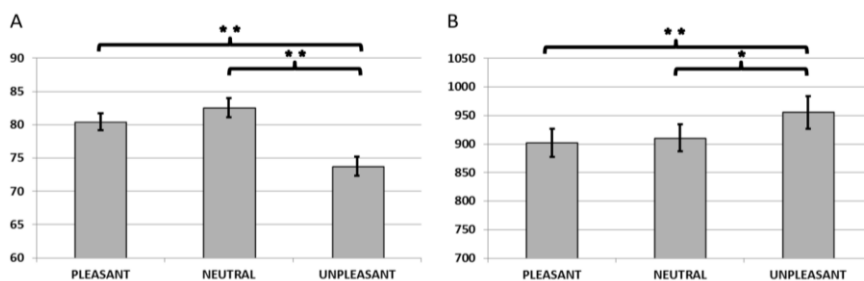
Figure 2. A: Mean accuracy (expressed as percent correct) in Experiment 1. Unpleasant distractors caused a detrimental effect on WM accuracy, compared to neutral and pleasant distractors (***p<.0001). B: Mean reaction times for accurate recognitions in Experiment 1. Unpleasant distractors caused a slower performance on WM, compared to neutral and pleasant distractors (* *p*<.05; ***p<.0001). Error bars represent standard error of mean.

2.2.4. Interference resolution in WM and performance

To test the relationship between individual inhibitory control and performance, results from TAVEC were used to develop an interference resolution measurement in WM. As in the CVLT, in the TAVEC, a list of items to memorize (list A) is presented and recalled five times before the presentation and recall of the interference list (list B). Then participants are asked to recall again as many items from list A as they can (post-interference recall of list A). Interference resolution scores were calculated by subtracting the amount of items successfully remembered at the first immediate recall

of list A from the amount of items successfully remembered at the post-interference recall of list A. Thus, scores below zero represent loss of information due to interference, or low interference resolution ability, while scores equal-to or over zero represent no loss of information after the interference, or high interference resolution ability. No significant correlations were found between interference resolution in WM and accuracy or reaction times for any experimental condition (see Table 3 for correlation coefficients and significance values).

Interference resolution	Accuracy			Reaction times		
	Pleasant	Neutral	Unpleasant	Pleasant	Neutral	Unpleasant
Rs	-.07	.04	-.22	-.14	-.12	-.15
Sig. (one-tailed)	.34	.41	.11	.22	.25	.20

Table 3. Spearman's correlation coefficients between individual interference resolution in WM and performance during the delayed-recognition WM task.

2.2.5. Item analysis

To test the relationship between the emotional features of pictures and their value as interference during the WM task, we calculated the correlation between their valence and arousal subjective ratings, and accurate recognition likelihood and reaction times for each trials in which they appeared as distractors. Valence correlated positively with accuracy (one-tailed Spearman's Rho=.22, p<.05) and negatively with reaction time (one-tailed Spearman's Rho=-.37, p<.0001), while arousal correlated positively with reaction time (one-tailed Spearman's Rho=.22, p<.05), and tended to negatively correlate with accuracy (one-tailed Spearman's Rho=-.26, p=.06). Since both pleasant and unpleasant stimuli were high arousing, partial correlations were calculated in order to test whether one of them was leading the correlation effect. Valence correlated positively with accuracy (one-tailed $\rho_{valence,\ accuracy\ \cdot\ arousal}$=.21, p<.05) and

negatively with reaction time (one-tailed ρvalence, accuracy · arousal=-.30, *p*<.005) when the effect of arousal was controlled. No significant correlation was found between arousal and accuracy (one-tailed ρvalence, accuracy · arousal=-.12, *p*>.1) nor arousal and reaction time (one-tailed ρvalence, accuracy · arousal=.11, *p*>.1) when the effect of valence was controlled.

2.3.   DISCUSSION

One of the major aims of this first experiment was to clarify previous results suggesting that unpleasant emotional stimuli disrupt WM maintenance of non-emotional information more than other neutral stimuli. In accordance to the literature (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008; Dolcos & McCarthy, 2006) unpleasant interference does affect WM more than neutral interference, resulting in enhanced forgetting in short-term memory. Analysis of reaction times for correct responses also showed this pattern, with slower responses after unpleasant interference than after neutral interference. This suggests that unpleasant interference not only increases the probability of forgetting but produces higher cognitive costs even for successful performance. This effect may be explained under the concept of motivated attention (Bradley et al., 2003) which refers to the automatic capture of attentional resources by stimuli which represent information linked to survival. As posed above, this capture of attentional resources means an advantage when emotion is task relevant, since it drives a deeper processing of those stimuli (Bradley et al., 2003). However, when emotion is not part of goal-task relevant information, this attentional capture turns emotional stimuli into powerful competitors which interfere with relevant information. This finally worsens performance of the

ongoing task (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008; Dolcos & McCarthy, 2006).

A second major aim of this experiment was to test whether pleasant emotional interference affect WM in a similar manner than unpleasant interference does. If we assume that emotional features of stimuli are key contributors to turn them into powerful interferences, pleasant stimuli, which also represent important information for survival, such as food or reproduction, should also recruit attentional resources, and therefore produce similar amount of forgetting. Unexpectedly, pleasant interference does not affect maintenance of information in WM more than neutral interference. These results suggest that, contrary to our initial hypothesis, the power of emotional stimuli as interference in WM is not only arousal-driven. If this were the case, pleasant distractors would have produced lower WM performance than neutral interference, but higher WM performance than unpleasant distraction. As this is not the case, the valence of emotional stimuli must have any contribution to the value of emotional stimuli as interference. Partial correlation analysis from our data confirmed this hypothesis. Valence correlated significantly with performance when the effect of arousal was controlled, so that the more unpleasant was the distractor the higher probability of forgetting information previously encoding, and the higher cognitive cost of giving a correct response, as reflected by reaction time.

Although this unexpected finding seems to partially contradict the hypothesis of biological relevance-based interference, a more thorough interpretation may clarify this issue. The reason that accounts for the salience of emotional stimuli is probably related to the potential consequences of ignoring them. If one do not pay attention to a

dangerous animal or to some food, our probability of surviving decreases. This probably explains why we are prepared to pay attention to and deeply process such stimuli. Nevertheless, consequences of ignoring pleasant and unpleasant stimuli, although critical for survival, differ in the immediate outcome of this behavior. Undoubtedly, medium to long-term survival or gene transfer to the next generation can be compromised when food or reproduction related stimuli are ignored. However, short-term surviving probability decreases when potentially dangerous cues are ignored. Therefore, it seems reasonable that our executive control, specifically our inhibitory control, can override the attentional response elicited by a pleasant stimulus for a moment, if we are performing another relevant task, since our survival is not immediately at risk (Ekman, 1992; Ohman, 1992).

Finally, we tried to relate individual differences in cognitive inhibition with task performance across the different experimental conditions. If cognitive inhibition and interference resolution are the key processes involved in control of distraction during WM maintenance, participants with higher inhibitory skills should show higher task accuracy. However, our data did not show any correlation between inhibitory control of memory as measured by TAVEC and performance in our WM task. Notwithstanding, the absence of a significant correlation here may be due to the test we chose to measure interference resolution in WM. In TAVEC, as well as in the original CVLT, a list of items to memorize is presented and recalled five times before the presentation of the interference list, whereas in our task, faces were only presented once before interference. Therefore, items to memorize in TAVEC might become more resistant to interference than faces in our task.

Even though, one may be concerned about the possibility that, for some reason, pleasant stimuli do not capture attention in the same way than unpleasant ones. That might easily explain why pleasant distractors produced the same amount of forgetting than neutral ones, instead of other interpretations based on differential effectiveness of cognitive control over pleasant and unpleasant distractors. However, a recent study has shown that pleasant does capture attention more than neutral stimuli during the attentional blink phenomenon (de Oca et al., 2012). This points to cognitive control as a putative responsible mechanism for the low detrimental effect of pleasant interference on WM. We approached this issue in Experiment 2 by changing the TAVEC administration to obtain individual measures of interference resolution in short term memory.

3.   EXPERIMENT 2

In the second experiment we first tried to confirm the unexpected finding of equivalent performance after pleasant and neutral interference showed in Experiment 1. Second, we attempted to reveal potential differences in the effect of emotional and non-emotional interference in comparison to a non-interference scenario. Additionally, we modified the administration of the TAVEC (see Participants in Experiment 1) to prevent items to be memorized from become more resistant to interference than faces in our task. Then, if cognitive inhibition and interference resolution in WM are the key processes involved in the control of distraction, participants with higher scores in this capacity will show better performance in distraction conditions, but not necessarily during the free-distractor condition. Finally, we adjusted the selection of distractors in order to make pleasant and unpleasant conditions equal in arousal.

3.1.   METHOD

3.1.1. Participants

Participants were 43 students from the Complutense University of Madrid and the Camilo José Cela University of Madrid (mean age 21.6 years; range from 18 to 40 years). They had normal or corrected-to-normal vision. 24 participants were females (18-33 years old and a mean age of 21.7 years) and 19 were males (18-40 years old and a mean age of 21.6 years). They all completed the Spanish version of the Spielberger State-Trait Anxiety Inventory for Adults (Spielberger et al., 2002), the Beck Depression Inventory (Beck et al., 2006) and the España-Complutense Verbal Learning Test (TAVEC), a Spanish version of the California Verbal Learning Test (CVLT) (Benedet & Alexandre, 1998) (see Table 1 for demographic information). In this experiment, items to memorize (list A) were presented and recall only one time (immediate recall), R before the presentation of the interference list. After this, participants were asked to recall the list A once again (post-interference recall). Participants received course credits for their time.

3.1.2. Materials

Items at encoding and recognition were exactly the same ones as those used in Experiment 1 (see Materials in Experiment 1), and they were also counterbalanced across experimental conditions. For the interfering items presented at the maintenance period, 90 pictures from the International Affective Picture System (IAPS) (Lang et al., 2005) were selected and matched in luminance, contrast, color and figure-ground relationships. They were divided in pleasant, neutral and unpleasant pictures. For this experiment we adjusted the criterion of selection to insure that pleasant and unpleasant conditions were equal in arousal (see Table 2 for mean normative values).

3.1.3. Procedure

A delayed-recognition WM paradigm with four experimental conditions non-interference, pleasant, neutral and unpleasant interference was used and all of them comprised 30 trials. The trial structure, times of presentation and instructions were the same as those used in Experiment 1.
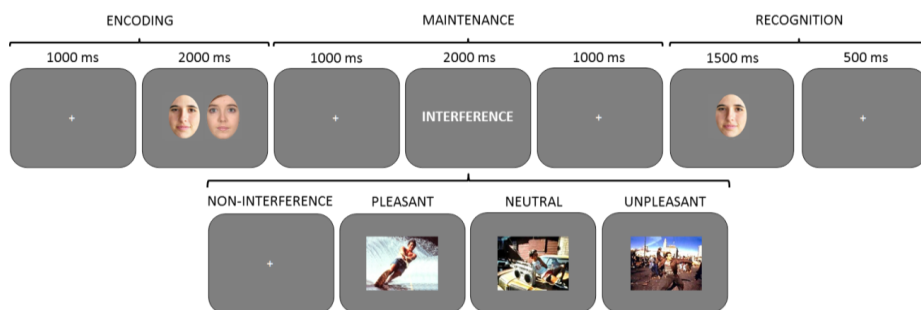
Figure 3. Diagram of the delayed-recognition WM paradigm in Experiment 2. Three types of distractors (pleasant, neutral and unpleasant) were pseudorandomly presented during the maintenance stage. Volunteers were trained to learn and maintain the pair of faces into WM, look at the distracter, and then decide whether the face at the recognition stage is one of the two previously encoded or not, by pressing one of two keys. In a separate block, volunteers performed a fourth experimental condition with a maintenance period free of distraction.

The order of trials was also constrained in the same way as in Experiment 1 (see Procedure in Experiment 1). However, non-interference trials were presented in a separate block to avoid potential experimental artifacts. Although a blocked presentation of non-interference condition may be considered a methodological inconvenience, results from previous studies has shown it as a suitable approach to avoid already reported experimental artifacts affecting performance after non-interference WM maintenance (Anticevic et al., 2010). That is, if presentation of all the 120 trials would have been intermixed, interference trials had been much more

common than non-interference trials. In addition, the period of time without any visual stimulation at the maintenance stage was much longer in non-interference trials (4 seconds) than in interference trials (1 second at the most) (see Figure 3). Therefore, volunteers might have been surprised by the appearance of a non-interference trial. This could produce a worsening in performance for this condition not related to the processes we are interested in (Anticevic et al., 2010). Additionally, the order of presentation of non-interference and interference blocks was counterbalanced across participants in order to eliminate any potential practice or fatigue effect.

3.2.   RESULTS

3.2.1. Accuracy

Figure 4a plots mean accuracy (hits and correct rejections) in each condition averaged across subjects. Non-parametric tests were employed since performance for non-interference, neutral and unpleasant conditions were not normally distributed.
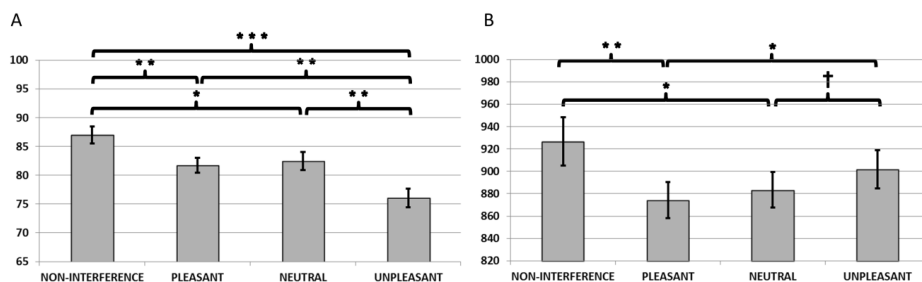
Figure 4. A: Mean accuracy (expressed as percent correct) in Experiment 2. Unpleasant distractors caused a detrimental effect on WM accuracy, compared to neutral and pleasant distractors, as well as to a scenario free of distraction (* $p<.01$; **$p<.005$; ***$p<.0001$). B: Mean reaction times for accurate recognitions in Experiment 2. Pleasant distractors caused a faster performance on WM, compared to unpleasant distractors and a scenario free of distraction (* $p<.05$; **$p<.01$). Performance during unpleasant distraction might also tend to be slower than during neutral distraction († $p=.07$). Error bars represent standard error of mean.

