

Tesis Doctoral

The Mind's eye

Orienting attention to categorical and idiosyncratic stimulus representations

Clara Aranda Carrasco

Directores:

Pío Tudela

Daniel Sanabria

María Ruz

El Ojo de la Mente

Orientando la atención a representaciones categoriales e idiosincrásicas del estímulo



Departamento de Psicología Experimental y Fisiología del comportamiento
Universidad de Granada

Editor: Editorial de la Universidad de Granada
Autor: Clara Aranda Carrasco
D.L.: GR 3793-2010
ISBN: 978-84-693-6016-3

Para que yo me llame Ángel González,
para que mi ser pese sobre el suelo,
fue necesario un ancho espacio
y un largo tiempo:
hombres de todo el mar y toda tierra,
fértiles vientres de mujer, y cuerpos
y más cuerpos, fundiéndose incesantes
en otro cuerpo nuevo.
Solsticios y equinoccios alumbraron
con su cambiante luz, su vario cielo,
el viaje milenario de mi carne
trepando por los siglos y los huesos.
De su pasaje lento y doloroso
de su huida hasta el fin, sobreviviendo
naufragios, aferrándose
al último suspiro de los muertos,
yo no soy más que el resultado, el fruto,
lo que queda, podrido, entre los restos;
esto que veis aquí,
tan sólo esto:
un escombros tenaz, que se resiste
a su ruina, que lucha contra el viento,
que avanza por caminos que no llevan
a ningún sitio. El éxito
de todos los fracasos. La enloquecida
fuerza del desaliento...

Ángel González (Oviedo, 1925-2008)

Índice General

Agradecimientos - Acknowledgments.....	9
Introducción	21
La Atención	23
1. El concepto de Atención.....	25
2. Formas y efectos de la atención.....	26
1. <i>El Modelo de las Redes Atencionales.....</i>	<i>26</i>
2. <i>El paradigma de Costes y Beneficios</i>	<i>28</i>
3. <i>Atención exógena versus Atención endógena.....</i>	<i>29</i>
3. El objeto de la atención.....	30
1. <i>El debate clásico.....</i>	<i>31</i>
2. <i>Panorámica actual.....</i>	<i>33</i>
4. El curso temporal de los efectos atencionales	34
1. <i>Correlatos electrofisiológicos de la atención endógena espacial.....</i>	<i>34</i>
2. <i>Correlatos electrofisiológicos de la atención endógena no espacial.....</i>	<i>36</i>
La Representación del conocimiento.....	41
1. El concepto de Representación	43
2. La naturaleza de la representación.....	44
1. <i>La existencia de imágenes mentales</i>	<i>45</i>
Expectativas acerca del objeto.....	49
1. Investigaciones precedentes.....	51
1. <i>Expectativas sobre categorías.....</i>	<i>51</i>
2. <i>Expectativas sobre estímulos particulares: Expectativas idiosincrásicas</i>	<i>52</i>
2. Expectativas: de lo general a lo particular, del objeto al sujeto	54
1. <i>Categorías: Caras y Palabras.....</i>	<i>54</i>

2. <i>Estímulos Idiosincrásicos: Caras familiares y no familiares</i>	56
3. <i>Estímulos Idiosincrásicos: El cuerpo propio y ajeno</i>	57
3. Planteamiento general de la investigación	59
Category Expectations:.....	63
Introduction	65
Methods	69
Results	73
Discussion	78
Equal but not the same:	85
Introduction	87
Methods	90
Results	94
Discussion	100
Focusing on the bodily self :.....	105
Introduction	107
Experiment 1	110
Experiment 2	115
Experiment 3	117
Experiment 4	120
Discussion	124
Were those my hands?	129
Introduction	131
Methods	133
Results	137
Discussion	143

Discusión General.....	149
1. Atención endógena centrada en el objeto.....	151
2. El vínculo entre la expectativa y la representación analógica.....	153
3. Atención a representaciones perceptivas del objeto.....	155
4. Conclusiones finales... ¿una propuesta de futuro?.....	158
Summary	163
1. Endogenous object-based attention	165
2. The link between expectations and visual representations	167
3. Orienting attention to perceptual object representations	169
4. Final conclusions... A proposal for future research?.....	171
Referencias - References.....	175

Agradecimientos - Acknowledgments

Después de tantas páginas escritas, las palabras se me escapan de entre los dedos...Intentaré, por ello, ser breve.

A Daniel Sanabria, María Ruz y Pío Tudela, cuyos improbables esfuerzos lograron canalizar mis pensamientos divergentes y darles la forma de algo parecido a una tesis doctoral. Os agradezco vuestro tiempo, ayuda y apoyo: Encantada de haber recorrido este camino junto a vosotros.

To the little “European fellowship of the Self”, which from Soria (the deepness of Spain) to Cargèse (the clear blue sky of Corsica) passing by London (the morning train to Egham and the RHUL), showed me that there are people like me there, outside, who encourage the effort to find common places and bridges between philosophy, neuroscience, psychopathology and the subjective experience of being. Thank you for your “amazing selves”.

A mi familia, que, al igual que mis intereses, se encuentra dispersa por toda la geografía española... y aún así, se mantiene unida, como una red fuertemente entrelazada que me impide caer mientras recorro los alambres de la vida, suspendidos en el vacío. No os quiero mucho, os quiero todo:

A mis abuelos, que no podrán ver este día con sus propios ojos pero que están y estarán siempre a mi lado.

A mi madre, Rosa M^a, el apoyo incondicional que me permite dar pasos cada vez menos vacilantes hacia el futuro, sabiendo que hay un lugar al que siempre es posible volver.

A mi padre, Jose Manuel, que ha guiado esos pasos vacilantes, mostrándome los múltiples caminos e inquietudes que puede ofrecer esta vida.

A mis pequeños Jimena y Fran, en plena ebullición adolescente...Ahora empieza realmente vuestra propia aventura, estaré a vuestro lado para levantaros y limpiar magulladuras cuando tropecéis.

A Miner, la primera psicóloga de esta familia, y a Eduardo, Edu y Celia. Porque gracias a todos ellos, tengo el privilegio de poseer dos hogares donde me siento querida.

A mis primos y tíos desde Madrid, Toledo, Murcia y Cuenca. En especial, a Alba y a Enrique, que son mucho más que primos, con los que las horas se

desvanecen entre conversaciones a la más pura esencia Aranda y Carrasco.

Asimismo, tengo la suerte de haberme topado con personajes, duendes de todas las latitudes, que son una parte extendida de mi familia...cuya risa, ánimo y apoyo, cuya “escucha activa” en el sentido más estrictamente psicoanalítico, me han alentado a continuar siempre adelante, brillando como luciérnagas en la oscuridad:

A Ignacio, porque apareció y, cogidos de la mano, descubrimos otras vidas. Soy, gracias a ti.

A Inma, mi reflejo neurótico especular con el que seguiré creciendo, llorando y riendo ante el sinsentido de la existencia.

A Elena, principal culpable de que me sienta hoy aquí a escribir estas palabras. Pure “nuts” girl con la que cantar y bailar hasta que salga el sol.

A mis Isabelinas, fieles y leales, caóticas y abrazables hasta el infinito : Conchi, risa libre y etérea; Mária, mi economista utópica con corazón de clown; y Laura y Ana, con las que constituimos el núcleo granaino, el lugar donde reencontrarnos todas desde y para siempre.

A mi narciso favorito, Manolo.

Algunos más se esconden entre las callejuelas de Granada, Málaga, Londres e incluso, Camboya. A ellos, que también se saben en este trabajo...

Creo que no es necesario decir lo importantes y únicos que sois todos y cada uno de vosotros para mí. Con esta tesis, termino un periodo de mi vida que no hubiera sido igual sin vuestra presencia.

Así que gracias... Gracias por existir.

Para esbozar una idea inicial de los objetivos que perseguimos con este proyecto doctoral, voy a pedir al lector que retroceda mentalmente a su infancia, a una mañana de Reyes cualquiera.

El niño que habita en nuestro interior se encuentra aún en la cama, nervios a flor de piel, repasando cada artículo que mencionó en su carta a los Reyes Magos. En especial, piensa en un robot. Podríamos considerar que el niño ha creado una *expectativa* de aquello que puede encontrar dentro de su paquete de regalo. Así, se levanta de la cama y corre a comprobarlo. El envoltorio tiene el tamaño perfecto: “Tiene que ser un robot”-piensa para sí-. En su mente se dibuja la forma y el tamaño de un posible robot. Posee la absoluta convicción de que cuando rasgue el papel, abra la caja y descubra su interior, verá el juguete deseado. Supongamos que el niño no tiene preferencia alguna por el tipo de robot, él simplemente espera un personaje de metal, de tamaño medio y formas cuadrículadas. Esta expectativa haría referencia a una categoría, donde pueden incluirse muchos tipos de robots. Pero, por el contrario, resulta probable que el niño tenga muy claro qué robot ha elegido: azul y blanco, con ojos rojos refulgentes y alas desplegadas en la espalda. En este caso, la expectativa sería mucho más específica, prácticamente única, ya que hace referencia a un objeto en particular. La descripción de una *expectativa idiosincrásica* es mucho más detallada que la descripción de una *expectativa categorial* y por tanto, más “exigente” en tanto a los complementos, colores y apariencia del robot.

¿Cuál es el efecto que generarán esas expectativas cuando el niño abra su regalo? Si finalmente, el regalo es el ansiado robot, el niño no tendrá más que echarle un leve vistazo para reconocerlo, alzarlo en sus manos y hacerlo volar. Sin embargo, si el niño descubre un coche teledirigido al abrir el paquete, es muy probable que el pequeño necesite mirarlo varias veces, sin creer lo que ven sus ojos, para comprobar que, de nuevo estas Navidades, los Reyes se han equivocado de regalo.

El objetivo de esta tesis es justamente estudiar el efecto que dichas expectativas, categoriales (un robot cualquiera) o idiosincrásicas (*el robot*, único e insustituible), poseen sobre el procesamiento visual del objeto. Estas expectativas son el resultado de dirigir voluntariamente la atención a un objeto, en base a su categoría o identidad

específica. Nuestro interés radica especialmente en identificar aquellas etapas del procesamiento que se ven moduladas por la atención durante el análisis visual del estímulo. Es decir, nuestro propósito es comprobar si dichas expectativas logran optimizar la percepción visual en sus etapas tempranas o, por el contrario, agilizan procesos post-perceptivos de categorización semántica o de selección de respuesta.

Pero no podemos seguir avanzando en nuestro planteamiento sin antes concretar el significado y el contexto teórico en el que se enmarcan algunos de los conceptos mencionados. Los siguientes capítulos nos ofrecen ese necesario encuadre. De manera que prepárense atencionalmente y dejen fluir sus expectativas.

Introducción

La Atención

y su relación con la percepción

1. El concepto de Atención

The world outside our minds is chaotic. Every moment threatens to submerge us beneath a welter of sensory experiences that compete for our attention and concentration. As a pre-condition for sanity, we must become selectively imperceptive [...]

Cited from E. J. Anthony (1955)

Resulta obvio mencionar que la definición de un concepto como la atención ha suscitado una gran controversia a lo largo de las décadas dedicadas a su investigación. La atención, como función cognitiva de alto nivel, está relacionada con múltiples aspectos de la conducta y esta complejidad puede conducirnos hacia posturas nihilistas que rehúsan ofrecer una definición concreta del constructo. Sin embargo, es necesario adoptar una perspectiva teórica, un enclave que guíe el desarrollo de una línea de investigación. La definición que hemos adoptado es fruto de la evolución histórica del concepto, supera algunas limitaciones identificadas en modelos anteriores y se enmarca, concretamente, dentro de la teoría de las redes atencionales de Michael Posner (e.g. Posner & Dehaene, 1994; Posner & Petersen, 1990). De ella, destacaremos varios aspectos fundamentales.

La atención es un mecanismo de selección. La capacidad de procesamiento de la cognición humana es indiscutiblemente limitada. De esta manera, la atención surge como un mecanismo que permite seleccionar aquellas representaciones internas o estímulos ambientales externos que son relevantes en un momento determinado (c.f. James, 1890). La atención se identificó con un *filtro* que protegía el sistema cognitivo (Broadbent, 1958), que ofrecía un procesamiento preferente del estímulo atendido en detrimento de los distractores existentes a su alrededor. Sin embargo, la metáfora del filtro generó un intenso debate sobre su localización específica a lo largo del procesamiento: la controversia sobre el *locus de selección* (see e.g. Broadbent, 1958; Deutsch & Deutsch, 1963), que puso de manifiesto las limitaciones de un modelo secuencial y poco flexible.

La atención es un mecanismo de control. Modelos posteriores enfatizaron el aspecto energético de la atención (*esfuerzo*) y de la regulación/control de sus recursos. Desde esta perspectiva, la atención adquirió así la forma de un *procesador central*, que evaluaba las demandas requeridas por la tarea y administraba de forma adecuada ese esfuerzo atencional (e.g. Kahneman, 1973; Norman & Bobrow, 1975). De esta manera, la atención parece que no sólo selecciona la información sensorial relevante sino que ejerce un control sobre la conducta mediante: la identificación de una necesidad, la selección de una estrategia cognitiva y/o motora y la distribución apropiada de los recursos atencionales requeridos para llevarla a cabo.

La atención se sitúa en una dimensión vertical. La evidencia empírica sugiere que atención actúa a múltiples niveles, incrementando la eficiencia del procesamiento desde etapas perceptivas hasta la ejecución de una respuesta específica. Esta flexibilidad no permite que la atención sea identificada con una estructura localizada en un lugar concreto del procesamiento. Por el contrario, la atención parece situarse en un plano vertical, desde el cual ejerce su influencia sobre diversos procesos cognitivos básicos (c.f. Norman & Shallice, 1986; Posner, 1978; Posner & Presti, 1987).

Así, bajo nuestro punto de vista, la atención ejerce un papel central en el control de la actividad consciente (e incluso, inconsciente) mediante múltiples funciones como la selección de estímulos sensoriales o de estrategias conductuales adecuadas, desde una dimensión independiente o vertical al flujo de procesamiento (c.f. Tudela, 1992).

2. Formas y efectos de la atención

1. El Modelo de las Redes Atencionales

La atención juega un papel crucial en el control de nuestro pensamiento y nuestra conducta: nos permite identificar metas, relacionarlas con aquellos estímulos relevantes y actuar selectivamente sobre esos estímulos para su consecución. No sólo moldea nuestro mundo perceptivo sino que guía nuestras acciones a través de él. Ante

esta complejidad, tiene sentido plantearse si la atención puede considerarse un sistema unitario o, mas bien, la acción integrada de un conjunto de mecanismos con diversas funciones específicas. La *Teoría de las Redes Atencionales* de Michael Posner ofrece una propuesta ante esta disyuntiva (Posner & Petersen, 1990). Su teoría distingue tres sistemas, funcional y anatómicamente dissociables entre sí, cuyos efectos pueden identificarse de forma independiente (Callejas, Lupiáñez, & Tudela, 2004; Fan, McCandliss, Sommer, Raz, & Posner, 2002; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005).

Según este modelo, la **Red de Vigilancia** se encargaría de producir y mantener el estado de alerta óptimo. Este sistema es el más primitivo de los tres, se encuentra íntimamente relacionado con el sistema reticular ascendente y establece el tono atencional de base. Algunos estudios de neuroimagen han relacionado el mantenimiento de la alerta con áreas del talámo y la corteza frontal y parietal derecha, regiones ricas en proyecciones norepinefrinéricas procedentes del locus coeruleus (Coull, Frith, Frackowiak, & Grasby, 1996; Marrocco & Davidson, 1998; Posner & Petersen, 1990).

La **Red Atencional Anterior (RAA)** podría identificarse con el ya mencionado procesador de carácter central. Este sistema se encuentra en contacto directo con las metas y objetivos del sujeto, llevándolos a cabo mediante la identificación de eventos conscientes, la detección del conflicto y la implementación de un control ejecutivo sobre la conducta. Las áreas neurales asociadas a estas funciones se han localizado en la región dorsal del cíngulo anterior y la corteza lateral prefrontal (Bush, Luu, & Posner, 2000; MacDonald, Cohen, Stenger, & Carter, 2000). Estas regiones presentan múltiples conexiones con el resto de la corteza, señalándolas como candidatos ideales para ejercer una modulación de arriba-a-abajo (del inglés, *top-down*) sobre diversos procesos básicos.

La **Red Atencional Posterior (RAP)** es un sistema de orientación sensorial, el cual controla y dirige el procesamiento perceptivo para extraer la información relevante del entorno. En su propuesta inicial, el sistema posterior comprende las operaciones de enganche, desenganche y movimiento de la atención que, a su vez, se asocian a áreas neurales específicas (véase Posner & Cohen, 1984a). Asimismo, el funcionamiento de

esta red puede iniciarse tanto *endógenamente*, a partir de los intereses del propio sujeto, como *exógenamente*, a partir de un evento llamativo externo (e.g. Posner, 1980). Sin embargo, publicaciones recientes han logrado caracterizar de manera más específica la RAP, identificando circuitos neurales dissociables encargados de estas dos formas de orientación (e.g. Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002). Según estos estudios, la orientación endógena implica la activación de regiones dorsales del lóbulo parietal (surco Intra-parietal) y frontal (Campo visual frontal, *FEF*), mientras que la orientación exógena se ha relacionado con la activación de un circuito ventral que incluye la unión temporo-parietal (TPJ) y áreas ventrales de la corteza frontal. Corbetta y colaboradores argumentan que la atención endógena está guiada por las metas y objetivos de la persona en un momento determinado, mientras que la atención exógena está constituida por un circuito neural que “rompe” esa concentración voluntaria (*circuit breaker*) y moviliza el sistema automáticamente hacia una fuente de estimulación externa, potencialmente peligrosa, que debe ser evaluada de forma prioritaria (e.g. Corbetta & Shulman, 2002).

Integrado en esta línea teórica, el presente proyecto doctoral investiga el funcionamiento de la red atencional posterior, focalizándose concretamente en el estudio de la orientación atencional endógena o voluntaria.

2. RAP: El paradigma de Costes y Beneficios

En un plano empírico, la red atencional posterior se ha investigado tradicionalmente mediante el uso del *Paradigma de Costes y Beneficios* (Posner, 1980). Este paradigma fue diseñado para explorar los efectos de la atención orientada a un lugar en el espacio. La tarea original consistía en detectar un estímulo cuando éste era precedido por una señal que dirigía la atención del participante hacia una de las posibles localizaciones. El estímulo podía aparecer en la localización atendida (ensayos señalados o válidos) o no atendida (ensayos no señalados o inválidos). Los resultados mostraron que el participante detectaba el estímulo con mayor rapidez y precisión en los ensayos señalados/válidos que en los ensayos no señalados/inválidos. Este hallazgo

llevó a la conclusión de que la atención, cuando se focaliza en un lugar en el espacio, favorece el procesamiento de la información presentada en esa localización (e.g. Posner, 1980).

Asimismo, la manipulación de la naturaleza de la señal permitió adaptar este paradigma al estudio de la orientación exógena y endógena. La orientación exógena de la atención es desencadenada por una señal periférica, que hace referencia a un estímulo saliente que se presenta en una de las localizaciones, capturando automáticamente la atención del participante. Por el contrario, la orientación endógena es desencadenada por una señal central o estímulo arbitrario informativo, el cual debe ser codificado e interpretado por el participante para que éste dirija su atención de forma voluntaria hacia la localización indicada. En función de la posición en la que posteriormente aparece el estímulo objetivo, los ensayos se denominan señalados o válidos (misma posición) y no señalados o inválidos (posición contraria).

3. *RAP: Atención exógena versus Atención endógena*

Entre investigadores comportamentales de la atención (medidas exclusivamente conductuales), la tendencia más extendida defendía que la orientación exógena y endógena eran dos maneras distintas de movilizar *un mismo* sistema atencional (e.g. Yantis, 1998, 2000). Así, ambas fuerzas se encontraban en continuo conflicto por el control del sistema, siendo el ganador de esta confrontación el que determinaría qué estímulo será atendido y procesado de forma preferente en cada momento. En la actualidad, no obstante, la evidencia empírica apoya la hipótesis de que ambas formas de orientación constituyen mecanismos atencionales distintos, no sólo a nivel neural, sino también a nivel conductual (e.g. Funes, Lupiáñez, & Milliken, 2007; Klein, 2004).

Estos hallazgos sugieren que el uso de una señal central o una señal periférica condiciona la manera en que se manifiestan los efectos atencionales a lo largo del procesamiento (i.e. el fenómeno de la Inhibición de Retorno, e.g. Posner & Cohen, 1984b; Chica & Lupiáñez, 2009). Las señales periféricas requieren un menor tiempo

que las señales centrales para focalizar la atención en una localización específica, aunque sus efectos decaen más rápidamente (Funes et al., 2007; Müller & Rabbitt, 1989). De esta manera, algunos autores defienden que la atención exógena operaría en etapas muy tempranas del procesamiento visual, mientras que la atención endógena se relacionaría con procesos más tardíos, tanto perceptivos como de selección de respuesta (Ciaramitaro, Cameron, & Glimcher, 2001; Klein & Shore, 2000; Lu & Doshier, 2005). Sin embargo, aunque ciertos estudios de registro electroencefalográfico apoyan esta hipótesis (e.g. Hopfinger & West, 2006), otros revelan que la atención endógena es igualmente capaz de modular componentes perceptivos tempranos (e.g. Clark & Hillyard, 1996; Luck, 1995).

Nuestra propuesta experimental utiliza una adaptación del Paradigma de Costes y Beneficios para investigar los efectos de la atención endógena sobre el procesamiento visual. Pero ¿cuál es la unidad específica hacia la que se dirige la atención? Como comentábamos, el tipo de orientación influye en la manifestación de los efectos atencionales a lo largo del procesamiento, pero éste no es el único factor en juego. Algunos estudios sugieren que el objeto de la atención o la unidad atendida constituye un elemento crucial en la determinación de aquellas etapas del procesamiento que se ven moduladas por la atención (e.g. Cristescu & Nobre, 2008; Ruz & Nobre, 2008). Por lo tanto, estas cuestiones nos llevan inevitablemente a centrar nuestro interés en el objeto de la atención y en sus posibles variantes.

3. El objeto de la atención

La unidad específica sobre la cual se focaliza la atención es un aspecto de suma importancia en el estudio de los efectos atencionales. De esta manera, no es lo mismo dirigir la atención a una localización en la que puede aparecer un estímulo, que hacerlo hacia un color que puede presentar ese estímulo. Este apartado realiza un breve recorrido sobre las unidades de selección atencional que se han investigado hasta el momento.

1. El debate clásico:

Atención espacial versus Atención centrada en el objeto

El objeto de la atención ha motivado intensos debates desde los comienzos de la investigación en atención visual (véase Scholl, 2001). Los planteamientos originales defendían la idea de que la atención se orientaba principalmente en el espacio. Resulta comprensible, por tanto, que las primeras metáforas conceptualizaran la atención como un foco de linterna ("spotlight", Posner, Snyder, & Davidson, 1980) o como un teleobjetivo ("zoom lens", Eriksen & St James, 1986) que facilitaba el procesamiento de aquellos estímulos contenidos en su perímetro de acción. Sin embargo, es evidente que la atención también puede dirigirse hacia otras características de la escena visual.

Las posturas clásicas más radicales ofrecían una explicación jerárquica de este hecho, defendiendo que la atención espacial constituía un medio y por tanto, un requisito previo imprescindible para seleccionar la característica objetivo (e.g. Navon, 1978; Treisman & Gelade, 1980; Tsal & Lavie, 1988, 1993). Así, la atención espacial poseía un estatus diferente con respecto a otras formas de selección. La existencia de efectos de interferencia provocados por estímulos irrelevantes próximos a la localización del estímulo atendido, ofrecía un apoyo empírico a este tipo de posturas (Cave & Pashler, 1995; Eriksen & Eriksen, 1974; Eriksen & Hoffman, 1972; Kim & Cave, 1995; Kramer & Jacobson, 1991).