Friedman's test revealed a significant main effect of condition [χ^2(3)=27.54, *p*<.0001)] and Wilcoxon's test for pairwise comparisons showed lower performance during unpleasant interference compared to non-interference (*p*<.0001), pleasant (*p*<.002) and neutral interference (*p*<.002). Performance during pleasant and neutral interference were also worse than during non-interference (*p*=.001 and *p*<.01, respectively).

3.2.2. Reaction times

Figure 4b shows mean reaction times for correctly recognized items in each condition. Friedman's test revealed a significant main effect of condition [χ^2(3)=8.38, *p*<.05)] and Wilcoxon's test for pairwise comparisons showed faster performance during pleasant interference compared to non-interference (*p*<.01) and unpleasant interference (*p*<.05). Results from post-hoc comparisons also showed a faster performance during neutral interference than during non-interference scenario (*p*<.05). Although no significant, our volunteers might tend to respond slower after unpleasant than after neutral interference (*p*=.07).

3.2.3. Subjective emotional ratings

As expected, subjective valence ratings differed as a function of affective category [F(2,28)=243.95, *p*<.0001, eta squared=.94], with pleasant pictures rated as most pleasant followed by neutral pictures, and unpleasant pictures rated as least pleasant [mean valence ratings: 7.09 sd=0.46 (pleasant), 5.09 sd=0.55 (neutral), 2.37 sd=0.97 (unpleasant), *p*<.0001 for all comparisons]. Arousal ratings also varied as a function of affective category [F(2,28)=258.91, *p*<.0001, eta squared=.94], with pleasant and unpleasant pictures rated as more arousing than neutral pictures [mean arousal

ratings: 5.40 sd=1.01 (pleasant), 1.92   sd=.66 (neutral), 6.71 sd=0.91 (unpleasant), p<.0001 for all comparisons]. Although both pleasant and unpleasant pictures were selected to be equal in arousal (see table 2 for mean normative values), our volunteers rated on average unpleasant pictures as more arousing than pleasant pictures (p<.0001) (see Table 2 for mean subjective values).

3.2.1. Interference resolution in WM and performance

In this experiment, interference resolution scores were calculated by subtracting the amount of items successfully remembered at the single immediate recall of list A from the amount of items successfully remembered at the post-interference recall of list A. Again, scores below zero represent loss of information due to interference, or low interference resolution ability, while scores equal-to or over zero represent no loss of information after the interference, or high interference resolution ability.

Using this modified measurement, interference resolution in WM correlates positively with accuracy during pleasant and neutral interference (Rs= .38, p=.005 and Rs=.39, p<.005, respectively) so that the higher interference resolution ability, the better accuracy at the recognition stage during the WM task.Interference resolution in WM did not significantly correlate with accuracy during non-interference and unpleasant interference (Rs= .13, p>.1 and Rs=-.008, p>.1, respectively. No significant correlations were found between interference resolution in WM and reaction times for accurate recognitions, during any condition (see Figure 5 and Table 4 for scatter plots and correlation coefficients and significance values, respectively).
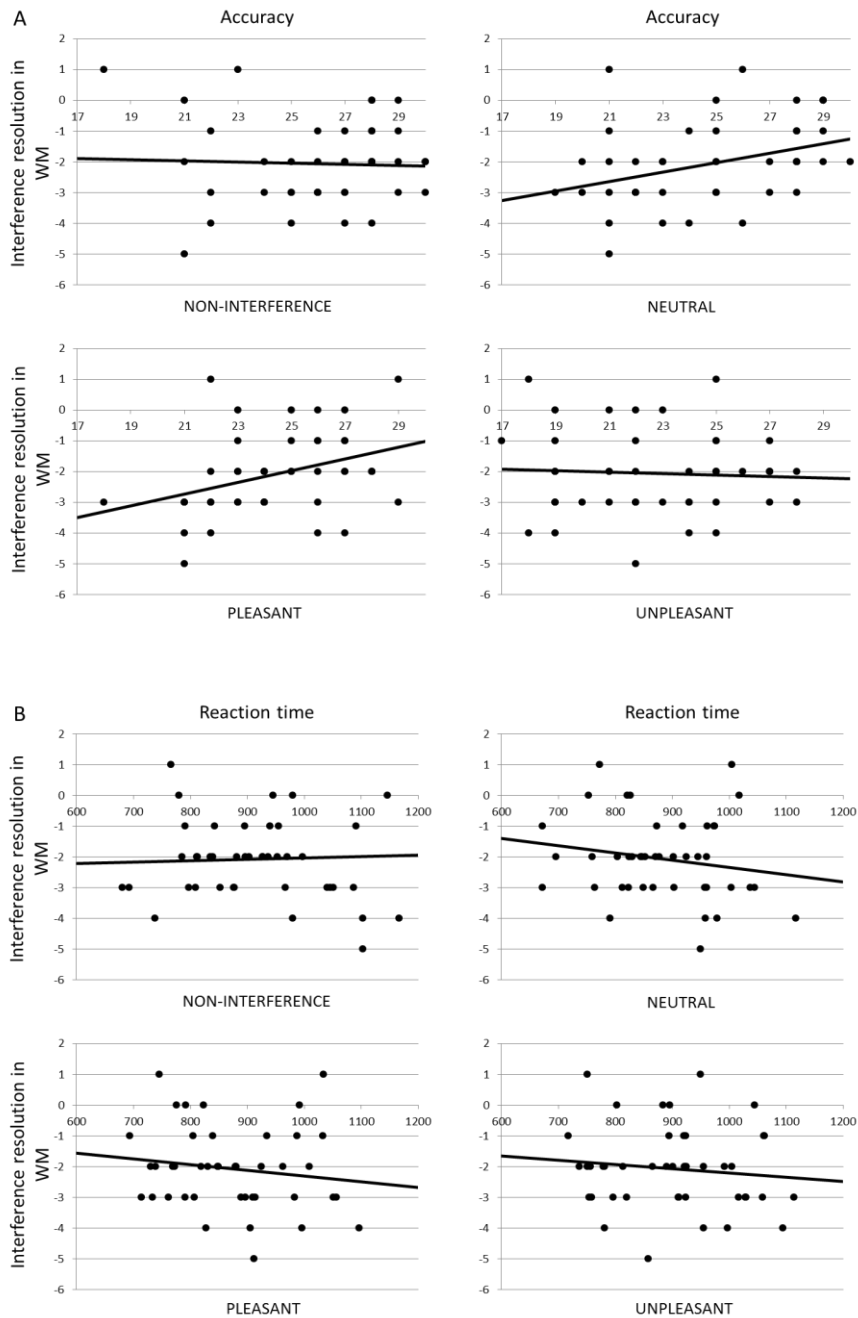
Figure 5. A: Scatter plots showing the relationship between interference resolution in WM and accuracy in each experimental condition of Experiment 2. B: Scatter plots showing the relationship between interference resolution in WM and reaction times for accurate recognitions in each experimental condition of Experiment 2.

Interference resolution	Accuracy				Reaction times			
	Non-interf	Pleasant	Neutral	Unpleasant	Non-interf	Pleasant	Neutral	Unpleasant
Rs	.13	.38	.39	-.008	-.59	-.16	-.15	-.13
Sig. (one-tailed)	.19	.005	.004	.47	.35	.15	.16	.19

Table 4. Spearman's correlation coefficients between individual interference resolution in WM and performance during the delayed-recognition WM task. Interference resolution in WM correlated positively with accuracy, during pleasant and neutral interference.

3.2.2. Item analysis

As we did in Experiment 1, we test the relationship between the emotional features of pictures and their value as interference during the WM task. To do this, we calculated the correlation between their valence and arousal subjective ratings, and accurate recognition likelihood and reaction times. Valence correlated positively with accuracy (one-tailed Spearman's Rho=.23, $p<.05$) and negatively with reaction time (one-tailed Spearman's Rho=-.27, $p<.005$), while arousal correlated negatively with accuracy (one-tailed Spearman's Rho=-25, $p<.05$) and positively with (one-tailed Spearman's Rho=-.20, $p<.01$). As previously mentioned, although we adjusted the criterion of selection to keep pleasant and unpleasant conditions equal in arousal, our volunteers rated unpleasant interferences as more arousing than pleasant ones. Therefore, partial correlations were also calculated in order to disentangle the effects of valence from the effects of arousal. In line with Experiment 1, valence correlated positively with accuracy (one-tailed ρvalence, accuracy · arousal=.19, $p<.05$) and negatively with reaction time (one-tailed ρvalence, accuracy · arousal=-.26, $p<.01$) when the effect of arousal was controlled. Again, no significant correlation was found between arousal and accuracy (one-tailed ρvalence, accuracy · arousal=-.13, $p=.1$) when

the effect of valence was controlled. Though, arousal positively correlated with reaction time (one-tailed ρvalence, accuracy · arousal=.19, *p*<.05).

3.3.   DISCUSSION

In accordance with the first experiment and previous literature, highest forgetting occurs after unpleasant interference, extending evidence in favor of a biological relevance-based interference (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008; Dolcos & McCarthy, 2006).

As in Experiment 1, pleasant interference does not affect WM more than neutral interference. In this regard, although we equated pleasant and unpleasant pictures in arousal, our volunteers rated unpleasant pictures as more arousing than pleasant ones, and this might account for their differences in performance. However, if the effect of emotional distractors in WM were exclusively due to the arousal value, performance after pleasant distraction should have been worse than after neutral distraction, since pleasant pictures were also rated as more arousing than neutral stimuli. But this was not the case, as both pleasant and neutral stimuli showed similar levels of interference. Furthermore, results from partial correlations between subjective valence and accuracy, blocking the effect of arousal, and between subjective arousal and accuracy, blocking the effect of valence, showed a greater contribution of valence to the power of emotional stimuli as distractors. This general effect resembles the one observed in the first experiment, so that the more unpleasant is perceived a distractor, the higher probability of forgetting previously encoded information. Neutral interference did lead to a higher forgetting than after a scenario free of distractor, in accordance to previous results employing similar tasks (Anticevic et al., 2010; Dolcos & McCarthy, 2006). These

findings provide further evidence in favor of the detrimental effect of both emotional and non-emotional distractors in WM and strengthen the interference-based forgetting theories (Berman et al., 2009).

If cognitive inhibition is the mechanism responsible for these differences between emotional and non-emotional interference, as well as between different emotional valence distractors, one would expect that individual differences in interference resolution capacity in short term memory predicted performance in each experimental condition. Therefore, higher interference resolution scores should correlate with better performance in the distraction conditions, but not necessarily in the condition free of distraction. According to this hypothesis, participants with higher interference resolution capacity showed less forgetting after neutral and pleasant distraction, but there was no relation between interference resolution and non-interference nor between interference resolution and unpleasant distraction. If one bear in mind the growing role attributed to cognitive inhibition in mental processes (McLeod, 2007) and specifically in WM (Hasher & Zacks, 1988), it seems reasonable that individual interference resolution control is related to performance in an experimental condition which requires it, such as neutral interference, but not when it is not required, such as non-interference condition. More interesting is the pattern observed in the emotional interference conditions. As commented above, emotional stimuli are powerful interferences due to its biological relevance. Therefore, one might expect that higher degree of interference control was needed to override the automatic attentional capture elicited by emotional stimuli. However, this relation is only observed in the pleasant interference condition, in which performance is equivalent to neutral, but not to unpleasant interference. This suggests that greater interference resolution capacity

does not necessarily help to override the attentional response elicited by unpleasant stimuli. This effect may be in accordance with the conclusion proposed based on results from Experiment 1. The key aspect which makes emotional stimuli powerful interferences is related to the severity and specially, to the immediacy of consequences derived from ignoring them. Therefore, our cognitive control might momentarily override interference when consequences of doing it would not affect us in the short term, releasing attentional resources for the current task.

Although results from reaction times were not as straightforward as in Experiment 1, they are in accordance with it, suggesting that unpleasant interference might produce higher cognitive cost even for successful performance. In addition, highest reactions times were recorded after non-interference WM maintenance. This may be motivated by the duration of maintenance stage without any stimulus (4 second without any stimulation), in combination with a relatively easy task (accuracy raised almost to 90% in this condition). Our volunteers might have experienced a decrease in their concentration level after encoding of information and might have been surprised by the probe stimulus, leading to slower responses to the test.

4.   DISCUSSION AND CONCLUSIONS

Few papers have addressed the effect of task-irrelevant emotional information during the maintenance of task-relevant non-emotional information, with the general finding that unpleasant interference mainly causes the worsening of WM performance (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008; Dolcos & McCarthy, 2006). Furthermore, the effect of pleasant emotional interference in WM remains unexplored. In two studies we attempted to unravel the effect of both

pleasant and unpleasant distractors in WM, when compared to non-emotional distractors, as well as to a non-interference scenario. Results from both experiments confirm the general finding that unpleasant interference increases the probability of forgetting in short-term memory (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008; Dolcos & McCarthy, 2006). This effect has been previously explained by the biological relevance of emotional stimuli. Provided that emotional stimuli represent crucial information for survival, our cognitive system tends to process them automatically (Bradley et al., 2003). In general, this supposes an advantage since it helps us to exert more adaptive responses (Dolan, 2002) but when the most adaptive behavior entails ignoring emotional stimuli, they strongly compete with maintenance of relevant information, worsening performance of the ongoing task (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008; Dolcos & McCarthy, 2006). According to this idea, pleasant emotional stimuli, which are also better remembered when they are task-relevant (Schmidt & Williams, 2001), should similarly worsen WM performance. Unexpectedly, results from both, Experiment 1 and 2, showed equivalent performance for neutral and pleasant interference, suggesting that valence might be the crucial dimension in the emotional-based interference effect. This was further supported by partial correlation analysis where the effect of arousal was controlled (see sections Item analysis in Experiment 1 and Experiment 2). But, why do not pleasant distractors affect WM more than unpleasant ones? It is probably related to the potential consequences of not to immediately pay attention to such stimuli, in an environment plenty of information which varies in relevance from time to time. Therefore, ignoring cues regarding feeding or predators just because our cognitive resources are dedicated to some other task, would definitively decrease our probably of

surviving. However, it is the immediacy of these consequences which makes the difference between ignoring pleasant and unpleasant stimuli. Medium to long-term survival or gene transfer are compromised when information related to food, reproduction opportunities or offspring care are ignored, while surviving probability is endangered in the short-term, if the individual ignores predator-related information (Ekman, 1992; LeDoux, 1990; Ohman, 1992). On the other hand, if any sort of survival-linked stimuli systematically recruited attentional resources, we would probably fail in many other tasks, which would finally reduce our effectiveness to deal with a changing environment. Therefore, it seems reasonable that our executive control, specifically our inhibitory control, can momentarily override the attentional capture evoked by pleasant stimuli while we are performing another relevant task, provided that our survival is not immediately compromised. Thus, we might benefit from the result of successfully performing an ongoing task. By contrast, it also seem logical that our inhibitory control was blocked and unable to override attentional responses elicit by unpleasant stimuli, since it would immediately endanger our survival in favor of just a potential secondary benefit. This hypothesis is also supported by the relationship found between individual interference resolution capacity and performance in Experiment 2. There is no doubt that individual differences in cognitive inhibition are related to performance in WM, particularly when interference resolution is required (Hasher & Zacks, 1988). According to this idea, we found that volunteers with higher interference resolution scores performed better after neutral interference, which was not the case for free-distractor maintenance period, where inhibitory control is not so required. More striking is the differential pattern of correlation with performance after pleasant and unpleasant interference. Individual interference resolution scores positively correlate with

performance after pleasant but not after unpleasant interference, supporting our postulate that inhibitory control could override attentional responses evoked by pleasant stimuli but would not be able to do it in face of unpleasant ones.