Por el contrario, líneas más flexibles argumentaban que la atención podía focalizarse sobre objetos o estímulos específicos, independientemente de su localización espacial (e.g. Duncan, 1984; Egly, Driver, & Rafal, 1994; Neisser, 1967; Neisser & Becklen, 1975). En uno de sus estudios clásicos, Duncan y colaboradores (1984) mostraron que cuando los participantes debían juzgar dos características pertenecientes a un objeto o a dos objetos distintos presentados en superposición espacial, el procesamiento de esas características era más rápido y eficiente cuando éstas pertenecían a un mismo objeto, a pesar de que la distancia entre características era

equivalente en ambas condiciones (Duncan, 1984). Este efecto se denominó “beneficio asociado al objeto” (del inglés, *same-object advantage*) y se interpretó como evidencia de que la atención podía optimizar el procesamiento visual de un estímulo particular sin favorecer la percepción de otros estímulos convergentes en el espacio, refutando el carácter exclusivamente espacial de la atención.

Egley y colaboradores (1994) aportaron nuevos hallazgos en esta misma dirección años más tarde, mediante un paradigma de orientación espacial que señalaba un extremo de dos rectángulos contiguos como lugar más probable de aparición del objetivo. Los resultados no sólo mostraron el clásico efecto de validez de atención espacial, sino que también revelaron un efecto de facilitación para los estímulos presentados en el extremo *no señalado* del mismo rectángulo, al compararlos con los presentados en extremo del rectángulo opuesto situado a una misma distancia. Los autores interpretaron este dato sugiriendo que la atención se propagaba automáticamente a través del objeto atendido. Esta hipótesis apoya la existencia de una selección basada en el objeto, ya que un modelo exclusivamente espacial hubiera predicho una propagación radial y homogénea de la atención, que hubiera beneficiado por igual ambas localizaciones equidistantes.

Sorprendentemente, la polémica sobre una selección basada principalmente en el espacio o en el objeto aún continúa viva (véase Kasten & Navon, 2008). A pesar del considerable número de estudios realizados, no se han logrado alcanzar conclusiones definitivas sobre qué dimensión prima en la selección de la información visual (para una revisión, véase Cave & Bichot, 1999; Scholl, 2001). Sin embargo, es posible que el debate se encuentre desenfocado y que en la actualidad resulte más relevante explorar la trascendencia y efectos que posee focalizar la atención en otros factores distintos a la posición espacial. En esta línea de pensamiento se encuadran las investigaciones más recientes en el área de la atención.

2. *Panorámica actual:*

La flexibilidad de la selección atencional

La investigación en este área ha experimentado un intenso avance en los últimos años. La emergencia de nuevos planteamientos, dirigidos a explorar el potencial y la capacidad de la orientación atencional, ha permitido dejar atrás la dicotomía clásica entre espacio y objeto (véase Nobre, 2004). Numerosos estudios han investigado el efecto de la atención no espacial focalizándola en características tan diversas como la forma (Eimer, 1997; Kanwisher, Driver, & Machado, 1995), el color (Anllo-Vento, Luck, & Hillyard, 1998; Sàenz, Buracas, & Boynton, 2003), la orientación del movimiento (Anllo-Vento & Hillyard, 1996; Nobre, Rao, & Chelazzi, 2006), el momento temporal de aparición del estímulo (Correa, Lupiáñez, Madrid, & Tudela, 2006; Miniussi, Wilding, Coull, & Nobre, 1999; Nobre, 2001), representaciones activas en la memoria de trabajo (Lepsien & Nobre, 2007), respuestas motoras específicas (Rushworth, Johansen-Berg, Göbel, & Devlin, 2003) y distintos aspectos del procesamiento lingüístico de palabras (Cristescu & Nobre, 2008; Ruz & Nobre, 2008).

Estos estudios apoyan la idea de que la atención es capaz de actuar de forma flexible sobre múltiples representaciones del estímulo. En general, los resultados obtenidos se asemejan a los identificados en la orientación espacial, revelando que focalizar la atención en una dimensión específica, optimiza el procesamiento del estímulo que presenta la dimensión atendida. Esta optimización del procesamiento se infiere a partir de medidas comportamentales. Pero éstas tan sólo muestran el resultado final de varios procesos cognitivos, sin permitirnos explorar qué etapa específica del procesamiento se ve modulada por la atención.

La técnica de registro electroencefalográfico [Potenciales Evocados asociados a Eventos (*ERPs*)] es una herramienta que logra ofrecer una respuesta adecuada a estos interrogantes. Los ERPs permiten obtener índices de la actividad eléctrica cerebral a lo largo de las distintas etapas de procesamiento con una alta resolución temporal. De esta manera, el registro electroencefalográfico informa sobre el efecto de la atención en cada

una de las fases sucesivas que componen el procesamiento visual de un estímulo. El siguiente apartado realiza una revisión de los hallazgos obtenidos en estudios de ERPs sobre atención endógena a distintos aspectos del estímulo. Esta revisión tiene el objetivo de comprobar si la unidad atendida determina el estadio del procesamiento en el que se manifiestan los efectos de la atención.

4. El curso temporal de los efectos atencionales

1. Correlatos electrofisiológicos de la atención endógena espacial

Como comentábamos en anteriores apartados, algunos estudios sobre atención espacial endógena sí describen una modulación inicial observada entre los 90 y los 190 ms tras la presentación del estímulo objetivo (Clark & Hillyard, 1996; Doallo et al., 2005; Eimer, 1993; Luck, 1995; Mangun, 1995). Este intervalo temporal contiene los componentes P1 y N1, cuya modulación atencional se interpreta como un incremento en la sensibilidad perceptiva que optimiza el procesamiento visual del estímulo (Mangun, Hansen, & Hillyard, 1987). El P1 se localiza en regiones occipito-temporales de ambos hemisferios y alcanza su máxima amplitud a los 100 ms (90-120 ms). El N1, por el contrario, muestra una distribución más extensa ya que está constituido por, al menos, tres subcomponentes distintos que se localizan en regiones frontales (140 ms), parietales (150-160 ms) y occipito-temporales (170-190 ms) y que, probablemente, reflejen distintos procesos cognitivos (Clark & Hillyard, 1996). Nosotros centraremos nuestro interés en el N1 occipito-temporal. Los análisis de dipolos correspondientes al P1 y N1 occipital identifican generadores neurales situados en la región ventro-lateral de la corteza extraestriada, por lo que ambos componentes se consideran índices del procesamiento visual en una de sus fases tempranas (Gómez, Clark, Fan, Luck, & Hillyard, 1994; Hillyard & Anllo-Vento, 1998; Mangun, Hillyard, & Luck, 1993). Así, el observar un incremento de la amplitud del P1 y N1 como resultado de una señal central, es consistente con la hipótesis de que la atención endógena es capaz de modular

etapas perceptivas del procesamiento, al menos bajo determinadas circunstancias (Doallo et al., 2005; Eimer, 1993; Luck, 1995; Mangun, 1995). Sin embargo, la existencia de una influencia temprana no excluye la posibilidad de la existencia de modulaciones posteriores.

El componente postperceptual más estudiado es el P3 (e.g. Rugg & Coles, 1995). Este componente se identificó inicialmente en tareas de atención sostenida que requerían la detección de un objetivo presentado de forma infrecuente (*paradigma oddball*). El término infrecuente define un número restringido de apariciones del estímulo objetivo en contraste con el alto porcentaje de aparición de otros estímulos no objetivos (Donchin, 1981). La distribución clásica del P3 se localiza en regiones centro-parietales y, a veces, se denomina P3b para distinguirla de otro subcomponente de la onda que aparece en zonas más frontales y es provocado por estímulos nuevos y no esperados (P3a). Su rango de latencia es muy variable, pudiendo observarse entre los 300 y los 800 ms. Dado que el P3 se observa ante estímulos designados como objetivo por el investigador o aquellos que requieren una respuesta, algunos autores proponen que este componente refleja las expectativas o la relevancia percibida por parte del sujeto, constituyendo un índice adecuado de la asignación de recursos atencionales (Kramer & Strayer, 1988). Los resultados revelan de forma consistente que la amplitud del P3 es mayor para estímulos que aparecen en la localización atendida que no atendida y para estímulos infrecuentes en comparación con los frecuentes (e.g. Donchin, 1981; Eimer, 2000d; Heinze, Luck, Mangun, & Hillyard, 1990).

En general, existe un consenso en interpretar una mayor amplitud de estas ondas como un incremento en la eficacia del procesamiento del estímulo, inducido por el efecto de la atención. Sin embargo, es importante señalar que no siempre un potencial de mayor amplitud da lugar a un procesamiento más rápido y eficiente de un determinado estímulo (e.g. caras invertidas: Rossion et al., 2000).

2. *Correlatos electrofisiológicos de la atención endógena no espacial*

Los primeros resultados de ERPs que se obtuvieron en relación a la atención no-espacial parecían diferir significativamente de los observados en atención espacial. Los estímulos atendidos en base a alguna característica específica mostraban frecuentemente una modulación atencional más tardía, entre los 150 y los 350 ms, que incluía deflexiones de carácter negativo en regiones posteriores (*selection negativity*) y de carácter positivo en regiones anteriores (*selection positivity*) (Anllo-Vento & Hillyard, 1996; Harter & Aine, 1984). A pesar de ello, algunos estudios lograron identificar efectos atencionales durante el rango temporal asociado al P1 y N1 occipitales (véase Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998).

Anllo Vento y colaboradores (1998) obtuvieron una modulación atencional muy similar a aquellas provocadas por atención espacial sobre el P1 en un estudio sobre atención selectiva al color. Aunque el análisis de dipolos no permitió certificar un absoluto paralelismo entre ambos efectos, estos resultados revelan que la atención no-espacial también logra influir en etapas perceptivas del procesamiento (véase también Andersen, Müller, & Hillyard, 2009).

Utilizando un paradigma de priming negativo, Nobre y colaboradores (2006) también lograron obtener efectos atencionales sobre componentes tempranos para atención selectiva al color o a la dirección del movimiento. Este estudio exploraba el efecto que la inhibición activa de una dimensión específica en estímulos bidimensionales (e.g. color) ejercía sobre el procesamiento de un estímulo unidimensional posterior, el cual presentaba la característica previamente ignorada. Sus resultados revelaron una modulación en etapas tempranas del procesamiento tanto para la dirección del movimiento como para el color. Resulta interesante señalar que para el movimiento, el efecto observado fue de supresión o reducción de la amplitud de onda como consecuencia de la inhibición previa, tal y como se esperaba. Sin embargo, en el caso del color, los resultados revelaron un aumento de la amplitud del N1 durante el procesamiento del estímulo que presentaba el color previamente ignorado.

Los estudios sobre atención orientada en el tiempo suscitaron una cierta controversia con respecto a su capacidad para modular etapas perceptivas del procesamiento. Las primeras investigaciones identificaron efectos atencionales sobre componentes de carácter postperceptual, como el P3 (e.g. Griffin, Miniussi, & Nobre, 2002). Así, en un primer momento, la orientación en el tiempo se relacionó principalmente con procesos anticipatorios y de preparación de respuesta. Sin embargo, Correa y colaboradores (2006) plantearon la posibilidad de que la modulación de componentes perceptivos pudiera estar mediada por factores como la dificultad o las demandas de la tarea. Siguiendo esta hipótesis, estos autores identificaron una modulación atencional del P1 bajo una tarea de alta demanda perceptiva, corroborando de nuevo la capacidad de atención endógena para modular, bajo determinadas circunstancias, fases tempranas del análisis visual. Pero ¿de qué depende el observar o no una modulación atencional en componentes perceptivos? Los estudios que exploran la influencia de la atención cuando se focaliza sobre distintos aspectos del procesamiento lingüístico, sugieren que la representación atendida juega un papel crucial en la manifestación de los efectos atencionales.

Ruz y Nobre (2008) llevaron a cabo un estudio para investigar cómo modulaba la atención el procesamiento visual de un estímulo lingüístico cuando la tarea enfatizaba distintos niveles de ese procesamiento. Los resultados revelaron que realizar un análisis visual, fonológico o semántico de la palabra modulaba componentes específicamente relacionados con esos niveles de procesamiento: el N200, asociado al procesamiento perceptivo; el N350 asociado al procesamiento fonológico; y el N400, asociado al procesamiento léxico-semántico. Estos datos pusieron de manifiesto que la dimensión atendida determinaba la fase del procesamiento que era modulada por la atención. De igual forma, Cristescu y Nobre (2008) compararon los efectos de la atención espacial y semántica sobre el mismo tipo de estímulos lingüísticos y describieron una clara disociación en su curso temporal. La orientación espacial, como era de esperar, afectaba a componentes perceptivos como el P1, mientras que dirigir la atención a los posibles significados de la palabra modulaba potenciales más tardíos, como el N300 y N400, de carácter léxico-semántico.