Previous studies in this field have addressed the effect of non-emotional distraction when compared to free-distraction maintenance. Some of them found equivalent performance after neutral distraction and after non-interference maintenance (Chuah et al., 2010; Denkova et al., 2010), while some others reported a better performance after non-interference scenario than after neutral interference (Anticevic et al., 2010; Dolcos & McCarthy, 2006). Our volunteers experience higher forgetting after neutral interference than during a free-distractor maintenance period. This result provides a further support in favor of the interference-based forgetting theories (Berman et al., 2009).

Finally, a possible limitation of the current study is in regard with the subjective arousal ratings of participants in Experiment 2. Although we selected pleasant and unpleasant pictures equal in arousal, based on their IAPS normative values, our volunteers rated pleasant pictures as less arousing than unpleasant stimuli, which might make difficult to disentangle the effects of valence from the effects of arousal. However, results from partial correlations between these emotional dimensions and accuracy, blocking first the effect of arousal and then the effect of valence, points to the valence as the primary responsible dimension for the power of emotional stimuli as distractors. Furthermore, if arousal instead of valence were the most contributory dimension, performance after pleasant interference would have been worse than after neutral distraction, since pleasant stimuli were rated as more arousing than neutral pictures.

Even though, a partial contribution of arousal cannot be completely discarded, and further studies should account for this issue, trying to keep the emotional distraction conditions equal in arousal, not only based on their normative values but in the participant's subjective ratings. Nevertheless, a potential partial contribution of arousal would not invalidate the immediacy of consequences of ignoring biologically relevant stimuli as the essential aspect that turns them into powerful interference. Indeed, it seems reasonable that those stimuli that immediately compromise our survival were perceived as slightly more arousing than those that do it in the medium or long-term.

In conclusion, the present study further supports previous evidences showing that unpleasant stimuli do affect the maintenance of non-emotional information when they are not goal-task relevant, leading to worse performance. At the same time, this study shows for the first time that pleasant interference does not necessarily affect WM as unpleasant interference does. Second, the relationship between performance and WM interference resolution capacity points to the immediacy of consequences of ignoring such irrelevant information as the key aspect that allows executive control, in particular cognitive inhibition, to override attentional responses. Finally, this study contributes to clarify the effect of neutral interference in WM in comparison to free-interference maintenance, showing that cognitive control cannot completely deal with neutral distraction, leading to a worsening of performance in comparison with non-interference maintenance.

SECOND STUDY

Early detection and late cognitive control of

emotional distraction by the prefrontal cortex

1.   INTRODUCTION

Emotion and cognition interact in the human brain in order to develop a complex and adaptive behavior. According to some theories, emotional stimuli preferentially recruit cognitive resources (Armony & Dolan, 2002; Mogg et al., 1997; Ohman et al., 2001), as they contain information that is closely linked to survival (Anderson & Phelps, 2001; LeDoux, 1996; Ohman et al., 2000). This preferential access to our cognitive system could be interpreted as a mechanism developed to prepare us to effectively process biologically relevant information, so that we are finally able to build up and exert more adaptive responses. In the memory domain, such an effect has been consistently observed (see Dolcos, Denkova, & Dolcos, 2012; Dolcos, Iordan, & Dolcos, 2011 for a review), and emotional memories has been reported as more vivid (Ochsner et al., 2000), accurate (Kensinger, 2007) and resilient to time (Bradley, Greenwald, Petry, & Lang, 1992; Dolcos, LaBar, K, & Cabeza, 2005; Weymar, Löw, & Hamm, 2011) than neutral memories. However, such a preferential access of emotional stimuli might be problematic when we are engaged in a relevant memory process, as our cognitive resources may be depleted in favor of emotional information. Several studies have

shown that emotional information, specifically unpleasant emotional stimuli, can impair the retention of task-relevant neutral information in short term memory (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006), and that individual differences in executive functioning as well as in the cognitive control of the emotional aspects of irrelevant information may account for differences in the ability to cope with emotional distraction (Denkova et al., 2010; Dolcos et al., 2013a, 2008). However, a recent study from our group (see the First Study of the present work) has explored the effect of other type of emotional distractors, those represented by pleasant stimuli. Results from that study showed that positively valenced emotional distractors do not affect WM maintenance, as unpleasant distractors do. That result led us to interpret that the key aspect that makes emotional stimuli powerful distractors is not directly related to their biological relevance, but to the immediacy of the consequences of ignoring such linked-to-survival information (see Discussion and conclusions of the First Study).

Over the last 10 years, a series of fMRI studies have been devoted to disentangle the brain mechanisms that mediate such cognitive control of emotional distraction in WM. Most of these studies identified a dissociable pattern of activity between dorsal cortical regions, including the DLPFC and the LPC, and ventral brain areas, including the OFC, the VLPFC, the OTC and the amygdala (see Dolcos et al., 2011 for a review). Specifically, unpleasant emotional distraction seems to produce a decreased activity over dorsal brain areas which are known to be related to executive processes implicated in attentional processes and active maintenance of information in WM (Berryhill & Olson, 2008; D'Esposito et al., 2000; Derrfuss et al., 2004; Koenigs et al., 2009; Nee et al., 2013; Smith & Jonides, 1999). This reduction of activity has been interpreted as the

cause of the impairment in the maintenance of task-relevant information observed at the behavioral level. Besides, unpleasant emotional distraction enhances activity in ventral cortical and subcortical regions, which has traditionally been related to emotional processing and emotional regulation (Davidson & Irwin, 1999; Kober et al., 2008; Lindquist et al., 2012; Phan et al., 2002). Thus, increases in ventral activity due to processing of emotional distraction appears to exert a bottom-up modulation over dorsal brain regions, reallocating processing resources (Vuilleumier, Armony, Driver, & Dolan, 2001) and finally impairing the behavioral performance. Moreover, this dorsal-ventral dissociation was found to be specific for emotional distraction (Dolcos et al., 2008).

Nevertheless, WM maintenance is not affected by every single emotional distractor, so our cognitive control mechanisms seem to be able to override such negative bottom-up influence. Specific regions over that ventral emotional processing system, such as the inferior frontal cortex (IFC) and the VLPFC, which are widely related to emotional regulation processes (Aron, 2007; Kober et al., 2008; Ochsner, Silvers, & Buhle, 2012), have been found critically involved in coping with emotional distraction in WM (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013a, 2006). Indeed, activation over those ventral prefrontal regions during emotional distraction processing seems to benefit WM maintenance of task-relevant information (Anticevic et al., 2010; Denkova et al., 2010; Dolcos et al., 2013a, 2006).

In addition to the evidence that points to a dorsal/executive-ventral/emotional dissociation as a general mechanism in response to emotional distraction, there are

several studies that found enhanced activity in dorsal cortices during unpleasant distraction in WM (Anticevic et al., 2010; Denkova et al., 2010; Dolcos et al., 2008). Furthermore, some of these studies showed that increases of activity in the medial frontal gyrus, the middle frontal gyrus and the postcentral gyrus were related to successful performance in the WM task (Anticevic et al., 2010; Denkova et al., 2010). These results are in line with extensive literature linking the DPFC with emotion processing (see Ochsner et al., 2012 for a review) and complement the whole picture regarding the spatial distribution of the brain systems that mediate the cognitive control of emotional distraction in WM.

Although all these studies have established the brain areas that underlie the mechanism that allow us to cope with biologically relevant distraction, the temporal dynamics of this process remains unexplored. In the present study, we use MEG to characterize the spatio-temporal patterns of the brain activity that underlies the cognitive control mechanisms involved in coping with emotional distraction. Based on previous evidence showing an early processing of emotional stimuli (Batty & Taylor, 2003; Bradley et al., 2003; Carretié et al., 2004; Pourtois et al., 2005), we predict that both, pleasant and unpleasant stimuli, but specially the latters, would increase the brain response at early latencies of distraction processing, when compared with neutral stimuli. Since such an early activation has been reported in perceptual tasks, in which the emotional stimuli do not have to be controlled, we also hypothesize that the effective overriding of emotional distractors would occur later in the processing, and that such cognitive control would be mediated by higher activation of prefrontal cortices, especially in the DLPFC and in the VLPFC. Finally, and based on previous results showing that positively valenced distractors do not affect WM maintenance as

unpleasant distractors do (see the First Study of the present work) we posit that differences between the cognitive control of unpleasant and pleasant distraction would appear at the brain activity level in a later time window.

2.   METHOD

2.1.   Participants

Participants were 19 students from the Camilo José Cela University of Madrid. Data from 4 volunteers were excluded from the analysis because of failure of the behavioral response recording system (3 participants) or performance lower than 60% at any condition of the WM task (1 participant). Hence, analyses of the behavioral and MEG data correspond to 15 volunteers (7 males and 8 females. Mean age 20.06 year and a range between 18 and 29 years). They had normal or corrected-to-normal vision. They all completed the Spanish version of the Spielberger State-Trait Anxiety Inventory for Adults (Spielberger et al., 2002) and the Beck Depression Inventory (Beck et al., 2006) (see Table 5 for demographic information). Participants received course credits for their time.

2.2.   Materials

Items at encoding and recognition stages consisted of colored images of neutral faces. An oval mask was applied along the contours of the faces to remove ears and hair and avoid any potential non-face specific cues. A pair of faces was presented at the encoding stage while just one face was displayed at the recognition stage. Faces were assigned to different experimental conditions across subjects. For the interfering items presented at the maintenance period, the International Affective Picture System (IAPS)

(Lang et al., 2005) were scanned to obtain three sets of images that formed the pleasant, neutral and unpleasant distractors. Pictures in the pleasant and unpleasant distraction conditions were selected as to differ in valence but not in arousal. 48 pictures between 8.5-6.5 valence and 7.5-5.5 arousal formed the pleasant condition. Other 48 pictures between 3.5-1.4 and 6.6-4.3 formed the unpleasant condition. Finally, 48 medium-valenced (5.5-4.0) and low-arousing (3.7-1.7) pictures were selected for the neutral distraction condition (see Table 6 for mean normative values).

	Age	STAI-S	STAI-T	BDI
Exp. 1				
Mean	20,06	15,07	12,36	6,46
SD	3,21	7,17	5,88	5,10

Table 5. Volunteer's demographic information in the First Study. STAI-S: Spielberger State-Trait Anxiety Inventory for Adults - State score; STAI-S: Spielberger State-Trait Anxiety Inventory for Adults - Trait score; BDI: Beck Depression Inventory.

Condition	IAPS Valence	IAPS Arousal	Subjective Valence	Subjective Arousal
Pleasant	7,42 (0,33)	6,16 (0,49)	7,30 (1,00)	6,33 (0,94)
Neutral	4,93 (0,35)	2,71 (0,38)	5,14 (0,49)	3,61 (1,33)
Unpleasant	2,48 (0,52)	6,16 (0,41)	2,42 (1,03)	6,77 (0,93)

Table 6. Mean normative values of pictures used in Second Study and mean subjective ratings of those pictures by our volunteers. Standard deviations are shown in parenthesis.

2.3.   Procedure

A very similar delayed-recognition WM paradigm to the one employed in the Experiment 2 of the First Study, with three experimental conditions, pleasant, neutral and unpleasant interference was used (Figure 1).

Each trial began with a 1000 ms intertrial interval (ITI), followed by the presentation of a pair of faces for 2000 ms (encoding phase). After a 1000 ms blank screen, an interfering stimulus was displayed for 2000 ms, followed by another 1000 ms blank screen (maintenance phase). Next, just one face appeared on the screen for 1500 ms, followed by a 500 ms blank screen (recognition stage). Participants had to decide whether the face at the recognition stage has been one of the two previously encoded or not, by pressing one of two buttons.

Each experimental condition included 96 trials in order to achieve an adequate signal-to-noise ratio for subsequent brain source estimation. Therefore, each one of the 48 previously selected interfering pictures was employed in two different trials. To avoid inducing long-lasting mood states, the order of trials was constrained so that no more than three trials of the same condition were consecutively presented. To prevent any potential habituation effect, the two presentations of the same interfering picture were separated by a minimum of thirty trials. Before the experiment, all the volunteers underwent four training trials in order to ensure that they completely understood the task. These trials were not used later in the analysis. Once the WM paradigm was completed, all the pictures used as interference were presented to the participants out of the MEG system, and they were asked to rate them regarding emotional valence and arousal, using the Self-Assessment Manikin (SAM) self-report scale (Lang, 1980). Participants were allowed to see each picture as long as they wanted, and the order of presentation of the pictures was also constrained in the same way, but in a different sequence, than for the WM task.