Todos estos hallazgos demuestran que la dimensión atendida determina el nivel de procesamiento en el que se observan los efectos de la orientación. Aquellas dimensiones que hacen referencia a la *naturaleza visual* del estímulo como el lugar, el momento de aparición o alguna de sus características perceptivas (color, movimiento, forma, apariencia ortográfica), logran modular etapas tempranas del procesamiento. Sin embargo, las dimensiones que hacen referencia a *procesos posteriores*, como el análisis de la fonología o la semántica del estímulo, influyen sobre etapas más tardías del procesamiento.

El objetivo de esta tesis doctoral es estudiar los efectos de la atención endógena mediante la creación de expectativas acerca de la aparición de estímulos determinados. Estas expectativas se generan en base a la descripción perceptiva del estímulo, atendiendo a su categoría o a su identidad idiosincrásica. En un interesante artículo, Lauwereyns (1998) retomó el debate clásico sobre la atención espacial y la atención centrada en el objeto, planteándolo desde sus dos posibles modalidades: la orientación exógena o endógena. Según este autor, hasta aquel momento la investigación había proporcionado evidencia empírica sobre tres de las formas que adquiriría la atención al cruzar ambas variables: atención espacial endógena, atención espacial exógena y atención exógena a objetos. Sin embargo, el cuadrante dedicado a prepararse voluntariamente para percibir un objeto específico, es decir, aquel destinado a la atención endógena dirigida al objeto se mantenía en blanco. En la actualidad, más de diez años después, aún son muy pocas las investigaciones que han abordado esta temática. Este proyecto constituye un intento de subsanar esta laguna de conocimiento.

Así, nuestros estudios no dirigen la atención hacia un objeto presente en la escena visual, sino que crean una expectativa en su ausencia. ¿Cuál es, entonces, la unidad sobre la que se focaliza la atención? Según Corbetta y Shulman (2002), la expectativa se define como “una habilidad para *representar* la información relevante de antemano, sesgando el procesamiento de la información visual procedente del exterior”. Esta definición sugiere que la expectativa se encuentra íntimamente relacionada con el concepto de *representación*. Según esta definición, el objeto de la atención en la serie de estudios que conforman este proyecto hace referencia a la representación interna que

poseemos sobre una categoría o un ejemplar particular dentro de una categoría. De esta manera, resulta ineludible preguntarnos acerca del concepto de representación, acerca de la organización del conocimiento en categorías y ejemplares individuales y esencialmente, acerca de la *naturaleza* de estas representaciones.

La Representación del conocimiento

y su relación con la percepción

1. El concepto de Representación

La representación mental constituye un elemento central en Psicología. Este concepto comenzó a adquirir relevancia cuando el esquema *Estímulo-Respuesta* (E-R), característico del conductismo radical, se quebró para incluir en su seno a un *Organismo* capaz de representar la información recibida y de seleccionar, en función de esa representación, una respuesta adecuada (E-O-R). La introducción de esta variable interviniente marcó el primer paso que finalmente desembocaría en la constitución de una nueva perspectiva: la orientación cognitiva, cuyo objeto de estudio son los procesos mentales y su representación.

La idea de representación implica la capacidad de un sistema de interiorizar información, codificarla, almacenarla y reproducirla posteriormente, en ausencia de su fuente sensorial directa. Desde la perspectiva del desarrollo cognitivo, este fenómeno se ha denominado como la *permanencia del objeto* (Piaget, 1929). Este proceso describe cómo el niño comienza a mantener una representación interna de los objetos, atribuyéndoles una existencia independiente que se extiende más allá de su percepción directa. Crucialmente, la adquisición de esta capacidad modifica radicalmente la relación del infante con la realidad, ya que las representaciones internas adquieren la forma de objetivos que organizan su conducta de forma coherente (véase e.g. Clifton, Rochat, Litovsky, & Perris, 1991).

A medida que el infante va adquiriendo la capacidad de representar los estímulos que le rodean, almacena este conocimiento en distintas categorías. Las categorías constituyen una forma de clasificación que permite agrupar varios ejemplares individuales en base a un conjunto de características compartidas. Se ha sugerido que las categorías presentan una *organización neuroanatómica* en nuestro cerebro, ya que la evidencia neuropsicológica ha revelado la existencia de déficits en categorías semánticas determinadas a consecuencia de daños cerebrales específicos. Así, estos déficits pueden mostrar un deterioro selectivo en la capacidad para identificar seres

vivos sin que la clasificación de seres inanimados se vea afectada, o viceversa (e.g. Capitani, Laiacona, Mahon, & Caramazza, 2003).

La mayoría de los modelos teóricos que intentan ofrecer una explicación a este tipo de disociaciones han sido formulados desde una *perspectiva semántica*, sugiriendo que las categorías se organizan anatómicamente en función de sus características [funcionales vs. perceptivas] o de su ámbito de conocimiento [seres vivos, seres inertes, seres de la propia especie o herramientas] (véase Mahon & Caramazza, 2009 para una revisión). Posturas recientes, por el contrario, defienden que ciertos déficits categoriales pueden explicarse desde una perspectiva *pre-semántica* (Gerlach, 2009). Gerlach define el conocimiento semántico como una forma de representación amodal y el conocimiento pre-semántico como una forma de representación ligada a una modalidad sensorial. Este autor propone que aquellos pacientes que muestran un déficit específico asociado a la categorización de un estímulo exclusivamente a través de una modalidad sensorial (i.e. afasia óptica)¹, mostrarían una alteración de la representación pre-semántica del objeto.

Basándonos en estos planteamientos, podríamos deducir que existen distintas formas de representar el conocimiento: mediante representaciones abstractas, basadas en la semántica del objeto o mediante representaciones concretas, ligadas a una modalidad sensorial. Esto, en definitiva, no es más que preguntarse acerca del formato que adopta la representación del conocimiento, es decir, preguntarnos acerca de la naturaleza de la representación.

2. La naturaleza de la representación

La naturaleza del objeto de la atención, como comentábamos en el capítulo anterior, constituye un factor determinante en la manifestación de los efectos atencionales. Por lo tanto, resulta ineludible abordar la cuestión de la naturaleza de la representación mental.

¹ Este déficit describe la incapacidad para categorizar un estímulo visualmente, a pesar de su reconocimiento (a diferencia de la agnosia visual). El conocimiento semántico del objeto se ve preservado ya que el paciente puede acceder a él a través de otras modalidades sensoriales (i.e. tacto).

Este tema dio lugar a un debate clásico en la literatura de la representación del conocimiento: el debate *analógico-proposicional*. La hipótesis analógica proponía la existencia de representaciones cuasipictóricas de la realidad. Estas *imágenes mentales* debían incluir información visuo-espacial como la forma, el tamaño, la orientación de una figura y la estructura de sus elementos (e.g. Richardson, 1969). Por el contrario, la hipótesis proposicionalista negaba su existencia y defendía el carácter semántico de toda representación simbólica, cuyo formato era conceptual, abstracto y amodal (e.g. Pylyshyn, 1973). A lo largo de las últimas décadas de investigación, la evidencia empírica ha logrado demostrar la validez de la hipótesis analógica en relación a la representación del conocimiento.

1. La existencia de imágenes mentales

El constructo de imagen como correlato de la actividad mental proviene de una experiencia fenomenológica incuestionable: los individuos de todas las culturas han experimentado la sensación de percibir imágenes con el *ojo de la mente* (1971). Sin embargo, el mismo carácter subjetivo de esta experiencia fue el responsable de su controversia. La imagen mental se considera un reflejo de la experiencia real que permanece en la mente del individuo, estableciendo una analogía entre representación y percepción. Pero, a pesar de que el concepto ya estaba presente en el pensamiento filosófico del siglo XVIII (e.g. Hume, 1739), la hipótesis sobre la existencia de una representación perceptiva de la realidad no se abordó de forma experimental hasta la mitad del siglo XX.

El estudio clásico de Shepard & Metzler (1971) sobre la rotación mental de objetos constituye un referente que ilustra la analogía entre la percepción de un objeto y su imagen mental. Este estudio reveló que el tiempo que necesitaban los participantes para juzgar si dos figuras desalineadas angularmente eran idénticas, dependía de la distancia de rotación existente entre ambas. La estrategia de los participantes, por tanto, parecía consistir en crear una imagen mental del modelo y rotarlo hasta alcanzar la

posición de la segunda figura. La equivalencia empírica entre los procesos de transformación real e imaginada constituyó una de las primeras evidencias a favor de las representaciones de naturaleza visual (Cooper & Shepard, 1973; Metzler & Shepard, 1974).

Sin embargo, los trabajos de Kosslyn y colaboradores establecieron las bases fundamentales de esta línea de investigación (e.g. Kosslyn & Alper, 1977; Kosslyn, Cave, Provost, & Von Gierke, 1988). Estos autores propusieron que si las representaciones percibidas e imaginadas eran equivalentes, el procesamiento de imágenes mentales se vería afectado por las mismas variables que el procesamiento perceptivo. De esta manera, comprobaron que determinadas características de la imagen mental, como su tamaño relativo o su complejidad, influían en los juicios perceptivos de los participantes de la misma forma que lo hubieran hecho durante la percepción de la imagen real (e.g. Kosslyn, 1975).

El conjunto de estos hallazgos condujo a la formulación del modelo de *Imaginación Visual* (Farah, 1984), que adaptó las hipótesis de Kosslyn y colaboradores al modelo de Memoria de Trabajo (Baddeley & Hitch, 1974). Este modelo considera el Búfer visuo-espacial como el dispositivo básico encargado de toda creación de imágenes, ya provengan del exterior a través de los mecanismos perceptivos (flujo de información de abajo-a-arriba, *bottom-up*) o se generen internamente, recuperadas de la memoria a largo plazo (flujo de información de arriba-a-abajo, *top-down*). Las implicaciones neuroanatómicas de este modelo revolucionaron el estudio de las representaciones mentales, al proponer la existencia de un mismo substrato neural para la percepción y la imaginación visual.

En la actualidad, numerosos estudios de neuroimagen han revelado que la creación de imágenes mentales genera actividad en áreas de la corteza visual, específicamente en regiones asociativas de la corteza occipitotemporal y occipitoparietal (e.g. D'Esposito et al., 1997; Klein, Paradis, Poline, Kosslyn, & Le Bihan, 2000; Mellet, Tzourio, Denis, & Mazoyer, 1998; Roland & Gulyás, 1995). Sin embargo, la evidencia indiscutible a favor de un substrato neural común proviene de

aquellos estudios que comparan de forma directa las áreas activadas durante la percepción y la representación interna de un mismo estímulo.

Las técnicas de neuroimagen han permitido descubrir la existencia de regiones de la corteza visual que responden de forma específica ante la presentación de distintas categorías (e.g. Cohen et al., 2000; Downing, Jiang, Shuman, & Kanwisher, 2001; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kanwisher, McDermott, & Chun, 1997). Basándose en esta evidencia, Ishai y colaboradores (2000) mostraron que imaginar casas, sillas o caras provocaba la activación de pequeñas subregiones de las áreas implicadas en el procesamiento visual de esas mismas categorías. O'Craven y colaboradores (2000) replicaron estos resultados con caras y paisajes, aunque su aportación crucial fue demostrar que el patrón de actividad asociado a cada imagen mental era lo suficientemente estable como para poder inferir su contenido mediante la sola inspección del registro cerebral.

Otro dato de interés es que, en determinadas ocasiones, las representaciones mentales logran activar áreas visuales de la corteza extraestriada (Chen et al., 1998; Kosslyn et al., 1999; Kosslyn, Thompson, Kim, & Alpert, 1995; Le Bihan et al., 1993; Thompson, Kosslyn, Sukel, & Alpert, 2001). Sin embargo, otras investigaciones no han identificado la activación de regiones implicadas en un procesamiento visual tan temprano (D'Esposito et al., 1997; Mellet et al., 1998; Mellet et al., 2000). Mediante una exhaustiva revisión de estos estudios, algunos autores han propuesto que dicha activación temprana se observa cuando la tarea requiere una focalización de la atención y un uso activo de los *detalles específicos* de la imagen mental (Kosslyn & Thompson, 2003), ya que la simple creación de una imagen detallada no logra inducir activación en la corteza extraestriada (Mellet et al., 2000).

En su conjunto, estos resultados han permitido consolidar varias ideas fundamentales en las teorías del conocimiento. En primer lugar, apoyan la existencia de representaciones mentales de carácter visual. En segundo lugar, sugieren que la representación de un objeto específico activa las mismas áreas que su percepción directa, pero en menor proporción. Y en tercer lugar, los resultados muestran que las regiones activadas se localizan en áreas visuales secundarias de la corteza

occipitotemporal pero, a medida que la imagen adquiere un mayor detalle, esa activación se extiende hacia áreas visuales primarias de la corteza extraestriada.

El objetivo fundamental que guía esta tesis explora qué etapas del procesamiento se ven moduladas por la atención como resultado de generar expectativas acerca de la categoría o identidad particular del estímulo objetivo. Los hallazgos expuestos en este apartado muestran que la representación de categorías y ejemplares pueden adoptar tanto un formato amodal/semántico como un formato visual/pre-semántico. Basándonos en previos resultados, si la expectativa hiciera referencia a una representación visual del estímulo, esperaríamos observar una modulación atencional en etapas perceptivas del procesamiento. Por el contrario, en el caso de que la expectativa hiciera referencia a una representación semántica, esperaríamos observar una modulación en etapas más tardías, encargadas del procesamiento léxico-semántico del estímulo.

Expectativas acerca del objeto

Efectos sobre la percepción

1. Investigaciones precedentes

Como comentábamos anteriormente, el estudio de las expectativas acerca de un estímulo, atendiendo a su categoría o identidad particular, es un campo que ha pasado prácticamente desapercibido dentro de la investigación experimental. Hasta donde alcanza nuestro conocimiento, muy pocos estudios han abordado esta temática y aquellos que lo han hecho, no han estudiado la manifestación del efecto de las expectativas mediante un registro electroencefalográfico. Debido a estas razones, creímos necesario y relevante iniciar este proyecto, que ofrece un pormenorizado estudio, mediante en uso de ERPs, sobre la modulación atencional que ejercen las expectativas acerca del objeto en el procesamiento visual. No obstante, las investigaciones precedentes aportan una base empírica fundamental para la elaboración de nuestras hipótesis.

1. Expectativas sobre categorías

A lo largo del 2009, dos investigaciones abordaron el estudio de las expectativas categoriales mediante fMRI. Esterman y colaboradores (2009) utilizaron dos señales predictivas que anticipaban la aparición de una cara o de un edificio con un 100% de probabilidad y una señal no predictiva que indicaba con la misma probabilidad la aparición de ambas. Tras la presentación de la señal, el estímulo objetivo surgía progresivamente de un patrón visual difuso. La tarea del participante consistía en discriminar el género (en el caso de las caras) o el número de plantas (en el caso del edificio) del estímulo percibido. Los resultados conductuales revelaron un claro efecto de validez al comparar los tiempos de reacción asociados a estímulos esperados con los no esperados de una misma categoría (válidos vs. neutros). Sin embargo, el hallazgo más interesante mostró que la señal atencional inducía actividad en áreas especializadas de la corteza visual (FFA para caras y el giro Parahipocampal para edificios) antes de que la imagen del estímulo alcanzara el umbral mínimo de percepción. Estos resultados

sugieren que la anticipación de una categoría facilita su procesamiento mediante la activación previa de áreas implicadas en su percepción.

Puri y colaboradores (2009) utilizaron un paradigma algo distinto para investigar el efecto de las expectativas categoriales. En su estudio, la señal consistía en una palabra que indicaba una de las categorías con un 70% de probabilidad (CARA vs. EDIFICIO). La tarea de los participantes consistía en decidir si el estímulo objetivo, presentado brevemente tras la señal, coincidía o no con la categoría señalada (igual vs. no igual). Este diseño permitía estudiar tanto el efecto de la expectativa en ausencia del estímulo, como el efecto de la atención durante el procesamiento de ese estímulo en función de la validez de la señal. Los resultados conductuales replicaron aquellos observados por Esterman y colaboradores. Asimismo, el análisis de la actividad inducida por las expectativas mostraron un mismo patrón de anticipación. Finalmente, el análisis de la actividad durante el procesamiento reveló un incremento selectivo de la actividad en regiones especializadas (FFA y PPA) ante estímulos de una misma categoría en función de la expectativa (ensayo válido > ensayo inválido).

2. Expectativas sobre estímulos particulares: Expectativas idiosincrásicas

Las expectativas idiosincrásicas se han investigado principalmente mediante estudios comportamentales. Dos de los tres estudios identificados sobre el tema (Faulkner, Rhodes, Palermo, Pellicano, & Ferguson, 2002; Puri & Wojciulik, 2008), utilizaron señales centrales asociadas a un 75% de validez (nombres propios), para indicar la aparición de una persona conocida o un lugar famoso (i.e. Tom Hanks, Taj Mahal). Los resultados de ambos estudios revelaron que estas expectativas reducían el TR necesario para identificar cuál del par de imágenes presentadas del mismo estímulo exhibía una distorsión (ensayos válidos < ensayos inválidos). Resulta importante señalar que Puri y Wojciulik también manipularon la presentación de un ejemplar específico tras una señal que indicaba un ejemplar distinto pero perteneciente a la misma categoría (ensayo inválido con respecto al ejemplar-ensayo válido con respecto a la categoría).

Según estos autores, la identificación de una optimización del procesamiento en este caso particular mostraría el efecto de expectativas acerca de la categoría del estímulo. Sus resultados no mostraron un beneficio comportamental, probablemente a consecuencia de la complejidad de su diseño.

Finalmente, un estudio reciente ha abordado la investigación de expectativas idiosincrásicas mediante fMRI (Stokes, Thompson, Nobre, & Duncan, 2009). Estos autores mostraron que generar una expectativa sobre una letra particular (X vs. O), incrementaba la precisión de los participantes para detectar esa letra en una sucesión de estímulos sobre fondo difuso. El análisis de la actividad cerebral inducida por la expectativa se llevó a cabo mediante un método avanzado de análisis, basado en algoritmos complejos de clasificación de patrones: “Análisis multi-voxel de descodificación de patrones” (de inglés, *Multi-voxel pattern analysis, MVPA*). Esta técnica, a diferencia de técnicas más tradicionales que analizan la activación voxel a voxel, se focaliza en identificar patrones de activación analizando simultáneamente una gran muestra de voxeles (véase e.g. Norman, Polyn, Detre, & Haxby, 2006). Este análisis permite caracterizar, con un alto nivel de precisión, patrones de actividad específicos dentro de una misma población neural. Los resultados revelaron que, en ausencia de estimulación visual, la expectativa sobre una letra activaba un circuito neural equivalente al observado durante la percepción directa de esa misma letra. La observación del patrón cerebral asociado a cada expectativa, por tanto, permitía deducir el contenido específico de la misma (X u O).

Estos resultados, tomados en su conjunto, constituyen una base fundamental para nuestra investigación. Esta tesis profundiza en el estudio de estas expectativas a través del registro de ERPs, el cual permite investigar la modulación atencional que ejerce esta forma de atención endógena sobre las distintas fases del procesamiento visual.

2. Expectativas: de lo general a lo particular, del objeto al sujeto

Las expectativas atencionales en este proyecto se estructuran en base a dos ejes: la dimensión de especificidad y la dimensión de relevancia personal. Así, la línea de investigación avanza a través del estudio de expectativas sobre categorías generales, neutrales con respecto al participante, hasta llegar al estudio de expectativas sobre estímulos particulares, de gran relevancia para el participante. El presente apartado expone aquellas categorías y estímulos ejemplares seleccionados para nuestro proyecto de investigación.

1. Categorías: Caras y Palabras

Nuestro cerebro es un órgano que posee un alto grado de especialización. El uso de técnicas de neuroimagen en las últimas décadas, así como los estudios clínicos de daño cerebral y registro unicelular en primates, han permitido identificar múltiples áreas especializadas en el análisis visual de distintos aspectos del estímulo (e.g. color, movimiento; Morita et al., 2004; Paradis et al., 2000). Asimismo, se han identificado regiones que responden no sólo a características específicas de un estímulo, sino también a patrones visuales complejos como caras (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Kanwisher et al., 1997), palabras (Cohen et al., 2000; Nobre, Allison, & McCarthy, 1994), animales (Chao, Martin, & Haxby, 1999), herramientas (Aguirre, Zarahn, & D'Esposito, 1998), paisajes (Epstein & Kanwisher, 1998), casas (Aguirre, Zarahn, & D'Esposito, 1998), sillas (Ishai et al., 1999) y partes del cuerpo humano (Downing et al., 2001).

Sin lugar a dudas, las áreas especializadas que han suscitado mayor investigación y controversia son las relacionadas con el procesamiento de caras y de palabras. La polémica sobre la especialización de estas áreas surgió en torno a tres aspectos básicos: la naturaleza de su origen (innato vs. aprendido; e.g. Carmel & Bentin,

2002), su nivel de especificidad (e.g. Gauthier, Behrmann, & Tarr, 2004) y su permeabilidad a procesos de alto nivel (e.g. Cauquil, Edmonds, & Taylor, 2000).

El área identificada en el procesamiento visual de caras se localiza en la región medial del giro fusiforme y muestra una mayor activación en el hemisferio derecho (FFA: Face Fusiform Area; e.g. Kanwisher et al., 1997; Puce, Allison, Gore, & McCarthy, 1995). En contraste, el área especializada en discriminar patrones lingüísticos visuales (palabras, no-palabras y símbolos) se localiza en una región similar del giro fusiforme pero muestra una clara lateralización sobre el hemisferio izquierdo (VWFA: Visual Word Form Area; e.g. McCandliss, Cohen, & Dehaene, 2003).

Los estudios de registro electroencefalográfico también han identificado potenciales específicos asociados al procesamiento visual de estas dos categorías. El componente N170 se registra en etapas perceptivas del procesamiento y parece mostrar una distribución espacial que se corresponde con el patrón de lateralización observado mediante técnicas de neuroimagen. Así, el N170 para caras se observa bilateralmente pero presenta una mayor definición sobre la región occipito-parietal del hemisferio derecho, mientras que el N170 para palabras muestra una fuerte lateralización hacia áreas occipito-parietales del hemisferio izquierdo (e.g. Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000a; Maurer, Brandeis, & McCandliss, 2005). De hecho, el análisis de dipolos y diversos estudios correlacionales sugieren la existencia de un vínculo funcional entre estos correlatos electrofisiológicos y la activación de las áreas mencionadas (Brem et al., 2005; Henson et al., 2003; Herrmann, Ehlis, Muehlberger, & Fallgatter, 2005; Itier, Herdman, George, Cheyne, & Taylor, 2006). Estos resultados permiten considerar al N170 como un índice adecuado de *procesamiento perceptivo categorial*.

Basándonos en estos hallazgos, decidimos seleccionar la categoría de caras y palabras para explorar los efectos de la atención endógena sobre el procesamiento de un estímulo atendiendo a su categoría. Sin duda, el potencial N170 constituye un parámetro excelente sobre el que comprobar si las expectativas categoriales logran modular el procesamiento perceptivo del estímulo esperado.

2. *Estímulos Idiosincrásicos: Caras familiares y no familiares*

El ser humano es un experto en la discriminación e identificación de caras individuales. Por esta razón, las caras se pueden considerar estímulos muy apropiados para el estudio de la atención a ejemplares específicos dentro de una misma categoría. Asimismo, consideramos interesante investigar la influencia que la familiaridad del estímulo esperado podía ejercer en la manifestación de los efectos atencionales.

La *familiaridad* es un término que ha sido ampliamente estudiado en el área de investigación en Memoria. En este área, la familiaridad hace referencia a un proceso de reconocimiento que se contrapone a la recuperación explícita y consciente de un recuerdo (e.g. Reder et al., 2000; Yonelinas, 1994). Sin embargo, en este proyecto no focalizamos nuestro interés en la recuperación de la experiencia pasada, sino en el efecto que la experiencia perceptiva previa ejerce sobre el procesamiento (e.g. Jackson & Raymond, 2008; Tong & Nakayama, 1999). Resulta fundamental señalar que esa experiencia es *explícita*, para no confundirla con el priming de repetición. Para considerar que un determinado estímulo es *familiar*, el participante debe haber experimentado un alto número de encuentros con el mismo durante un periodo extenso de tiempo. Por el contrario, un estímulo *no familiar* es aquel que se ha presentado un escaso número de veces o que es completamente nuevo para el participante.