2.4.   Data acquisition and preprocessing

MEG data was continuously recorded (1000 Hz sample rate, 0.01–330 Hz online filter) during the performance of the WM task using a 306-channel (102 magnetometers and 204 planar gradiometers) system (Elekta©, VectorView), inside a magnetically shielded room (Vacuumschmelze GmbH, Hanau, Germany). Activity in electrooculogram channels was also recorded to keep track of ocular artefacts. Maxfilter software (version 2.2., Elekta Neuromag) was used to remove external noise with the temporal extension of the signal space separation method (Taulu & Simola, 2006).

Raw data was band-pass filtered with low and high cutoffs of 1 and 45Hz, respectively, and segmented for each trial beginning 300 ms prior to distractor onset and continuing for 2,000 ms. Baseline correction was performed for each trial, using the 300 ms prior to distractor onset. Epochs were discarded from the analysis when containing eye, muscular or movement artefacts identified by visual inspection, or amplitudes higher than 3 pT.

The output of this preprocessing stage was a set of artefact-free trials for each condition and for each MEG channel. For the subsequent analysis we decided to use exclusively the magnetometer data, since magnetometers will enable the analysis of deeper sources such as the orbital part of the frontal lobe and the cingulate cortex, which have been reported active in previous studies involving memory control mechanisms and emotional processing (see Iordan, Dolcos, & Dolcos, 2013 for a review). The whole analysis was performed using the Fieldtrip toolbox (http://fieldtrip.fcdonders.nl/) in combination with in-house-MATLAB©-code (The Mathworks, Natick, MA).

2.5.   Statistical analysis at sensor level

A minimum of 52 artifact-free epochs were averaged to obtain an event related field (ERF) for each participant and condition. To determine the time windows and channel locations of significant differences in magnetic amplitude between the three distraction conditions, dependent samples F-tests were used. To control for the familywise error rate in the context of multiple comparisons (time points and sensors), a cluster-based nonparametric permutation statistic (Maris & Oostenveld, 2007) was performed. Accordingly, clusters of channels and time samples with significant differences ($p<0.05$) were created by temporal and spatial adjacency (a cluster had to consist of minimum of two significant neighboring sensors). Then, a set of 2000 permutations were created by randomly assigning condition labels and F-values were computed for each permutation. A cluster was considered have a significant effect if the sum of F-values in the original dataset was greater than the 95th percentile ($p<0.05$) of the distribution of the corresponding values in the randomized data.

2.6.   Source reconstruction

Based on the statistical analysis of the ERF in sensor space, three time windows of interest showing significant results were established: 70-130ms, 280-320ms and 360-455ms. To estimate the changes in brain activity that originated these differences, a source reconstruction in these time intervals was performed.

2.6.1.   Headmodels

A regular grid of 2471 points with 1cm spacing was created in the template Montreal Neurological Institute (MNI) brain (Collins et al., 1998). An anatomical label was assigned to each grid point with the AAL atlas (Tzourio-Mazoyer & Landeau, 2002),

as implemented in the WFU software (Maldjian, Laurienti, Kraft, & Burdette, 2003). Then, this set of points was transformed into subject's space and constituted the source locations. For that, an iterative closest point algorithm was used, that yielded a 4x4 matrix (translation, rotation and resizing) that transformed a standard MNI skin into the subject's headshape. The forward model was solved with a local spheres method (Huang, Mosher, & Leahy, 1999).

2.6.2. Beamforming

Source reconstruction was performed with Linearly Constrained Minimum Variance Beamformer (Veen, 1997). We followed a common filter approach that would ease the comparison between conditions (pleasant, neutral and unpleasant distraction): the spatial filter's coefficients were obtained from the average covariance matrix from trials belonging to all three conditions and then this filter was applied to each condition separately. This procedure is performed for each time window separately, so that the output of this source reconstruction step consists in a power estimate per source location, condition, time window and subject.

2.7.   Statistical analysis on source space

To search for differences in source power between conditions, dependent samples T-tests were performed. A clustering and permutation procedure was used to correct for multiple comparisons, as introduced for the Statistical analysis at sensor level section. However, the clustering step groups now spatially adjacent sources that show significant differences ($p<0.05$), and employs for that their 3D coordinates. 2000 permutations were used to obtain the final and corrected p-value.

3.   RESULTS

3.1.   Working memory performance

As expected, Friedman's test revealed a significant main effect of condition in WM accuracy [$\chi^2(3)=12.21$, $p=.001$)] (see Figure 6). Wilcoxon's test for pairwise comparisons revealed that accuracy after unpleasant distraction was lower than after pleasant ($p<.05$) and neutral ($p<.01$) distraction. No differences were found between neutral and pleasant distraction ($p>.1$).
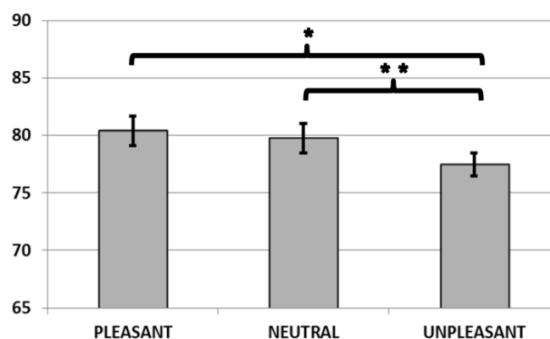
Figure 6. Mean accuracy (expressed as percent correct) in Experiment 2. Unpleasant distractors caused a detrimental effect on WM accuracy, compared to neutral and pleasant distractors, as well as to a scenario free of distraction (* $p<.05$; **$p<.01$). Error bars represent standard error of mean.

As each one of the 144 interfering pictures (48 pictures per condition) was used two times in each condition (see Procedure), one might be concerned about the possibility that a specific distraction might have produced less interference the second time it appeared than the first one, due to potential habituation effects. Although there was a minimum of thirty trials between the two presentations of the same interfering picture, and behavioral performance was similar than in the two experiments of the First Study (see Accuracy in Experiment 1 and Accuracy in Experiment 2), we compared

the mean accuracy for distractors presented for the first and second time, for each condition separately. Wilcoxon's tests showed that distracting pictures produced the same amount of interference both times they were presented as distractors for pleasant (p>.1), neutral (p>.1) and unpleasant (p>.1) conditions.

3.2.   Subjective emotional ratings

As expected, Friedman's test revealed a significant main effect of affective category in subjective valence ratings [χ^2(2)=30.00, p<.0001)], and Wilcoxon's test for pairwise comparisons showed that pleasant pictures were rated as the most pleasant followed by neutral pictures, and unpleasant pictures rated as the least pleasant [mean valence ratings: 7.14, sd=0.52 (pleasant), 5.09, sd=0.52 (neutral), 2.23, sd=0.82 (unpleasant), p<.0001 for all comparisons]. Arousal ratings also varied as a function of affective category [χ^2(2)=25.20, p<.0001)], with pleasant and unpleasant pictures rated as more arousing than neutral pictures [mean arousal ratings: 5.35, sd=1.20 (pleasant), 2.27, sd=0.5 (neutral), 6.48, sd=0.48 (unpleasant), p=.001 for both comparisons]. Unpleasant pictures were rated as more arousing than pleasant pictures (p<.01) (see Table 6 for mean subjective values).

3.3.   Event-related fields

The non-parametric cluster-based analysis performed on sensor-level data revealed three significant clusters of sensors that arose at three different temporal windows, indicating that the neuromagetic response to distracting emotional stimuli varied across conditions and in time. The first significant cluster (p>0.05) involved 35 right sensors and emerged between 70 and 130 ms after the onset of the distracting picture. The second cluster (p<0.05) emerged about 280-320 ms, across 23 right anterior

sensors. Finally, a third significant cluster ($p<0.05$) was composed by 36 sensors bilaterally distributed and arose between 360 and 455 ms. Figure 7 plots the time course of the average neuromagnetic response for each significant cluster (see Figure 7).
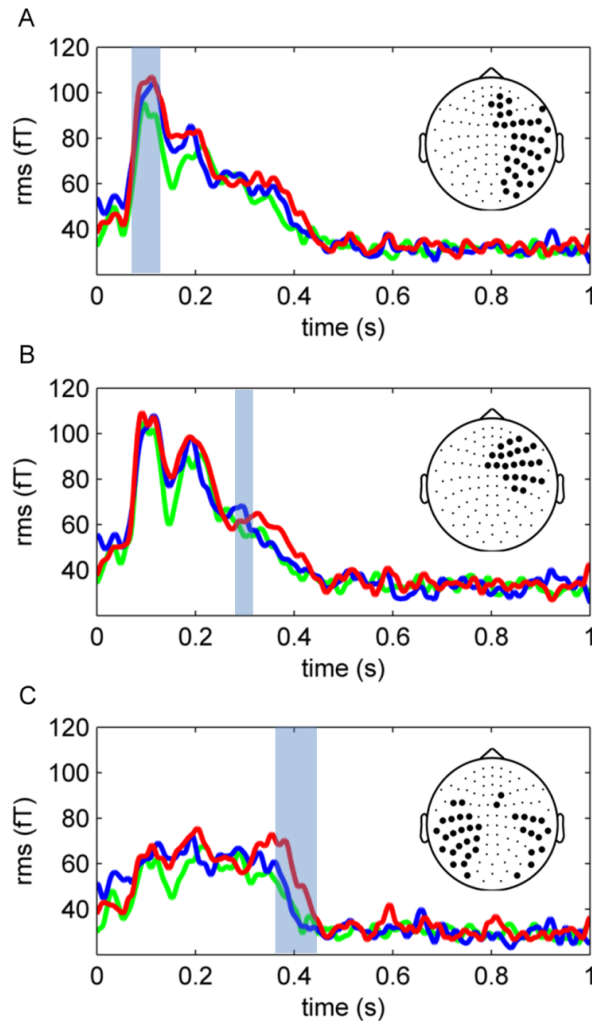
Figure 7. Root-mean-square of grandaverage ERF waveforms in significant clusters of sensors as detected by permutation statistics between 70-130 ms (A), 280-320 ms (B) and 360-455 ms (C). Insets depict sensor cluster locations.

Although the topographical distribution at sensor space does not faithfully represent the actual distribution of the underlying cortical sources, this first analysis showed significant effects of distraction type and pointed out the specific time windows were these differences emerged. Thus, source reconstruction was performed for these time intervals, to investigate the changes in brain activity originating the observed ERF differences.

3.4.   Source-space activity

Results from pairwise comparisons in each of one of the significant time windows identified at sensor level revealed differences between emotional and neutral distraction at early latencies (70-130 ms and 280-320 ms) and between unpleasant and both, pleasant and neutral distraction, at medium latencies (360-455 ms) at the source level.

Figure 8. Cortical distribution of statistical differences in source power between 70-130 ms. Emotional distractors enhanced source power in the DLPFC, the VLPFC, the OFC, the MPFC and the PosFC. Unpleasant distraction also produced increased activity in OC when compared with neutral distraction.

3.4.1. Early prefrontal enhanced activity by emotional distraction

Both emotional distractions produced a significantly increased brain activity about 70-130 ms when compared to neutral distraction. Particularly, pleasant distractors enhanced source power in a cortical bilateral cluster ($p < 0.0005$) composed by a number of frontal regions, including the DLPFC, the VLPFC, the OFC, the medial prefrontal cortex (MPFC) and the posterior frontal cortex (PosFC). Unpleasant distracters also increased activity in two clusters, one of them over left frontal cortices including the DLPFC, the VLPFC, the OFC, the MPFC and the PosFC ($p < 0.01$), while the other one ($p < 0.05$) was composed by the occipital cortex (OC) (see Figure 8 for cortical distribution of statistical differences in source power and Table 7 for specific cortical regions included in the clusters, as defined in the Automated Anatomical Labeling Atlas (AAL atlas) (Tzourio-Mazoyer & Landeau, 2002)).

3.4.2. Increased temporal activation by unpleasant distraction

Unpleasant distraction significantly enhanced activity in a left cortical cluster ($p < 0.05$), relative to neutral distraction.
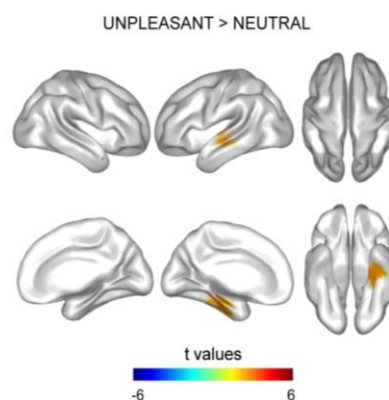
Figure 9. Cortical distribution of statistical differences in source power between 280-320 ms. Unpleasant distraction enhanced source power in the LTL, the MTL and the VTL.

This cluster of activity comprised regions over the superior (STC), lateral (LTC), medial (MTC) and ventral temporal cortex (VTC) (see Figure 9 for cortical distribution of statistical differences in source power and Table 7 for specific cortical regions included in the cluster, as defined in the AAL atlas (Tzourio-Mazoyer & Landeau, 2002)).

3.4.3. Cognitive control of emotional distraction at medium latencies

Negatively valenced emotional distraction significantly enhanced brain activity at 360-455 ms relative to neutral and positively valenced distractors. When compared with neutral distracters, unpleasant distraction increased brain signal in a bilateral cluster ($p<$ 0.005) distributed over the DLPFC, the VLPFC, the OFC, the MPFC and the PosFC, as wells as over the parietal cortex (PC) and the medial parietal cortex (MPC).
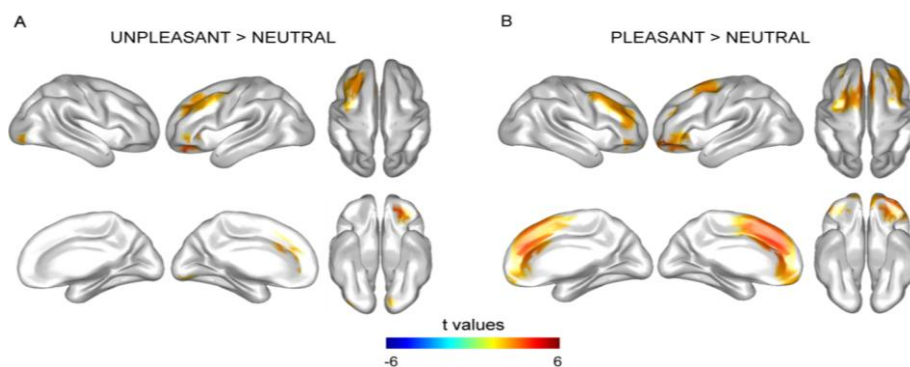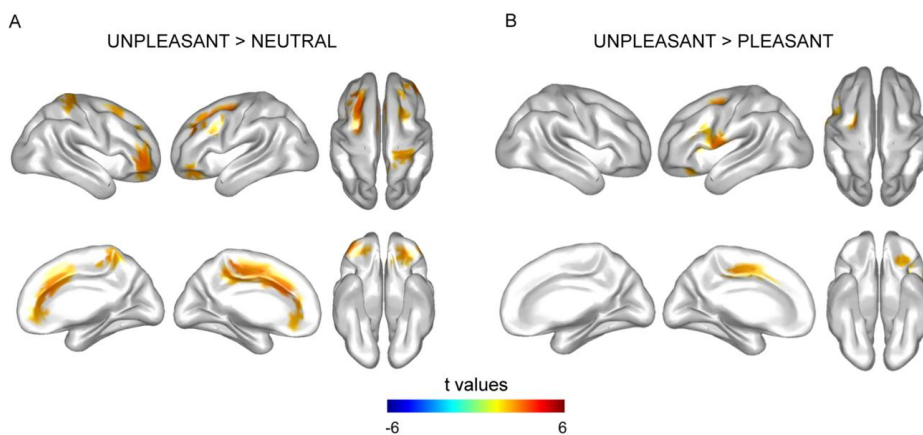

Figure 10. Cortical distribution of statistical differences in source power between 360-455 ms. Unpleasant distraction enhanced source power in the DLPFC, the VLPFC, the OFC, the MPFC, the PosFC and the PC when compared with both neutral and pleasant distraction.

Unpleasant distracters also increased cortical activity when compared with pleasant ones, in a left lateralized cluster ($p<0.05$) which included the DLPFC, the VLPFC,

the OFC, the MPFC, the PosFC and PC (see Figure 10 for cortical distribution of statistical differences in source power and Table 7 for specific cortical regions included in the cluster, as defined in the AAL atlas (Tzourio-Mazoyer & Landeau, 2002)).

3.4.4. Brain activity and behavioral performance

To further investigate the physiological meaning of the reported differences in brain activity while coping with emotional distraction, we segmented significant clusters into smaller regions as defined in the AAL atlas (Tzourio-Mazoyer & Landeau, 2002) (see Table 7) and correlated the activity of the source that showed the maximal power in each region with task accuracy, for every experimental condition in each contrast and time window.
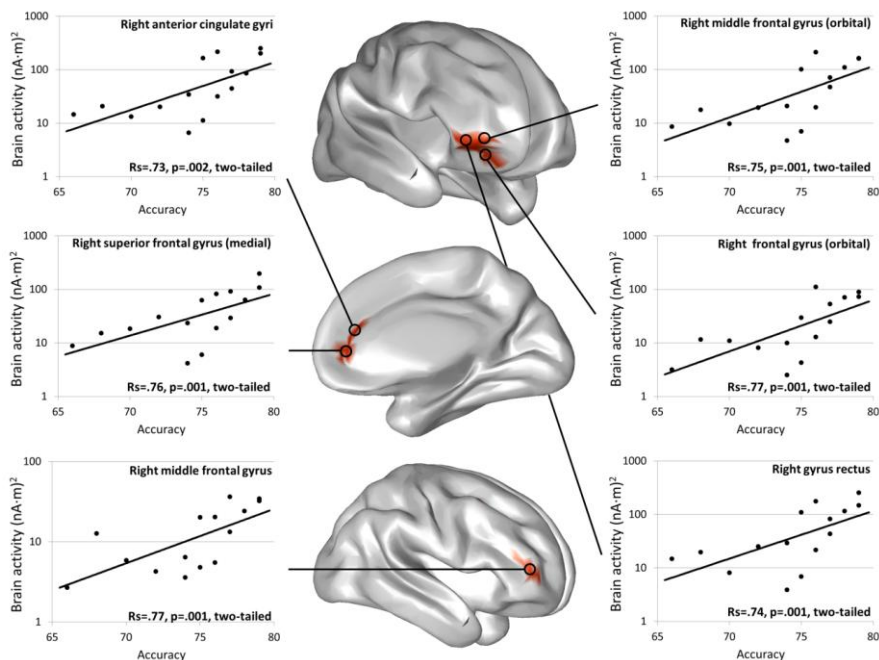
Figure 11. The role of the prefrontal cortex in coping with emotional distraction. The brain activity in specific regions of the DLPFC, the MPFC and the OFC at the 360-455 ms latency of unpleasant distraction processing positively correlated with successful performance at the recognition stage of that condition of the WM task.

No significant correlations for any condition were found during the first and second temporal windows [False discovery Rate (FDR) corrected q=.05, for all correlations]. In the third temporal window, activity in specific regions of the right OFC, DLPFC and MPFC in unpleasant distraction positively correlated with accuracy, so that volunteers with greater activity over those prefrontal cortices were those who performed better at the recognition stage of that condition (p<.05, FDR corrected q=.05, for all the reported correlations) (see Figure 11 for specific localizations of brain regions, scatter plots, correlation coefficients and significance values).No significant correlations were found between brain activity and accuracy for neutral or for unpleasant distraction (FDR corrected q=.05, for all correlations), during this time window.

L Hemisphere	R Hemisphere

70-130 ms Pleasant > Neutral

DLPFC	DLPFC
Superior frontal gyrus	Superior frontal gyrus
Middle frontal gyrus	Middle frontal gyrus
VLPFC	**VLPFC**
Inferior frontal gyrus (triangular part)	Inferior frontal gyrus (triangular part)
	Inferior frontal gyrus (opercular part)
OFC	**OFC**
Superior frontal Gyrus (orbital part)	Superior frontal Gyrus (orbital part)
Middle frontal gyrus (orbital part)	Middle frontal gyrus (orbital part)
Inferior frontal gyrus (orbital part)	Inferior frontal gyrus (orbital part)
Superior frontal gyrus (medial orbital part)	Superior frontal gyrus (medial orbital part)
Gyrus rectus	
MPFC	**MPFC**
Superior frontal gyrus (medial part)	Superior frontal gyrus (medial part)
Anterior cingulate gyri	Anterior cingulate gyri
Median cingulate gyri	Median cingulate gyri
PosFC	**PosFC**
Precentral gyrus	Precentral gyrus
Supplementary motor area	Supplementary motor area

70-130 ms Unpleasant > Neutral

DLPFC	MPFC
Superior frontal gyrus	Anterior cingulate gyri
Middle frontal gyrus	

VLPFC	OC
Inferior frontal gyrus (triangular part)	Inferior occipital gyrus Middle occipital gyrus
OFC	
Superior frontal Gyrus (orbital part) Middle frontal gyrus (orbital part) Inferior frontal gyrus (orbital part) Superior frontal gyrus (medial orbital part) Gyrus rectus	
MPFC	
Superior frontal gyrus (medial part) Anterior cingulate gyri Median cingulate gyri	
PosFC	
Precentral gyrus Supplementary motor area	

280-320 ms Unpleasant > Neutral

STL	
Superior temporal gyrus Heschl gyrus	
LTC	
Middle temporal gyrus Inferior temporal gyrus	
MTL	
Hippocampus Parahippocampal gyrus	
VTL	
Fusiform gyrus	

360-455ms Unpleasant > Neutral

DLPFC	DLPFC
Superior frontal gyrus Middle frontal gyrus	Superior frontal gyrus Middle frontal gyrus
VLPFC	**VLPFC**
Inferior frontal gyrus (triangular part) Insula	Inferior frontal gyrus (triangular part)
OFC	**OFC**
Superior frontal gyrus (orbital part) Middle frontal gyrus (orbital part) Inferior frontal gyrus (orbital part) Superior frontal gyrus (medial orbital part) Gyrus rectus	Middle frontal gyrus (orbital part) Inferior frontal gyrus (orbital part) Superior frontal gyrus (medial orbital part)
MPFC	**MPFC**
Superior frontal gyrus (medial part) Anterior cingulate gyri Median cingulate gyri	Superior frontal gyrus (medial part) Anterior cingulate gyri Median cingulate gyri

PosFC	PosFC
Precentral gyrus	Precentral gyrus
Paracentral lobule	Paracentral lobule
Supplementary motor area	Supplementary motor area
PC	PC
Postcentral gyrus	Postcentral gyrus
Precuneus	Precuneus
	Inferior parietal gyrus

360-455ms Unpleasant > Pleasant

DLPFC	
Superior frontal gyrus	
Middle frontal gyrus	
VLPFC	
Inferior frontal gyrus (triangular part)	
Inferior frontal gyrus (opercular part)	
Insula	
OFC	
Middle frontal gyrus (orbital part)	
Inferior frontal gyrus (orbital part)	
MPFC	
Anterior cingulate gyri	
Median cingulate gyri	
PosFC	
Precentral gyrus	
Paracentral lobule	
Supplementary motor area	
Rolandic operculum	
PC	
Postcentral gyrus	

Table 7. Parcellation of significant clusters into smaller regions, as defined in the AAL atlas (Tzourio-Mazoyer et al., 2002). Segmentation was performed for clusters obtained from every statical contrast, within each temporal window of interest.

4.   DISCUSSION AND CONCLUSIONS

Previous studies have shown that emotional stimuli can impair the retention of task-relevant information when they are presented as distractors in WM. Most of those studies have focused on the effect of unpleasant emotional distractors and their power as interfering stimuli have been linked to its biological relevance for survival (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006). However, a recent study from our group (see the First Study of the present work) has

shown that other type of emotional distractors, those represented by pleasant stimuli, were not so able to interfere WM maintenance, as unpleasant distractors were. Results of the present study further replicate that behavioral effect, showing greater impairment of WM maintenance after unpleasant distraction, while pleasant distracters did not affect WM retention more than neutral ones.

However, the main objective of the present work was to unravel the temporal profile of the brain mechanism that underlies the cognitive control of emotional distraction in WM. To date, all the studies in this field have focused on establishing the brain areas responsible of that mechanism, while the temporal dynamics of that process have remained unexplored. Using a spatio-temporal cluster-based approach, we identified three temporal windows of interest, in which differences of activity between distractor types arose. During the earliest significant temporal window, about 70-130 ms, both types of emotional distraction increased the brain activity when compared with neutral distraction, specifically over frontal cortices including prefrontal regions such as the DLPFC, the VLPFC, the OFC, and the MPFC. Activity in these prefrontal regions, particularly in the DLPFC and the anterior cingulate cortex (ACC) has been traditionally related to cognitive control processes during WM maintenance (D'Esposito et al., 2000; Nee et al., 2013; Smith & Jonides, 1999), and activity in ventral cortices such as the VLPFC and the OFC has also been linked to mechanisms of coping with emotional distraction in WM (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013a, 2006). However, the very early latency of those differences overlapped stages of processing that are mainly linked to the detection of visual stimulation, rather than to the cognitive control of this stimulation (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Di Russo, 2003; Hillyard & Anllo-

Vento, 1998). Besides, activity in those areas did not correlate with successful performance in the WM task, so that it does not seem probable that the early engagement of those prefrontal cortices was implicated in coping with emotional distraction. Many studies have highlighted the central role of top-down modulation in visual processing (see Bar, 2003 for a review), since the prefrontal cortex has been reported active in visual recognition (Freedman, Riesenhuber, Poggio, & Miller, 2001; Parker, Wilding, & Akerman, 1998; Wilson, Scalaidhe, & Goldman-Rakic, 1993) and, more interestingly, during visual processing of emotional stimuli (Kawabata & Zeki, 2004; Kawabata et al., 2001; Northoff et al., 2000; Paradiso et al., 1999; Simpson et al., 2000). Moreover, activity in the prefrontal cortex during both emotional and non-emotional visual stimulation has been shown at very early latencies, about 100 ms after the onset of the stimuli (Freedman et al., 2001; Funahashi, Bruce, & Goldman-Rakic, 1990; Kawabata et al., 2001; Thorpe, Rolls, & Maddison, 1983). Such an early response of the prefrontal cortex during visual processing has been interpreted as a top-down mechanism that facilitates visual recognition, based on three components: 1) Low spatial frequencies in the visual stimuli are rapidly projected from early visual cortices to the prefrontal cortex, through the magnocellular pathway, which is known to early and quickly carry low frequency information (Bullier & Nowak, 1995; Maunsell, Nealey, & DePriest, 1990; Merigan & Maunsell, 1993; Shapley, 1990); 2) such a low frequency information activates simultaneous expectations for the recognition of the visual stimuli, in the prefrontal cortex; 3) finally, these expectations would be back-projected to posterior areas such as the inferior temporal cortex, where they activate the corresponding object representations that are combined with the bottom-up information for the final object recognition (Bar, 2003). This top-down processing of

partial visual information reduces the possible interpretations of the input and minimizes the amount of time required for the object recognition, which may be extremely helpful when the visual stimulus represents biologically relevant information. According to this model proposed by Bar (2003), increased prefrontal activation at early latencies of both pleasant and unpleasant distraction processing would reflect a top-down mechanism that may improve our preparation to adaptively respond to linked-to-survival stimuli. Particularly, enhanced activity in the OFC, which has been related to guessing processes and generation of expectations (Bechara, Tranel, Damasio, & Damasio, n.d.; Browning & Harmer, 2012; Elliott, Rees, & Dolan, 1999; Noonan, Mars, & Rushworth, 2011), would be crucial for the rapidly identification of biological information, as such contained in emotional distractors.

Notwithstanding, the fast detection of emotional information *per se* is not enough for the cognitive control process required to override its influence when presented as a distractor. Our results also identified a later significant temporal window, about 360-455 ms, in which unpleasant distraction increased the brain activity when compared with both pleasant and neutral distraction. Differences in activity were distributed over the DLPFC, the VLPFC, the OFC, the MPFC and the PosFC, as well as over the PC. As commented above, activity in the DLPFC, the ACC and the PC has been largely related to successful performance in WM tasks (Berryhill & Olson, 2008; D'Esposito et al., 2000; Derrfuss et al., 2004; Koenigs et al., 2009; Nee et al., 2013; Smith & Jonides, 1999), and these regions, along with the VLPFC and the PosFC, have been reported as important areas for interference resolution and inhibition of prepotent responses (Braver, Cohen, & Barch, 2002; Derrfuss et al., 2004; Jha, Fabian, & Aguirre, 2004; Menon, Adleman, White, Glover, & Reiss, 2001; Petrides, 2000; Picard & Strick, 2001).