Dentro del área de investigación en percepción, diversas investigaciones han mostrado que la familiaridad visual que se posee con un estímulo es un factor que influye en su procesamiento, agilizando el proceso de análisis visual y el reconocimiento (e.g. Gauthier & Tarr, 1997). Esta influencia es particularmente remarcable en el procesamiento de caras. Las caras familiares no sólo muestran un beneficio en procesos relacionados con la extracción de la identidad (Balas, Cox, & Conwell, 2007; Bruce, Henderson, Newman, & Burton, 2001; Bruck, Cavanagh, & Ceci, 1991; Hancock, Bruce, & Burton, 2000) sino que también facilitan juicios perceptivos independientes (Balas et al., 2007; Bruyer, Lafalize, & Distefano, 1991; Bruyer, Leclere, & Quinet, 2004; Buttle & Raymond, 2003; O'Donnell & Bruce, 2001; Rossion, 2002). En base a esta evidencia, se ha sugerido que las caras familiares y no

familiares poseen representaciones perceptivas distintas (véase Johnston & Edmonds, 2009 para una revisión).

3. *Estímulos Idiosincrásicos: El cuerpo propio y ajeno*

Finalmente, con el propósito de investigar el efecto de expectativas muy detalladas acerca del estímulo y de avanzar un nivel más en la dimensión de relevancia personal, decidimos seleccionar una categoría que nos permitiera incluir un estímulo perteneciente al propio sujeto: el cuerpo.

Nuestro cuerpo constituye un objeto único para la percepción. La experiencia subjetiva de sentirse un ser individual pasa por percibir el cuerpo como propio (c.f. Blanke & Arzy, 2005). Ese cuerpo puede ser percibido externamente, como el resto de los estímulos que nos rodean, pero también puede percibirse desde el interior, como sujeto de experiencia. El cuerpo es objeto y sujeto: siente y, a su vez, es sentido. Debido a estas características, el cuerpo es considerado por numerosos autores como la primera fase emergente de la conciencia del *Yo* o el *Self* (Damasio, 1999; Gallagher, 2000; James, 1890).

A lo largo de las últimas décadas, numerosos estudios han puesto de manifiesto que la información relacionada con uno mismo (*Self-related information*) parece procesarse de forma diferente a otro tipo de información (e.g. Craik et al., 1999; Fischler, Jin, Boaz, Perry, & Childers, 1987; Gilboa, 2004; Graham, Lee, Brett, & Patterson, 2003; Kelley et al., 2002). Basándose en estos hallazgos, algunos autores han propuesto que esta información sustenta una representación interna cualitativamente distinta, una representación *especial* (véase Gillihan & Farah, 2005 para una revisión). ¿Es posible que la representación de nuestro cuerpo difiera de la que poseemos sobre otros cuerpos?

Esta cuestión adquiere un matiz singular en el caso de la representación corporal, ya que la evidencia neuropsicológica sugiere que nuestro cuerpo posee múltiples representaciones internas (e.g. Head & Holmes, 1911; Sirigu, Grafman,

Bressler, & Sunderland, 1991). La principal división propuesta distingue entre el *esquema corporal* y la *imagen corporal*, que presenta un estrecha analogía con las dos vías neurales encargadas del procesamiento de un estímulo: la vía del *cómo/dónde* y la vía del *qué* (e.g. Haxby et al., 1994). De esta forma, el *esquema corporal* describe el conocimiento implícito que poseemos sobre la localización de nuestros distintos miembros y la coordinación visuo-motora de la acción en el espacio (e.g. Paillard, 1999; Sirigu et al., 1991). Por el contrario, la *imagen corporal* hace referencia al conocimiento explícito que poseemos sobre nuestro propio cuerpo: el conocimiento semántico sobre las funciones corporales (i.e. función de la boca), el uso correcto de complementos (i.e. lugar donde se colocan los guantes) y, por supuesto, la representación consciente de nuestra apariencia visual (e.g. Frassinetti et al., 2009; Moro et al., 2008; Schwoebel & Coslett, 2005).

El estudio de la representación visual que poseemos de nuestro cuerpo se ha centrado principalmente en el reconocimiento del propio rostro, otorgando a otras partes del cuerpo menos distintivas un papel secundario (Kircher et al., 2000; Sugiura et al., 2000, 2006, 2005). A pesar de ello, el interés por explorar cómo procesamos imágenes visuales de nuestro cuerpo o partes de él ha ido creciendo progresivamente en los últimos años. Estos estudios investigan las diferencias que emergen al comparar el procesamiento visual del propio cuerpo con cuerpos ajenos, tanto a nivel comportamental (Frassinetti et al., 2009, 2009; Frassinetti, Manuele Maini, Romualdi, Galante, & Avanzi, 2008) como a nivel neural (Hodzic et al., 2009; Hodzic, Muckli, Singer, & Stirn, 2009; Myers & Sowden, 2008), revelando que efectivamente el procesamiento visual de nuestro cuerpo sustenta un estatus *especial*. Estos resultados sugieren la posibilidad de que la representación perceptiva de nuestro cuerpo sea intrínsecamente distinta a la representación que poseemos sobre otros cuerpos.

3. Planteamiento general de la investigación

El objetivo principal de esta serie de estudios es comprobar si la atención endógena, adoptando la forma de expectativas acerca del objeto, logra optimizar el procesamiento del estímulo esperado. Estas expectativas se crean en base a la categoría a la que pertenece el estímulo o a su identidad idiosincrásica. Una vez identificada una facilitación del procesamiento a nivel comportamental, el interés de la investigación se centra en explorar si este tipo de expectativas modulan etapas perceptivas o post-perceptivas del procesamiento visual mediante ERPs. El estudio de la modulación atencional en las distintas etapas del procesamiento nos permite hipotetizar acerca del tipo de representación que constituye el objeto de la atención en este proyecto.

Esta serie experimental se subdivide en tres bloques principales. El primer bloque (Capítulo 2) aborda la posibilidad de anticipar la aparición de un estímulo específico atendiendo a la categoría a la que pertenece: caras o palabras. Ambas categorías son neutrales con respecto al sujeto. Estas categorías fueron seleccionadas debido a la extensa información que se posee acerca de su procesamiento visual, la lateralización opuesta de las áreas implicadas en su percepción y la existencia de un índice perceptivo de procesamiento categorial que distingue estas dos categorías: el N170. El objetivo general de este estudio, por tanto, es investigar si las expectativas categoriales logran facilitar el procesamiento de aquellos estímulos pertenecientes a la categoría esperada. El objetivo secundario, aunque no menos importante, es examinar si la atención endógena modula etapas perceptivas asociadas al procesamiento categorial, cuyo índice es el componente N170. Resulta importante señalar que no esperamos encontrar efectos en componentes perceptivos previos a este índice, ya que la expectativa generada incluye información visual a un nivel medio de especificidad. Esta información es suficientemente concreta como para distinguir entre categorías y suficientemente abstracta como para incluir a todos los estímulos individuales pertenecientes a cada categoría. Según nuestro planteamiento, una modulación atencional más temprana se observaría tan sólo induciendo una expectativa detallada

sobre el estímulo esperado, capaz de activar áreas primarias del procesamiento visual (véase Kosslyn & Thompson, 2003).

El segundo bloque (Capítulo 3) investiga la capacidad de la atención para optimizar el procesamiento de estímulos particulares dentro de una misma categoría perceptiva. Con este propósito, seleccionamos dos caras pertenecientes a personas que compartían una serie de características generales como la edad, el sexo y el color de pelo. La búsqueda de similitud entre estímulos respondía a la intención de forzar a los participantes a que focalizaran su atención en los detalles idiosincrásicos de cada rostro. Según nuestro planteamiento, una expectativa detallada modularía componentes perceptivos tempranos del procesamiento visual (véase Kosslyn & Thompson, 2003). Por otra parte, dado que la familiaridad parece influir en la representación interna (c.f. Johnston & Edmonds, 2009), decidimos examinar si las expectativas basadas en representaciones previamente establecidas (cara familiar) o recién creadas (cara no familiar) ejercían un efecto diferencial sobre el procesamiento visual del estímulo.

Finalmente, el tercer bloque (Capítulos 4 y 5) explora el efecto de la atención endógena sobre estímulos particulares aún más semejantes entre sí. Dado que las caras son estímulos muy distintivos, a pesar de pertenecer a una misma categoría, decidimos seleccionar imágenes corporales pertenecientes a dos personas diferentes. Las manos de distintas personas, cuando éstas son equivalentes en tamaño, género, edad y color de piel, presentan un gran parecido, requiriendo que los participantes generen expectativas con un alto grado de definición. Avanzando un nivel más en la relevancia personal del estímulo esperado, decidimos investigar la influencia de la identidad propia o ajena en la modulación atencional del procesamiento. Dado que el propio cuerpo presenta una serie de características únicas, este bloque experimental incluye varios objetivos específicos.

En primer lugar, nuestras manos constituyen una parte del cuerpo que utilizamos constantemente pero a cuya apariencia no prestamos especial atención. Por esta razón, uno de nuestros objetivos es investigar si las expectativas facilitan el procesamiento visual del estímulo (activando una impresión visual o *imagen*) o simplemente preparan una respuesta manual (activando un conocimiento motor o *esquema*). En segundo lugar,

las imágenes sobre el propio cuerpo se procesan de forma distinta en relación a otros cuerpos (Frassinetti et al., 2008; Hodzic et al., 2009; Myers & Sowden, 2008). Basándonos en estos resultados, investigamos la posible existencia de un efecto diferencial de la atención en el procesamiento en función de la identidad propia o ajena del estímulo.

Clara Aranda
Eduardo Madrid,
Pío Tudela
María Ruz

Manuscript submitted for publication

Category Expectations:

A differential modulation of the N170 potential for faces and words

Abstract

The goal of the present study was to explore whether endogenous attention can be oriented to different perceptual categories and to examine how these expectations modulate stimulus visual processing. We designed a cueing paradigm that prepared participants, on a trial by trial basis, for the most likely stimulus category of the target, which could be either a face or a word. Participants were asked to perform a gender discrimination task of the stimuli, independently of their category. We measured participants' brain activity by means of a high-density electroencephalographic recording system to investigate the neural correlates of orienting attention to faces and words. As expected, we observed a behavioural facilitation for valid compared to invalid trials. In addition, target expectations influenced stimulus processing at several points in time. Most importantly, attention modulated the lateralized N170 component in a category-specific fashion. These results show that, at least under certain circumstances, orienting endogenous attention to different categories can influence the perceptual stages of face and word visual processing.

Introduction

Voluntary attention has been mainly investigated in the context of spatial locations (e.g. Posner, 1980), simple perceptual features (e.g. Anllo-Vento & Hillyard, 1996) and objects (e.g. Duncan, 1984). This body of research has repeatedly shown that attended attributes are processed more efficiently than unattended ones. However, attention can also be directed to more complex or abstract features (see Scholl, 2001), such as specific motor responses (Rushworth et al., 2003), instants of time (Correa, Sanabria, Spence, Tudela, & Lupiáñez, 2006; Nobre, 2001), representations held in memory (Lepsien & Nobre, 2007) or different aspects of linguistic processing (Cristescu & Nobre, 2008; Ruz & Nobre, 2008, 2008a). However, the effects of expectations that concern the perceptual configuration of a target stimulus, describing a category or an individual identity, have been scarcely explored (Esterman & Yantis, 2009; Puri & Wojciulik, 2008; Puri et al., 2009). It is important to note that none of the published investigations have approached this goal by means of Event-Related Potential recordings (ERPs). Therefore, here we explored the electrophysiological correlates of category expectations to investigate whether they were able to influence initial stages of stimulus visual processing.

Converging evidence in Neuroscience has revealed that our brain sustains a high degree of specialization. Thus, there are regions that respond specifically to the visual presentation of different categories such as human faces (Allison et al., 1994; Kanwisher et al., 1997), words (Cohen et al., 2000; Nobre et al., 1994), body parts (Downing et al., 2001), buildings (Aguirre et al., 1998), tools (Chao, Haxby, & Martin, 1999) or animals (Chao et al., 1999). Among them, faces and words are the perceptual categories that have boosted more interest by researchers. These stimuli are identified faster and more accurately than other type of objects, which suggests that humans processed them in a highly efficient manner (e.g. McCandliss et al., 2003; Rayner & Pollatsek, 1989; Yin, 1969). On the one hand, face processing is severely disrupted by stimuli inversion, which has been taken as an evidence of a holistic analysis of up-right

faces (e.g. Hochberg & Galper, 1967). On the other hand, several authors have suggested that letters are grouped together, resulting in an individual unit that is also perceived as a whole (Riesenhuber & Poggio, 1999; Warrington & Shallice, 1980). As a result, it has been proposed that the efficient processing of faces and words reflects a configurational perceptual analysis.