Further analysis of our data revealed that activity in specific regions of the right DLPFC, the right MPFC -including the ACC- and the right OFC -including a portion of cortex that overlaps the inferior section of the VLPFC- positively correlated with successful recognition after unpleasant distraction. Although the VLPFC and specific regions of the DLPFC and the MPFC has previously been linked to mechanisms of coping with unpleasant emotional distraction in WM (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013a, 2008, 2006), the OFC has not been extensively related to successful control of such distraction (Anticevic et al., 2010). However, it does play an important role in tasks that require to inhibit prepotent responses (Casey et al., 1997; B. Jones & Mishkin, 1972; Kowalska, Bachevalier, & Mishkin, 1991), specially when such responses were established upon their previous reward value (Iversen & Mishkin, 1970). Taking into account that the attentional capture by emotional distraction may be seen as a prepotent attentional response that should be overridden in our task, it is conceivable that the OFC appeared implicated in inhibition of such an attentional response. Altogether, these results are in consonance with previous fMRI studies that have highlighted the implication of the VLPFC in coping with unpleasant emotional distraction (Anticevic et al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013a, 2006), and extend the evidence of activity in the DLPFC, the MPFC and the OFC in relation to the cognitive control of unpleasant distractors in WM (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008). Furthermore, that significant enhancement of activity about 360-455 ms, when effective control of distraction seemed to take place, were restricted to unpleasant distraction. This fact suggests that such a control mechanism may be exclusive for unpleasant distraction. The absence of differences

between pleasant and unpleasant distractors also suggests that coping with positively valenced distractors would not require additional resources to those engaged when coping with neutral ones, as reflected by an equivalent WM performance at the behavioral level (see the First Study of the present work and the Working memory performance section of the present study).

Finally, results from our analysis also revealed a third significant temporal window that arose about 280-320 ms, between those temporal windows commented above. Pairwise comparisons at the source space revealed that unpleasant distraction enhanced the brain activity when compared with neutral distraction. Particularly, this enhancement of activity appeared over the superior, lateral, medial and ventral surfaces of the left temporal lobe. Dolcos and cols. (2013) have recently proposed that the impairing effect of unpleasant emotional distraction in WM may co-occur with the consistently observed effect of enhanced episodic memory for emotional events (see Dolcos et al., 2012, 2011 for a review). Their results showed greater activity in the MTL for those unpleasant distractors that impaired WM performance but were successfully remembered one week later. Furthermore, emotional distractors that did not impair WM were also accurately remembered on the episodic memory test. We proposed that the higher activity over the left temporal lobe in the unpleasant distraction condition of our task might be reflecting this effect of episodic memory enhancement for the unpleasant distractors themselves. However, this interpretation is only tentative, as we did not test the subsequent episodic memory for the distractors in our volunteers, and therefore we were not able to test a potential relation between temporal lobe activity and subsequent episodic memory for the distractors.

Although most of the previous studies in this field have identified a dissociable pattern of activity between dorsal cortical regions and ventral brain areas (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013a, 2008) when coping with emotional distraction, our results did not show any deactivation over the DLPFC and PC. Moreover, the dorsal activity identified in our analysis was always higher for emotional distracters than for neutral ones. However, all the previous studies that found such dorsal deactivations employed fMRI for their experiments. As the functional signal recorded in fMRI has a different origin than the MEG signal, since the first relies in the slow hemodynamic response while the latter records the very fast electromagnetic changes (Buckner & Logan, 2006; Lopes da Silva, 2010), our results may not be straightforward compared with previous fMRI results. Nevertheless, the present study is not the first one reporting enhanced activity in dorsal cortices while coping with emotional distraction (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008) and extends the wealthy literature that links the DPFC with emotion processing (see Ochsner et al., 2012 for a review). In spite of these differences, the enhanced activity over ventral prefrontal cortices for emotional distraction in our results is consistent with previous literature concluding that the right VLPFC is critically engaged in coping with emotional distraction. Further, our results suggest that specific regions of the right OFC, partially overlapping the VLPFC, would also be important for overriding the emotional distraction.

In summary, the present study reveals for the first time the temporal dynamics of the brain mechanisms that are responsible for our capacity to deal with emotional distractors in WM. At the very early latencies of the distractor processing, prefrontal mechanisms are engaged for the rapid detection of both pleasant and unpleasant

emotional distraction. Later in the processing, unpleasant distractors seem to recruit a specific cognitive control mechanism when compared with neutral and pleasant distractors. Such a mechanism depends on activity over the DLPFC, the MPFC and the OFC. Finally, in the meantime between the early detection and the effective control of the emotional distraction the increased activity in the temporal lobe, specially in the MTL, might be reflecting the well-known enhancement memory effect for emotional materials. The present findings contribute to extend our knowledge regarding the brain mechanisms of coping with emotional distraction in WM, and clarify for the first time the temporal dynamics of those cognitive control mechanisms.

THIRD STUDY

Dynamics of functional brain networks of coping

with emotional distraction in working memory

1.   INTRODUCTION

Active maintenance of information is the result of synchronized and sustained activity within local groups of neurons and over functional networks widely distributed across the brain (Fuster & Alexander, 1971; E. K. Miller, 1996; Uylings, 1990). Traditional approaches in neuroscience have demonstrated that several cortical regions across the fronto-parietal cortex support WM maintenance (Curtis & D'Esposito, 2003; Linden et al., 2003; Pessoa et al., 2002; Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000; Rowe et al., 2000; Todd & Marois, 2004) and that occipital and temporal areas are related with the formation of sensory representation in visual WM (Desimone, 1998; Fuster, 1990; E. K. Miller & Desimone, 1994; E. K. Miller, Li, & Desimone, 1991; Miyashita, 2000; Ranganath, DeGutis, & D'Esposito, 2004). Moreover, recent investigations have shown that sustained long-range functional coupling between frontal and posterior areas is a key mechanism for maintaining information in WM (Gazzaley et al., 2004; Palva et al., 2010; Rissman et al., 2004, 2008; Sarnthein, 1998; Sauseng et al., 2005). Since interference effects of irrelevant information in short-term memory have become an exciting field of research in cognitive psychology (see Jonides et al., 2008 for a review),

there is also an increasing interest in how interfering information affects such fronto-posterior network and how our cognitive system is able to override the influence of distraction in such dynamic functional interactions.

Several neuroimaging studies that have explored the effect of distraction on the functional network that sustains WM have focused in the prefrontal cortex and the posterior areas of the brain. Yoon and cols. (Yoon et al., 2006) have focused on the functional coupling of the DLPFC and the visual associative cortex during the delay period of a WM task with distraction. They showed that distractors with high similarity to the memorized material produced a disruption of the functional coupling between the DLPFC and the visual associative cortex, suggesting that the active maintenance of information is an emergent function of cooperative activity between the lateral PFC and the posterior sensory cortex. More interestingly, such a disruption of the fronto-posterior functional connectivity has been shown to be restored after the presentation of the interfering stimuli (Clapp et al., 2010). This result was interpreted as a mechanism responsible for the reactivation of the information previously encoded, as the middle frontal gyrus is known to be implicated in refreshing the memorized information during the delay period (Johnson, 2003; B. T. Miller, Verstynen, Johnson, & D'Esposito, 2008).

However, to the best of our knowledge, no studies have addressed the effect of emotional distraction in the cortical functional networks that sustains WM maintenance, as all the studies have focused on cortico-subcortical connections (Chuah et al., 2010; Dolcos et al., 2006). In accordance with previous literature, activity in the VLPFC, the DLPFC and the MPFC were shown highly coupled with activity in the amygdala during successful coping with emotional distraction. Finally, a recent fMRI

study (Clarke & Johnstone, 2013) has assessed the effective connectivity pattern during the maintenance period of a WM task, in which anxiety was inducted by threat of electric shock. Results of this study showed that the VLPC and the ACC exerted a top-down modulation of the amygdala and its output to the prefrontal cortex, inhibiting threat processing and enabling WM performance without threat-related interference.

In this study we address the potential effect of emotional distraction in fronto-posterior cortical networks that have been related to the active maintenance of information in WM. Based on the existent literature showing a disruption of those functional connections (Clapp et al., 2010; Yoon et al., 2006) we expect that the fronto-posterior network would be more disrupted by emotional distractors than by neutral ones. Given the emotional nature of our distractors, and according with the extensive literature that links the VLPFC to the successful coping with emotional distraction (Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013a, 2006; Iordan, Dolcos, & Dolcos, 2013; see also the Second Study of the present work) we also hypothesize that this prefrontal region would be highly functionally coupled with posterior areas.

2.   METHOD

2.1.   Participants, materials, procedure and data acquisition and preprocessing

Since participants in this study were the same than in the Second Study, age and demographic information was exactly the same (see Table 5). Procedure, materials, data acquisition and preprocessing were also the same than in Second Study: WM task, faces at the encoding and recognition stages as well as emotional pictures from IAPS (Lang et

al., 2005), MEG data collection and preprocessing (see Materials, procedure and Data acquisition and preprocessing of the Second Study).

2.2.   Source reconstruction

Based on the results obtained in the ERF analysis (see Event-related fields in the Second Study), we focused on three time windows for source reconstruction: 70-130ms, 280-320 ms and 360-455ms. As longer time series generate more robust entropy and Mutual Information estimates (Knuth, 2006), temporal windows were enlarged to 100 ms, so that the final temporal windows of interest for source reconstruction and further functional connectivity analysis were 50-150 ms, 250-350 ms and 360-460 ms. The same headmodels were used as in section Headmodels in the Second Study: 2471 points in MNI space that were transformed to each individual, and a local spheres method was employed for the forward modelling. The inverse problem was solved with beamforming (see Beamforming section, in the Second Study), yielding a time series per source location, condition, time window and subject.

2.3.   Functional connectivity

Functional connectivity was computed between each pair of Regions of Interest (ROIs). Sources were first grouped into ROIs using their MNI coordinate and the AAL atlas (Tzourio-Mazoyer & Landeau, 2002), as implemented in the WFU software (Maldjian et al., 2003). For each hemisphere, 41 cortical regions (a total of 82 cortical regions) were included. Next, the correlation between all sources belonging to a same cortical region was computed and the time series of the source with higher correlation values was selected as the representative time series for this cortical region, as proposed by Hillebrand and cols. (Hillebrand, Barnes, Bosboom, Berendse, & Stam,

2012). Then, functional connectivity between each pair of cortical region and trial was computed, using Mutual Information (MI). MI assesses the relationship between two time series using Shannon Entropy (Shannon & Weaver, 1949) and Information Theory (Pereda, Quiroga, & Bhattacharya, 2005), capturing both linear and nonlinear interactions. It quantifies the amount of information that is shared between two source time series. Mutual Information values were averaged over trials, yielding an 82x82 connectivity matrix per subject and condition.

2.4.   Statistical analysis

To compare functional connectivity between conditions, Friedman tests were first performed and a set of links with significant effects (p<0.005) was obtained. For significant links, pairwise comparisons were performed using Wilcoxon tests. Links with p-values under 0.005 were further submitted to a permutation procedure applied to correct them for multiple comparisons (Maris & Oostenveld, 2007). This procedure was similar to the one described in Statistical analysis on source space section of the Second Study. MI values were randomized and new Wilcoxon tests were performed, yielding a set of 2000 randomized W values. Then, the original W value was compared with the distribution of randomized W to obtain the final and corrected p-value. Only results with p<.005 were considered as significant links.

3.   RESULTS

3.1.   Working memory performance and emotional ratings

As participants and WM task were the same than those described in the Second Study, WM performance was different across distraction conditions [$\chi^2(3)$=12.21,

p=.001)]. Accuracy after unpleasant distraction was lower than after pleasant (*p*<.05) and neutral (*p*<.01) distraction, and no differences were found between neutral and pleasant distraction (*p*>.1). Subjective emotional ratings were equal to those reported in the Second Study (see Working memory performance and Subjective emotional ratings of the Second Study for complete information).

3.2.   Brain Connectivity

Results from pairwise comparisons after correction for multiple comparisons (see Statistical analysis) revealed higher level of brain connectivity in neutral distraction than in both emotional distractions, as well as higher level of connectivity in pleasant than in unpleasant distraction, at the very early temporal window (50-150 ms). By contrast, at the subsequent temporal windows (250-350 ms and 360-460 ms), unpleasant distraction increased the level of connectivity when compared with both pleasant and neutral distraction. Pleasant distraction also yielded higher connectivity values than neutral distraction in the last two temporal windows.

3.2.1. Emotional-based depletion of brain functional connectivity

Functional connectivity between brain hemispheres was higher in neutral distraction than in emotional distraction during the first temporal window of interest, between 50 and 150 ms. Specifically, functional coupling between parietal cortices, temporal cortices, as well as posterior frontal and posterior parietal cortices was higher in neutral than in unpleasant distraction. Interhemispheric functional connectivity between the posterior cingulum and the PC was also higher in neutral than in pleasant distraction. Finally, functional coupling between left anterior temporal regions and the left posterior PC was higher in pleasant than in unpleasant distraction (see Figure 12 and

Table 8 for specific functional connections between cortical areas, as defined in the AAL

atlas (Tzourio-Mazoyer & Landeau, 2002)).
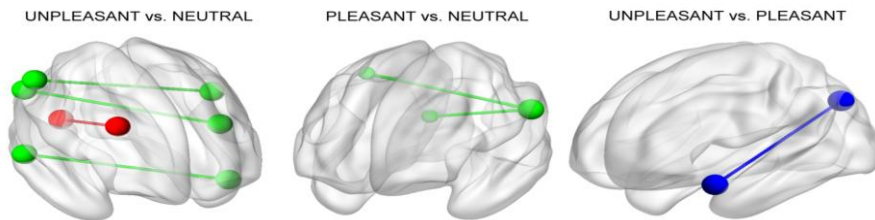
Figure 12. Statistical differences in functional brain connectivity at 50-150 ms. Interhemispheric functional connectivity over parieto-temporal cortices was higher in neutral distraction than in both pleasant and unpleasant distraction. Functional coupling between temporal and parietal regions was also higher in pleasant than in unpleasant distraction. Links in green represent significant higher connectivity for neutral distraction; links in red represent significant higher connectivity for unpleasant distraction; and links in blue represent significant higher connectivity for pleasant distraction.

3.2.2. Prefrontal-posterior coupling and the restoring of WM network

Unpleasant distraction significantly increased the level of connectivity between

the prefrontal cortex and the posterior as well as the temporal cortex, between 250-350

ms. Specifically, functional coupling between the right VLPFC cortex and the right PC-OC,

and between the right DLPFC cortex and the left PC was higher in unpleasant than in

neutral distraction, as well as between the ventral occipital cortex of both hemispheres.

Unpleasant distraction also increased functional coupling between the right OFC and the

right anterior temporal lobe when compared with pleasant distraction. Finally, pleasant

distraction produced higher functional connectivity between the VLPFC and the PC of

the right hemisphere than neutral distraction (see Figure 12 and Table 8 for specific

functional connections between cortical areas).
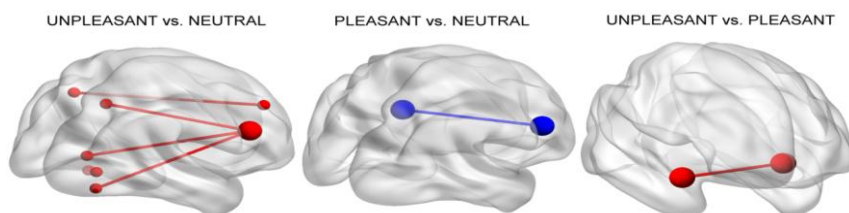
Figure 13. Statistical differences in functional brain connectivity at 250-350 ms. Functional connectivity between the right frontal and posterior areas was higher in both pleasant and unpleasant than in neutral distraction. Functional coupling between the right OFC and the temporal cortex was also higher in unpleasant than in pleasant distraction. Links in red represent significant higher connectivity for unpleasant distraction; and links in blue represent significant higher connectivity for pleasant distraction.

3.2.3. Increased functional coupling by unpleasant distraction

Unpleasant distraction significantly increased the level of connectivity between the prefrontal, the parietal, the medial temporal cortex, and the superior temporal cortex more than neutral distraction.
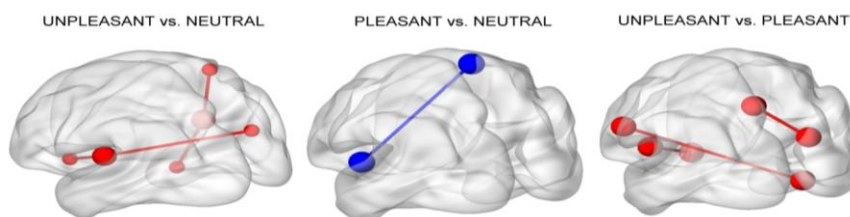
Figure 14. Statistical differences in functional brain connectivity at 360-460 ms. Unpleasant distraction enhanced functional connectivity in a network that comprised prefrontal, parietal and temporal cortices more than both neutral and pleasant distractors. Functional interhemispheric coupling between the PosFC and the temporal cortex was also higher in pleasant than in neutral distraction. Links in red represent significant higher connectivity for unpleasant distraction; and links in blue represent significant higher connectivity for pleasant distraction.

Unpleasant distraction also increased functional coupling between the bilateral OFC and the right ventral OC, as well as with the left insula, and between the left PC and the right OC, when compared with pleasant distraction. Finally, pleasant distraction increased interhemispheric functional connectivity between the PosFC and the STC more than neutral distraction (see Figure 12 and Table 8 for specific functional connection between cortical areas).

### 3.2.4. Brain connectivity and behavioral performance

In order to explore the meaning of the differential connectivity patterns described above, in the context of coping with emotional and non-emotional distraction, we correlated the mutual information value of every single significant link between brain areas with task accuracy, for every experimental condition in each contrast and time window. No significant correlations for any condition were found during the first temporal windows (FDR corrected q=.05, for all correlations).

In the second temporal window, functional coupling between a specific region of the right VLPFC and the right occipital cortex in unpleasant distraction positively correlated with accuracy, so that participants with stronger coupling between those brain regions were those who achieved higher accuracy at the recognition stage of that condition (p<.01, FDR corrected q=.05). Finally, in the last temporal window, functional coupling between a specific portion of the left OFC and the left STC in neutral distraction positively correlated with accuracy, so that volunteers with stronger coupling between those brain regions were those who performed better at the recognition stage of that condition (p<.001, FDR corrected q=.05). No more significant correlations were found between other significant links and accuracy for any condition during these latters

temporal windows (FDR corrected q=.05, for all correlations) (see Figure 15 for specific brain functionally coupled regions, scatter plots, correlation coefficients and significance values).

50-150 ms

UNPLEASANT > NEUTRAL	UNPLEASANT < NEUTRAL
R Mid FG - R Calcarine	L Rolandic Operc - R Angular G R Inf Pariet G - L Supramarg G L Temp Pole - R Mid Temp G

PLEASANT > NEUTRAL	PLEASANT < NEUTRAL
	L Supramarg G - R Post Cing G L Supramarg G - R Inf Pariet G

UNPLEASANT > PLEASANT	UNPLEASANT < PLEASANT
	L Temp Pole - R Angular G

250-350 ms

UNPLEASANT > NEUTRAL	UNPLEASANT < NEUTRAL
R Mid FG - L Supramarg G R Inf FG oper - R Inf Occip G R Inf FG oper - R Calcarine R Inf FG oper - R Precuneus R Lingual G - R Fusiform G	

PLEASANT > NEUTRAL	PLEASANT < NEUTRAL
R Mid FG orb - R Precuneus	

UNPLEASANT > PLEASANT	UNPLEASANT < PLEASANT
R Mid FG orb - L Temp Pole	

360-460 ms

UNPLEASANT > NEUTRAL	UNPLEASANT < NEUTRAL
L Rectus G - L Heschl G R Cuneus - L Heschl G R Poscentr G - R Heschl G R Parahippoc G - R Heschl G	

PLEASANT > NEUTRAL	PLEASANT < NEUTRAL
R Paracentr Lob - L Sup Temp G	

UNPLEASANT > PLEASANT	UNPLEASANT < PLEASANT
L Inf FG orb - R Fusiform G R Rectus G - L Insula R Cuneus - L Precuneus	

Table 8. Significant connections between cortical regions as defined in the AAL atlas (Tzourio-Mazoyer et al., 2002). A total of 82 cortical regions (41 regions per hemisphere) were included in the analysis. R: Right hemisphere; L: Left hemisphere; Mid FG: middle frontal gyrus; Mid FG orb: middle frontal gyrus (orbital part); Inf FG oper: inferior frontal gyrus (opercular part); Rectus G: gyrus rectus; Post Cing G: posterior cingulate gyrus; Rolandic Operc: Rolandic operculum; Paracentr Lob: paracentral lobule; Poscentr G: postcentral gyrus; Inf Pariet G: inferior parietal gyrus; Supramarg G: supramarginal gyrus; Angular G: Angular gyrus; Sup Temp G: superior temporal gyrus; Mid Temp G: middle temporal gyrus; Heschl G: heschl gyrus; Temp Pole: temporal pole (superior temporal gyrus); Parahippoc G: parahippocampal gyrus; Lingual G: Lingual gyrus; Fusiform G: fusiform gyrus; Inf Occip G: inferior occipital gyrus; Calcarine: calcarine fissure and surrounding cortex.

4.   DISCUSSION AND CONCLUSIONS

Previous research has shown that long-range functional coupling between frontal and posterior areas plays an important role in maintaining information in WM (Gazzaley et al., 2004; Palva et al., 2010; Rissman et al., 2004, 2008; Sarnthein, 1998; Sauseng et al., 2005). Additionally, recent studies have demonstrated that interfering information can impair WM retention by disrupting the functional coupling between the prefrontal cortex and the PC and other posterior areas (Clapp et al., 2010; Yoon et al., 2006). However, the specific effect of emotional distraction in such a fronto-posterior network has not been explored yet, although the VLPFC is thought to be crucial as it has been reported active in coping with emotional distraction (Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013, 2006; Iordan et al., 2013; see also the Second Study of the present work), and functionally coupled with amygdala while overriding this kind of distractors (Chuah et al., 2010; Dolcos et al., 2006).
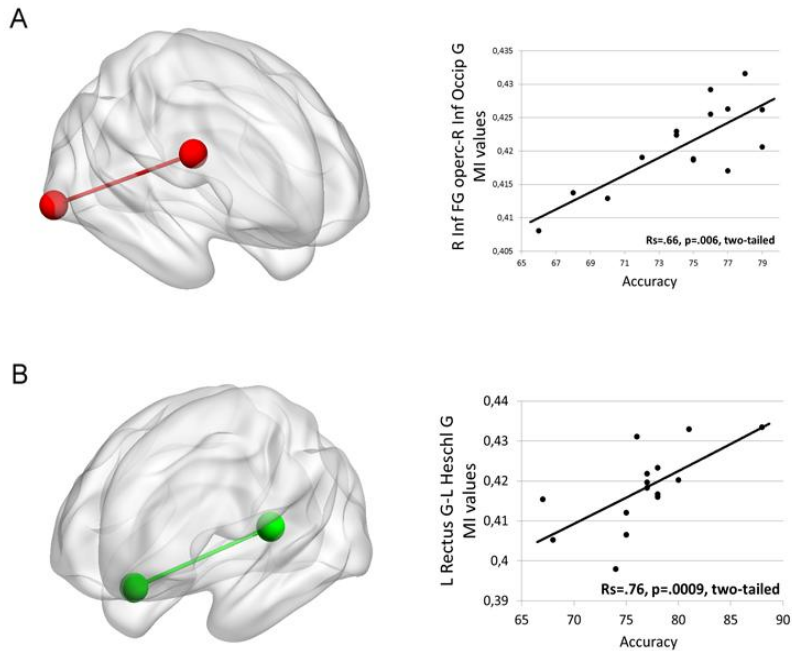
Figure 15. The role of dorsal fronto-posterior functional connectivity in coping with emotional distraction. A: The functional coupling between the right VLPFC and the right occipital cortex at the 250-350 ms latency of unpleasant distraction processing positively correlated with successful performance at the recognition stage of that condition of the WM task. B: The functional coupling between the left OFC and the left temporal lobe at the 360-460 ms latency of neutral distraction processing positively correlated with successful performance at the recognition stage of that condition of the WM task. The red link represents functional connectivity between cortical regions while coping with unpleasant distraction; the green link represents functional connectivity between cortical regions while coping with neutral distraction.

Based on results obtained in a previous ERF analysis (see Event-related fields in the Second Study), we focused on three temporal windows of interest, in which differences between emotional and neutral distraction arose at the brain activity level, and we performed a whole-brain functional connectivity analysis.During the earliest temporal window of interest, between 50 and 150 ms, both types of emotional distractors seemed to reduce functional connectivity when compared with neutral

distraction, and this reduction appeared mostly between parieto-temporal cortices of both hemispheres. The parieto-temporal cortex is part of the fronto-posterior network widely related with WM maintenance (Gazzaley et al., 2004; Palva et al., 2010; Rissman et al., 2004, 2008; Sarnthein, 1998; Sauseng et al., 2005) and it has been consistently reported active during retention of information in WM (e.g. Corbetta, Kincade, & Shulman, 2002; Courtney, Ungerleider, Keil, & Haxby, 1997; Curtis & D'Esposito, 2003; Miyashita, 2000; Ranganath et al., 2004; Todd & Marois, 2004). Moreover, cortical regions surrounding the intraparietal sulcus are considered a primary hub in the network that sustains WM (Palva et al., 2010). Therefore, the observed functional disruption of this component of the fronto-posterior network, in comparison with neutral distraction, would be reflecting the attentional capture of emotional distractors while maintaining relevant information in WM. This interpretation is consistent with previous findings of disrupted functional connectivity in WM at the time an interfering stimulus is encountered (Clapp et al., 2010; Yoon et al., 2006). At the same time, unpleasant distraction also increases functional connectivity between the DLPFC and the OC of the right hemisphere. Since the DLPFC, among other prefrontal regions, has been reported active during visual recognition and, at early latencies of such a processes (Barbas, 1995; Funahashi et al., 1990; Paradiso et al., 1999; see also the Second Study of the present work) it has been proposed as a part of a top-down visual processing mechanism that would be highly adaptive in the fast detection of biologically relevant information (Bar, 2003; see also the Dicussion and conclusions section of the Second Study). Thus it is conceivable that functional coupling between the prefrontal cortex and the visual cortex was strengthened at an early stage of emotional distraction processing, when such a distraction may comprise linked-to-survival information.

However, a sustained depletion of the parieto-temporal component of the fronto-posterior network responsible of WM maintenance might lead to the interruption of such maintenance of information, and may finally produce the forgetting of the initially encoded materials (Clapp et al., 2011). According with previous studies showing that the functional fronto-posterior coupling is reactivated after the presentation of an interfering stimuli (Clapp et al., 2010) and that the degree of this reactivation can predict WM performance (Clapp et al., 2011), the disturbed parieto-temporal coupling returned to levels observed in neutral distraction, in the second temporal window of interest, about 250-350 ms. More interestingly, both types of emotional distraction increases functional coupling between the prefrontal cortex and parieto-temporal cortices. Specifically, unpleasant distractors produced an increase in functional connectivity between the DLPFC and the PC, which can be considered as a part of the network that sustains WM maintenance (Gazzaley et al., 2004; Palva et al., 2010; Rissman et al., 2004, 2008; Sarnthein, 1998; Sauseng et al., 2005), when compared with neutral distractors. This particular result that did not appear in the contrast between pleasant and neutral distraction, is consistent with the behavioral performance, as pleasant distractors did not lead to lower performance than neutral ones (see Working memory performance and subjective emotional ratings section). Thus, this enhancement of the DLPFC-PC connectivity might be related to the necessity of increasing the functional coupling in the network that sustains WM maintenance, when the most interfering distractor is encountered. In parallel, both emotional distractors strengthen the functional coupling between the right VLPFC-OFC and parieto-temporal cortices. As commented above, although cortico-cortical connectivity while coping with emotional distraction in WM has not been previously addressed, the

VLPFC is highly coupled with the amygdala and modulates projections from this nucleus to the prefrontal cortex while facing to emotional distractors (Chuah et al., 2010; Clarke & Johnstone, 2013; Dolcos et al., 2006). Moreover, the VLPFC is considered a crucial cortical region in the successful cognitive control of emotional distraction (Anticevic et al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013a). Therefore, we suggest that this specific fronto-posterior coupling might sustain specific control mechanisms of the emotional distractor. This hypothesis is supported by the positive correlation between the strength of this link and the behavioral performance found for the unpleasant distraction condition.