Regarding the particular neural substrates of face and word processing, fMRI studies have shown that the visual presentation of faces evokes activation in the lateral fusiform gyri, which is generally greater on the right hemisphere (Kanwisher et al., 1997; McCarthy, Puce, Gore, & Allison, 1997), while words recruit a specific area on the left fusiform gyrus (Cohen et al., 2000; Dehaene, Le Clec'H, Jean-Baptiste Poline, Le Bihan, & Cohen, 2002; Polk & Farah, 2002; for a review, see McCandliss et al., 2003; although see Price & Devlin, 2003). These regions have been labelled as the Face Fusiform Area (FFA) and the Visual Word Form Area (VWFA), respectively. Neuropsychological cases support these claims by showing deficits in face processing after right occipito-temporal damage (Prosopagnosia; e.g. Damasio, Damasio, & Van Hoesen, 1982; Farah, 1995; although see Gauthier et al., 2004) and deficits in word processing after left occipital damage (Pure alexia; Binder & Mohr, 1992; Warrington & Shallice, 1980).

Crucially, electroencephalographic studies have also identified specific potentials that reflect the distinct processing of face and word stimuli. Faces evoke a negative event-related peak over occipito-temporal regions, named N170, which shows a bilateral pattern, although it is more pronounced in the right hemisphere (e.g. Bentin et al., 1996; Eimer, 2000c; Lueschow et al., 2004; Watanabe, Kakigi, Koyama, & Kirino, 1999). On the other hand, words evoke an analogous negative potential, which is also observed over occipito-temporal regions and presents a strongly left-lateralized pattern (e.g. Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Maurer et al., 2005; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). It is important to note that source localization analyses and correlation studies have suggested the existence of a functional link between the neural and electrophysiological correlates identified for face and word processing, respectively (e.g. Brem et al., 2005; Henson et

al., 2003; Herrmann et al., 2005; Itier et al., 2006). These findings suggest that the N170 is a satisfactory index of categorical stimulus processing (although see Dering, C. D. Martin, & Thierry, 2009; Thierry, Martin, Downing, & Pegna, 2007).

The attentional modulation of the N170 potential has evoked a notable controversy. Numerous studies have reported that orienting attention to faces or words does not exert an influence on the N170 amplitude (e.g. Carmel & Bentin, 2002; Cauquil et al., 2000; Lueschow et al., 2004; Thierry et al., 2007; see also Nobre, Allison, & McCarthy, 1998), which has led some authors to claim that the initial stages of categorical processing were *cognitively impenetrable* (Cauquil et al., 2000; Fodorian modules; see Fodor, 1983). However, recent findings indicate that face and word N170 potentials can be modulated by top-down factors, at least under certain circumstances.

Regarding the face N170, working memory (WM) demands seem to play a critical role in observing amplitude modulations. Several studies have reported such modulations as a result of the particular requirements related to different phases of a WM task: increased N170 amplitudes during face encoding and reduced N170 amplitudes during retrieval, in response to face distractors or target stimuli (e.g. Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Morgan, Klein, Boehm, Shapiro, & Linden, 2008; Sreenivasan & Jha, 2007). These opposite patterns emphasized the role of attention during encoding, which optimizes target processing, and during retrieval, which preserves the maintenance of face representations by restraining current stimulus processing. In contrast, pure attentional paradigms have rarely induced an influence on the face N170 amplitude. As an exception, we can cite three studies: two of spatial visual attention and a recently published study of selective attention. These studies reported attentional N170 modulations to attended in contrast to unattended faces, while using complex visual arrays within a spatial paradigm (Crist, Wu, Karp, & Marty G. Woldorff, 2008; Holmes, Vuilleumier, & Eimer, 2003) or under deprived perceptual conditions (Sreenivasan, Goldstein, Lustig, Rivas, & Jha, 2009). Overall, these data show that the face N170 is susceptible to attentional modulation in certain circumstances, although most of the time faces appear to be processed in a

highly automatic fashion (e.g. Lavie, Ro, & C. Russell, 2003; Liu, Harris, & Kanwisher, 2002).

In contrast to the high number of publications reported on the face N170, the attentional modulation of the word N170 has not been so extensively explored. However, a recent study that manipulated task instructions reported an attentional modulation of the word N170 potential (Ruz & Nobre, 2008). In this study, focusing attention to the orthographic nature of the letters within words as compared to their phonology or semantics, enhanced the amplitude of the N170. This outcome was at odds with previous results that failed to find an attentional influence on early visual stages of word processing (e.g. Nobre et al., 1998).

The main goal of the present study was to explore whether expectations about different perceptual categories, i.e. faces or words, optimize the visual processing of an upcoming stimulus belonging to one of these categories. In addition, we investigated whether these expectations modulate early perceptual stages of processing by focusing specifically on the N170, which is thought to reflect a categorical perceptual analysis of the stimuli.

We used a central cueing paradigm to create expectations about the most likely category of the target stimulus, which could be either a face or a word. Our hypotheses were the following. First, we expected that attention to a perceptual category would enhance the processing of the exemplars belonging to it and as a consequence, participants' responses would be faster for valid than for invalid trials. In addition, we predicted that expectancies would modulate the category-specific N170 potentials to faces and words. In order to assess these two hypotheses, we obtained high-density electrophysiological recordings (EEG) while participants performed a gender evaluation task on cued face and word target stimuli.

Methods

Participants. Twenty-four right-handed students (14 females, mean age: 24, age range: 18-46) from the University of Granada participated in the study in exchange of course credits. All participants reported normal or corrected to normal vision and had no history of neurological disorders. They all signed a consent form approved by the Ethics committee of the University of Granada.

Experimental task. Participants were asked to discriminate the gender of visually presented faces or words as fast and accurately as possible. To help them to perform this task, a symbolic cue that predicted the most likely category of the upcoming stimulus was presented prior to target onset. Cues were valid in 75% of the trials and were invalid in the remaining 25%. Note that the gender discrimination task was independent of the dimension signalled by the cue (Target category), which avoided confounds related to the preparation of specific motor responses.

We used 80 first-names, displayed in black, and 80 human faces, displayed in black and white, as targets. Half of the names and faces were female and the other half were male. The words had 3 to 7 letters (5.48 in average, matched across genders) and were collected from a Spanish word database. The faces were obtained from the Max-Planck-Institute for Biological Cybernetics database (Tuebingen, Germany). All of them had the hair removed and were equated in terms of size and luminance. The cue was a star coloured in blue or red. Each colour was associated with one stimulus category in a counterbalanced manner across participants. All stimuli were presented centrally in a 17'' monitor controlled by Biological E-prime software (Schneider, Eschman, & Zuccolotto, 2002).

Each trial comprised a fixation point (1.5°), a cue (3.48°) and a target, all displayed on a grey background, as can be seen in Figure 1. After a fixation point of 750 ms of duration, the cue was flashed for 200 ms, followed by a blank inter-stimulus-interval (ISI of a random duration between 1300-2300 ms). Then, the target stimulus,

either a word (5.22°/ 2.73° on average) or a face (4.38°/ 4.80° on average), was presented for 1200 ms. Participants had 1200 ms to give a response and afterwards, they received a visual feedback of their performance for 500 ms (Correct, Incorrect or Missing response). The feedback helped to keep participants engaged on the task during the experiment.

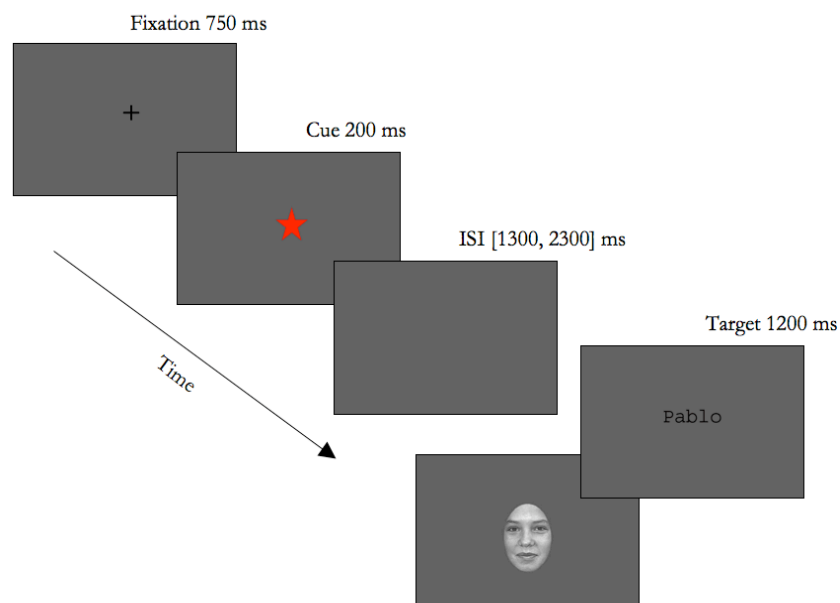


Figure 1. Sequence of events in a trial.

Procedure. Participants sat in a dimly illuminated and electrically shielded room facing a computer screen placed 50 cm in front of them. At the beginning of the experiment, they read the instructions that explained the task and the relationship between the coloured cues and the predicted target categories. Participants were asked to keep their eyes fixated on the centre of the screen and to avoid eye movements and blinks during the presentation of the stimuli. Responses were given by pressing one of two buttons with the left and right index fingers. The association between hand and response was counterbalanced across participants.

The experiment was composed of three blocks of 160 trials each (480 trials in total), with brief breaks between them. The assignment of the validity conditions across individual stimuli was achieved by creating lists with different validity value-item associations, which were counterbalanced across blocks and participants. This controlled assignment made sure that each stimulus (i.e. an specific face) was associated to each validity condition (invalid, valid) an equal number of trials, as well as presented in a different order of blocks. In addition, the presentation of stimuli within each block was randomized. At the beginning of the session, participants performed a training block of 100 trials to familiarize with the task and the electrophysiological recording set-up. The whole EEG recording session lasted for about 50 minutes.

EEG was collected with a high-density EEG system [Geodesics Sensor Net with 128 electrodes from *Electrical Geodesics, Inc. (EGI)*], referenced to the vertex channel. The electrodes located above, beneath and to the left and right of the external canthi of the eyes were used as electrooculograph leads to detect eye movements. The EEG net was connected to an AC-coupled, high-input impedance amplifier (200 MOhm); impedances were kept below 50k Ω , as recommended for the Electrical Geodesics high-input impedance amplifiers. The signal was amplified (0.1 to 100-Hz band pass) and digitized at a sampling rate of 250 Hz (16 bits A/D converter). Data were filtered off-line with a 30 Hz low-pass filter.

The EEG continuous recording was segmented into epochs, 200 ms before and 500 ms after target onset, and subsequently submitted to software processing for identification of artefacts. Epochs showing an excessively noisy EEG ($\pm 100 \mu\text{V}$ from one sample to the next), eye-movements artefacts (blinks or saccades: $\pm 70 \mu\text{V}$ on EOG channels) or incorrect behavioural responses were rejected. Data from individual channels that were consistently bad for a specific subject ($> 20\%$ of trials) were replaced using a spherical interpolation algorithm (Perrin, Pernier, Bertrand, & Echallier, 1989). Trials with reaction times (RTs) faster than 300 ms or slower than 800 ms were regarded as anticipations or late responses, and were also excluded from the

analyses (9,25%). Finally, we established a minimum criterion of 30 artefact-free trials per subject and condition to maintain an acceptable signal-to-noise ratio.

Four group-averaged ERPs waveforms were constructed according to the Target category (face, name) and cue Validity (valid, invalid trials). ERPs were re-referenced to the average to eliminate the effects of reference-site activity and to generate an accurate estimation of the scalp topography of the recorded electrical fields (Dien, 1998; Tucker, Liotti, Potts, G. S. Russell, & Posner, 1994). The 200-msec pre-stimulus epoch served as baseline.