During the last temporal window of interest, between 360 and 460 ms after the onset of the distractor, unpleasant distraction increased the parieto-temporal component of the abovementioned fronto-posterior WM network, in comparison with both neutral and pleasant distraction. Again, this effect might be reflecting the higher difficulty of maintaining relevant information in WM, when a powerful distractor is encountered. Besides, functional coupling between the OFC and posterior temporal cortices were stronger during unpleasant distraction than during both pleasant and neutral distraction. The OFC is known highly implicated in the inhibition of prepotent responses (Bokura, Yamaguchi, & Kobayashi, 2001; Casey et al., 1997; B. Jones & Mishkin, 1972; Kowalska et al., 1991; Malloy, Bihrle, Duffy, & Cimino, 1993; Perret, 1974), specially when such responses were established upon their previous reward value (Iversen & Mishkin, 1970), and so on it is likely to be involved when the most detracting stimuli appears. Unexpectedly, the strength of the connection between left OFC and STC during the processing of neutral distraction correlated positively with WM accuracy in this condition, while no links involving the left OFC correlated with

behavioral performance in pleasant or unpleasant conditions. Although this result seems surprising, as we have found the ventral and lateral parts of the prefrontal cortex strongly active and connected with posterior areas while processing emotional distraction (see Results section of the present study and the Second Study of the present work), we exclusively found positive correlations between both activity and functional connectivity of OFC in the right hemisphere (see Brain activity and behavioral performance section of the Second Study and Brain connectivity and behavioral performance section of the present study). Thus, it is possible that left OFC was generally engaged in overriding a different sort of distraction, and the right OFC was especially engaged in coping with emotional distraction. This tentative explanation would be in accordance with traditional theories that suggest that the left hemisphere is specialized in a number of cognitive processes, while the right hemisphere is predominantly involved in processing emotion (e.g. Erhan, Borod, Tenke, & Bruder, 1998; Levine & Levy, 1986; Sauseng et al., 2005; Schwartz, Davidson, & Maer, 1975).

The present study constitutes the first approximation to the temporal dynamics of the functional networks implicated in the maintenance of information in WM, while coping with emotional distraction. Consistent with previous literature in the study of the cognitive control of distraction in WM, our results showed that emotional stimuli produce a transient disruption of the parieto-temporal component of the well-known fronto-posterior network that is supposed to sustain the WM maintenance (Clapp et al., 2010, 2011; Yoon et al., 2006). Indeed, such a disruption mostly affected an important hub in this fronto-posterior WM network (Palva et al., 2010). Our results also confirmed that this network can be reestablished for a successful behavioral performance (Clapp et al., 2010, 2011), extending previous findings from non-emotional distraction to the

emotional domain. More interestingly, functional connectivity between prefrontal cortex and OC is strengthened during the early detection of unpleasant distractors, as they might potentially contain threatening information (Bar, 2003; see also Second Study of the present work), while the enhancement of functional connectivity between the right VLPFC-OFC and posterior regions, probably reflects specific control mechanisms of the emotional distractor at medium latencies.

The present findings highlight the temporal dynamics of the distributed network that sustains our ability to cope with emotional distraction, while providing evidences for differential mechanisms implicated in the maintenance of information in WM and in the effective control of emotional distractors.

GENERAL DISCUSSION

In the General Introduction section we revisited the existent literature regarding the cognitive control of emotional distraction in WM, from the behavioral level to the most advance approaches consistent in applying functional connectivity methods to the study of the dynamical networks that sustain such a cognitive process. Our review identified several gaps in the current knowledge about how our cognitive system is affected by emotional distractors, and how it is able to override this effect, in order to accomplish a number of relevant tasks.

At the behavioral level, it seems clear that unpleasant distractor can be powerful interferences in WM due to their biological relevance, although the effect of other type of linked-to-survival stimuli has not been addressed. In our First Study we replicated previous results showing that unpleasant distraction does affect the maintenance of non-emotional elements in WM (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008; Dolcos & McCarthy, 2006). However, pleasant distractors did not produce higher rates of forgetting than neutral ones, as one would have expected since they also represent very important information for our survival (i.e. food). Then, if both pleasant and unpleasant stimuli are relevant for survival and we

tended to preferentially process them (Armony & Dolan, 2002; Mogg et al., 1997; Ohman et al., 2001), why only unpleasant distractors work as potent interferences for the maintenance of other elements in short-term memory, while pleasant distractors behave like neutral ones? In the Discussion and conclusion section of that study we argued that the reason because we are prepared to pay attention to and deeply process emotional stimuli is probably related to the potential consequences of ignoring them. Thus, if we do not pay attention to a dangerous animal our survival is immediately compromised. However, if we ignore food or reproduction-related stimuli, our survival will be compromised in the medium or long term. Therefore, it is reasonable that our executive control can override the attentional response elicited by pleasant stimuli for a moment, if we are performing another relevant task, since our survival is not immediately at risk (Ekman, 1992; Ohman, 1992). Hence, we may benefit from the result of successfully performing an ongoing task without compromising our survival. By contrast, it is also logical that our inhibitory control is blocked and unable to override attentional responses elicit by unpleasant stimuli, since it would immediately endanger our survival just for a potential secondary benefit. Further analysis confirm this idea, as the individual capacity of overriding interference in WM correlated positively with performance after neutral and pleasant distraction, but not after unpleasant distraction.

At the brain activity level, several studies have provided substantial information about the particular brain regions involved in the cognitive control of emotional distraction in WM (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos & McCarthy, 2006; Dolcos et al., 2013b, 2008, 2006; Iordan, Dolcos, Denkova, et al., 2013), showing that unpleasant emotional distraction may produce a decreased activity over dorsal/executive brain areas while increases activity in ventral/emotional

cortical and subcortical regions. This dissociation has been interpreted as an unpleasant distraction-based enhancement of bottom-up influences from ventral/emotional to dorsal/executive brain areas, which reallocates attentional processes deploying WM performance (see Dolcos et al., 2011 for a review). In addition, those studies have highlighted specific regions over both the ventral/emotional and the dorsal/executive systems, i.e. the VLPFC and DLPFC, that are critically involved in successful coping with emotional distraction in WM (Anticevic et al., 2010; Denkova et al., 2010; Dolcos et al., 2013a, 2006).

In the Second Study we explore the temporal dynamic of the neural activity that supports our capacity of coping with emotional distraction in order to understand the exact nature of this highly adaptive cognitive process. Our results revealed that prefrontal mechanisms were engaged at very early latencies of the distractor processing, allowing the rapid detection of both pleasant and unpleasant emotional distraction. Later in the processing, unpleasant distractors recruited a specific cognitive control mechanism that depended on the activity over the DLPFC, the MPFC and the OFC, for the effective control of such a distraction. The specificity of this mechanism in the unpleasant distraction is in accordance with behavioral results from our First Study, as it provoked higher rates of forgetting than both neutral and pleasant distraction. Therefore, it is reasonable that we need a specific high-order cognitive control mechanism for overriding such a powerful distraction.

Despite of the increasing evidence regarding the brain mechanisms of coping with emotional distraction, very few experiments have investigated the effect this type of distraction on functional brain networks of WM, even though recent evidence has

suggested that long-range functional coupling between frontal and posterior areas as the key mechanism for maintaining information in WM (Gazzaley, Rissman, & D'Esposito, 2004; Palva, Monto, Kulashekhar, & Palva, 2010; Rissman, Gazzaley, & D'Esposito, 2004, 2008; Sarnthein, 1998; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005). Indeed, only three papers have applied functional connectivity methods in this field and all of them have limited their analysis to the particular connections between the amygdala and the prefrontal cortex (Chuah et al., 2010; Clarke & Johnstone, 2013; Dolcos et al., 2006), leaving aside posterior cortical networks known to be engaged in WM maintenance (e.g. Corbetta, Kincade, & Shulman, 2002; Todd & Marois, 2004).

In the Third Study we applied a functional connectivity analysis to the data collected in the Second Study in order to address the potential effect of the emotional distraction in fronto-posterior cortical networks that have been related to the active maintenance of information in WM. Our results showed that emotional stimuli produced an early and transient disruption of the parieto-temporal component of the above described fronto-posterior network. Such a disruption was found at the same latency in which emotional distractors were detected, as reported in the Second Study, indicating that this early detection immediately provoke the disturbance of the fronto-posterior WM network. However, and according with previous literature (Clapp et al., 2010, 2011), such a disruption was reestablished for a successful behavioral performance. Moreover, both emotional distractors strengthen the functional coupling between the right VLPFC-OFC and parieto-temporal cortices at a relatively early latency of processing. For the unpleasant emotional distraction condition this coupling also appeared to be crucial for a successful WM performance and was accompanied by an enhancement of the DLPFC-PC coupling. This particular result that was exclusively

observed in the unpleasant condition is also consistent with behavioral results from our First Study and brain activity reported in our Second Study. Interesting enough, results from this Third Study suggest that the effective cognitive control of emotional distraction may begin even earlier than reported in Second Study, and that this fast and subtle mechanism could relies in long-range functional coupling.

In summary, the present series of studies investigated for the first time the cognitive mechanisms of coping with emotional distraction, starting at the behavioral level, exploring the spatio-temporal profiles of the brain activity and finally investigating the underlying dynamical changes in brain functional networks.

GENERAL CONCLUSIONS

The present series of studies show that unpleasant stimuli do affect the maintenance of non-emotional information when they are not goal-task relevant. At the same time, these studies show for the first time that pleasant interference does not necessarily affect WM as unpleasant interference does. These results indicate that not any sort of emotional information can distract us when we are engaged in a relevant task, as our cognitive system seems to be able to resist pleasant distractors as well as non-emotional events.

The relationship between performance and WM interference resolution capacity points to the immediacy of consequences of ignoring irrelevant information as the key aspect that allows executive control to override attentional responses. In other words, our cognitive control is able to inhibit our tendency to pay attention to pleasant events, as our survival will not be immediately compromised. Yet, we are unable to resist the attentional capture elicited by aversive events, since doing so, we will endanger our survival in the very short-term.

Our exploration of the neural mechanisms involved in the processing of irrelevant emotional events shows that prefrontal cortices are highly activated at very

early latencies of the distractor processing, allowing the rapid detection of both pleasant and unpleasant emotional distraction. However, these prefrontal areas are also engaged in the actual cognitive control of emotional distraction later in the processing. Interestingly, the control of unpleasant events requires a higher level of activity over the DLPFC, the MPFC and the OFC, which is actually in accordance with the higher difficulty in controlling those events observed at the behavioral level.

Nowadays, we know that active maintenance of information is not just the result of the neural activity over concrete brain regions, but it is rather sustained by synchronized activity over functional networks, widely distributed across the brain. Our analysis of functional connectivity shows that the early detection of emotional distraction produces a transient disruption of an important hub of the fronto-posterior network that contributes to sustain WM maintenance. Nevertheless, functional connectivity between prefrontal cortex and OC is strengthened during the early detection of unpleasant distractors, as they potentially contain threatening information.

In line with our analysis of regional activity, the cognitive control of emotional distraction occurs later in the processing. At this point, the fronto-posterior network is reestablished for a successful behavioral performance, while the right VLPFC-OFC and posterior cortices become strongly connected as a mechanism to cope with emotional distractors.

In contrast to the popular idea regarding the effect of emotion on cognition, this work reveals for the first time that not any sort of emotional information can affect our capacity to keep focused on important matters. Although we are able to cope with emotional distractors most of the times, unpleasant events are more difficult to control

and affect our cognitive efficiency more frequently than pleasant or neutral ones. Our results also reveal two different mechanisms that underlie our capacity to override the negative effect of emotional distraction. First, we need to detect the potential biological relevance of distracting events, as it is highly adaptive to be prepared to process them. This mechanism is underpinned by the prefrontal cortex, although such an early detection induces a disruption of the functional brain network that sustains relevant information for the ongoing task. Afterwards, the prefrontal cortex contributes to control the emotional distraction by means of higher local activity and by strong functional connections with posterior cortices of the brain.

LIMITATIONS AND FUTURE DIRECTIONS

This series of studies have explored our capacity to cope with emotional distracting events while we are keeping in mind some relevant information, from the behavioral level to the neural basis of such capacity, using both, a traditional approach based on regional brain activations as well as a more cutting-edge methodology that allows us to study how distant areas in the brain work together. Despite the results obtained at those different levels of analysis, there are still some relevant questions that future research should address.

Our First Study was based on the concept of motivated attention, and therefore, we assumed that both types of emotional stimuli recruit attentional resources to the same extend. However, it was possible that differences between pleasant and unpleasant distractors were due to differences in the amount of attention captured by them. Such hypothesis could be tested if volunteers processed every type of distractor to the same depth. A possible way to achieve that goal might be asking participants to evaluate some aspect of the distractors, for example whether the scene represented in the picture takes place indoor or outdoor. If volunteers performed equally well this secondary task at all types of distractions, one could be sure that they pay attention to

them to the same extent and therefore, differences between conditions could not be attributed to differences in attentional capture.

In the Second Study, we used a correlation analysis to explore the relationship between brain activity and behavior. Although this is a common strategy, the most reliable way to address this issue would have consisted in comparing the brain activity during successfully performed and unsuccessfully performed trials. Still, the limited number of error trials in our experiment prevented us from applying source reconstruction to the corresponding data. Future research should increase the total numbers of trials to try to obtain enough data from unsuccessfully performed trials.

Finally, in our Third Study, we explored the long-range functional connectivity in a wide band of frequencies. As this is the first study that explores the functional connectivity dynamics of our ability to cope with emotional distraction, we decided to focus on the three temporal windows in which differences between emotional and neutral distraction arose at the brain activity level. Hence, our decision to use the same range of frequencies that we used in the Second Study, in order to keep both analyses consistent. However, increasing evidence suggest that specific frequency bands, i.e. the alpha band, might be strongly related with inhibitory processes that are strong candidates to be engaged in our capacity to cope with any sort of distracting events. Future studies should analyze different frequency bands to unravel the potential contribution of each rhythm to our capacity to control the emotional distraction.

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