Electrophysiological analysis

We analyzed the voltage of specific ERP potentials to study the effect of cue validity on the processing of target stimuli across categories. The factors tested were Target category (face, name), Validity (valid, invalid) and Hemisphere (right, left), where relevant.

Prior to voltage analyses, we performed a topographical analysis of the ERP data. This analysis shows how the distribution of scalp voltage (i.e. topographies) evolves over time in each experimental condition. Topographical maps represent stable periods of electrical field patterns that correspond to dissociable functional states of the brain, which usually match identifiable ERPs on the grand-averaged waveforms (see Pascual-Marqui, Michel, & Lehmann, 1995). Therefore, a sequence of different maps is thought to reflect a succession of different stages of information processing (Murray et al., 2004; Thierry et al., 2007). In accordance, we used the topographical analysis to explore different brain states during face and word processing and to guide the selection of optimal spatio-temporal windows for voltage comparisons. To obtain the topographical maps on a group-average level, we used a *Segmentation-into-microstates procedure* implemented in Cartool software (developed by Denis Brunet: <http://brainmapping.unige.ch/Cartool.php>). This procedure was applied with several constraints: the maps had to remain stable for 20 ms and the maximum correlation between different topographies should not exceed 92%. The finding of distinct maps for

different conditions was tested by a *Fitting procedure*, which provides information about the percentage of times that the different maps are found in the data from individual participants (see Murray et al., 2002 for a detailed description of these procedures). These values, susceptible to statistic analyses, were then introduced into multifactorial analyses of variance (ANOVAs). A significant interaction between Map and Experimental condition suggests that the explored conditions involve distinct neural configurations (Brandeis, Lehmann, Michel, & Mingrone, 1995; Lehmann & Skrandies, 1980).

We carried out the voltage analyses on selected spatio-temporal windows that were determined by visual inspection, within the time-interval of the corresponding ERP topographical map. The mean amplitude values were computed with reference to the 200 ms pre-stimulus baseline.

Results

Behavioural results.

Reaction times shorter than 300 ms and longer than 800 ms (9,91%), and errors (3,98%) were excluded from the analysis. Participants' mean response time (RT) and accuracy were submitted to a within-subjects repeated-measures ANOVA with the factors of Target category (face, name) and Validity (valid, invalid).

The mean accuracy on the task was 95.5 % with no significant differences between valid and invalid trials ($F < 1$). Participant's accuracy was numerically higher for faces (95.9 %) than for names (95.2 %), although the effect only approached statistical significance, $F(1,23)=3.36$; $p = .08$.

The RT analysis showed that participants were faster on validly cued targets (553 ms) than on invalidly cued targets (564 ms), resulting in a significant main effect of Validity, $F(1,23)=17,81$, $p < .001$ (see Figure 1). The main effect of Target category also reached significance: responses to faces were faster than responses to words (551

ms and 561 ms, respectively, $F(1,23)=16,27, p=.001$). However, the interaction between Target category and Validity was not significant, $F<1$, revealing that the validity effects were comparable across categories.

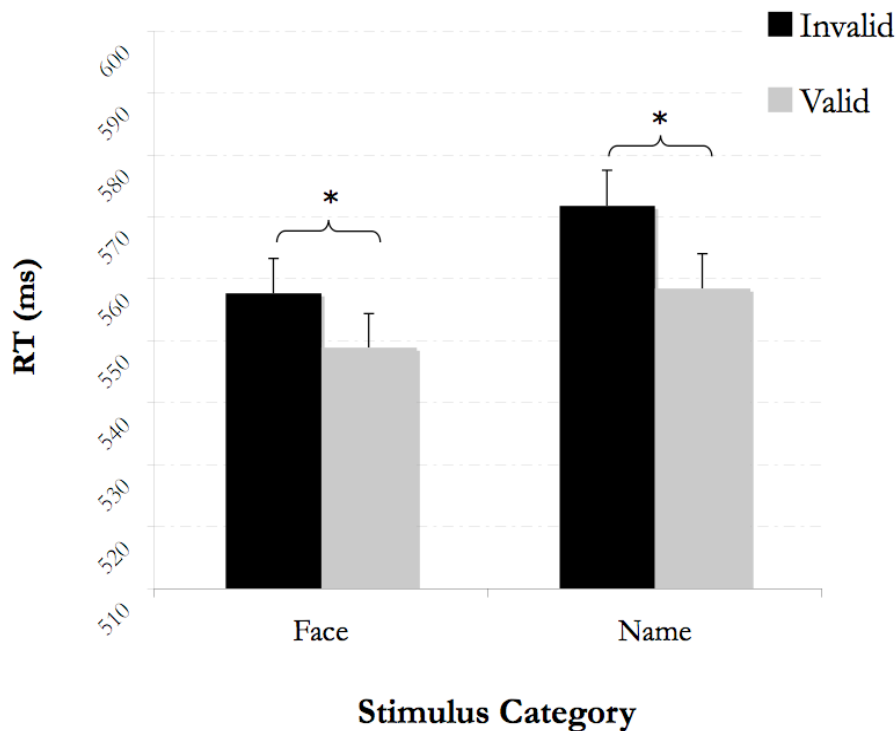


Figure 2. Validity effect on Reaction Times.

ERP results

Topographical analyses. After data pre-processing, the average number of trials retained for target analyses was 140 in both valid conditions (out of a possible maximum of 180) and 46 in both invalid conditions (out of a possible maximum of 60).

The segmentation analysis yielded seven different maps explaining 95.5% of the variance in the ERPs associated to word and face processing, which are displayed in

Figure 3². The first map was common for both types of stimuli and corresponded to the P1 component: it showed a bilateral distribution of positive voltages at posterior regions and negative values at frontal regions. At 150 ms, however, face and word topographies became different from each other. Although both maps showed negative voltages over occipito-parietal regions, this negativity presented a differential hemispheric pattern: it was highly left-lateralized for word stimuli and bilateral but slightly right-lateralized for face stimuli. These topographies encompassed from 150 to 220 ms in the case of faces and from 150 to 200 ms in the case of words. A *fitting procedure* was carried out on these two maps to test the differences at a statistical level (temporal interval: 152 to 192 ms). The ANOVA revealed a significant Map x Target category interaction, $F(1,23)=16.3$, $p<.001$, which supported the predominance of right and left lateralized topographies on face and word processing, respectively.

Faces generated a different topography at 220 ms, which had a positive polarity in central channels and negative voltages over lateral frontal areas. The topographies for words, in contrast, remained negative in posterior channels until 300 ms. We performed two additional fitting analyses to corroborate that face and word topographies were actually different also during these temporal windows (temporal intervals: 200 to 250 ms and 250 to 300 ms). Both ANOVAs involving Map and Target category on these intervals showed significant interactions, $F(1,23)=13.8$, $p<0.01$ and $F(1,23)= 6,05$, $p<0.05$, respectively. These findings suggest that the distinct sequence of maps for face and word processing resulted from the activation of different neural generators. However, after 300 ms both perceptual categories shared again the same topographical distributions, as can be seen in Figure 3.

² As invalid and valid conditions for both categories did not revealed any differential topography, we have not included further topographical analyses involving the Validity factor.

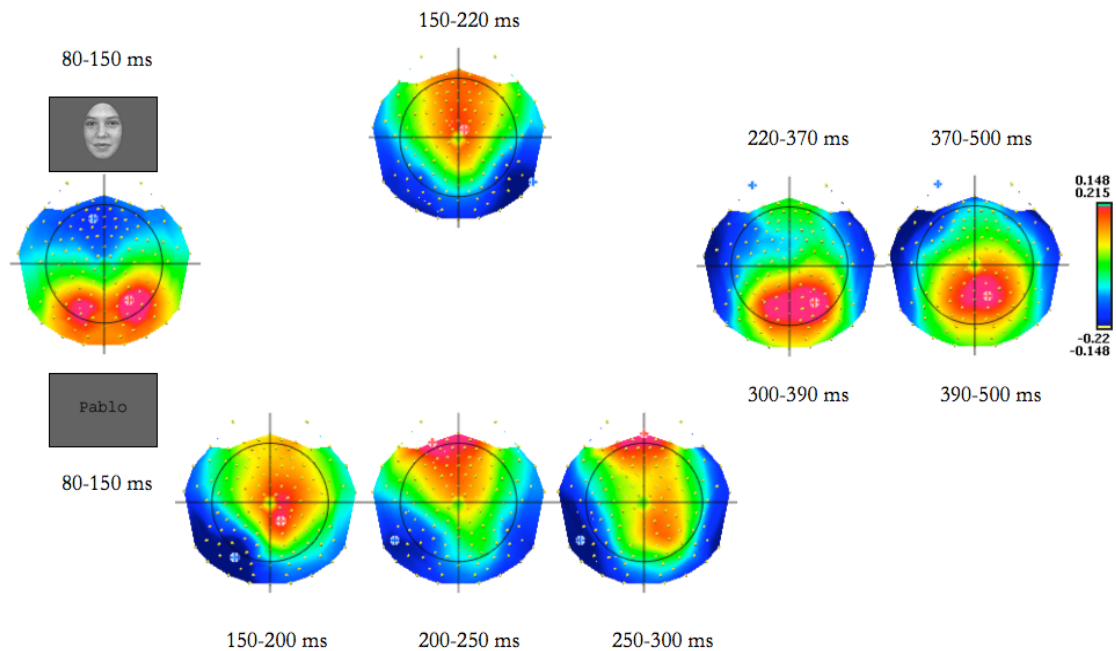


Figure 3. Sequence of topographies associated with face and word processing.

Voltage analyses. Voltages comparisons were performed on three temporal windows that encompassed the peaks of the P1, N170 and P3 potentials. Although we specifically focused on the attentional modulation of the category-specific N170, we also found relevant to investigate the influence of endogenous attention on earlier and later stages of processing. Spatio-temporal windows for specific ERPs were determined by visual inspection to capture their peak component, although we made sure that optimal intervals were selected within their corresponding topographical maps. Mean amplitude voltages over the selected electrodes and time windows were submitted to repeated measures ANOVAs with the factors Target category (face/word), Validity (valid/invalid) and Hemisphere (left/ right).

The peak of the P1 potential was analyzed from 116 to 136 ms, over 10 occipitoparietal electrodes on both hemispheres. The analysis yielded a significant main effect of Target category, $F(1,23)=11.47$; $p<0.01$, as the P1 amplitudes for faces were larger than for words. In addition, we observed a significant main effect of Hemisphere, $F(1,23)=4.4$; $p<0.05$, which revealed larger amplitudes for both stimuli on the right than the left hemisphere. Crucially, neither the main effect of Validity nor any of the interactions reached statistical significance.

The N170 potential was maximal from 164 to 188 ms, over 18 occipital electrodes from both hemispheres. The ANOVA revealed a significant Target category x Validity interaction, $F(1,23)= 6.7$, $p<0.05$. Subsequent analyses showed that Validity significantly influenced the N170 amplitude for both faces, $F(1,23)=4.36$, $p<0.05$, and words, $F(1,23)=4.86$, $p<0.05$. Therefore, the significant two-way interaction emerged as a result of a reversed pattern of modulation, as can be seen in Figure 4. For words, valid trials elicited a larger N170 than invalid trials (-3,71 μV vs. -3,24 μV) while for faces, invalid trials showed an enhanced amplitude as compared to valid trials (-5,13 μV vs. -4,68 μV). Given our a-priori hypotheses, we used planned comparisons to explore further the lateralization of the validity effect, although the Target category x Validity x Hemisphere interaction did not reach statistical significance, $p=.4$. The results showed that the validity modulation was only significant on the right hemisphere for faces, $F(1,23)=10.23$, $p<.01$ [left hemisphere: $F(1,23)=1.131$, $p=0.29$]. In a similar way, the attentional effect on the word N170 was statistically significant on the left hemisphere, $F(1,23)=4.64$, $p<0.05$, while it only approached significance on the right hemisphere, $F(1,23)= 3.47$, $p=.075$.

Finally, we analysed the influence of endogenous attention on the P3 potential. The voltages of 8 central electrodes from 480 ms to 500 ms were submitted to a repeated measures ANOVA. We found a significant main effect of validity, $F(1,23)=5.01$, $p<0.05$, with the P3 amplitude significantly larger for valid as compared to invalid stimuli. None of the rest of the terms in the analysis reached statistical significance.

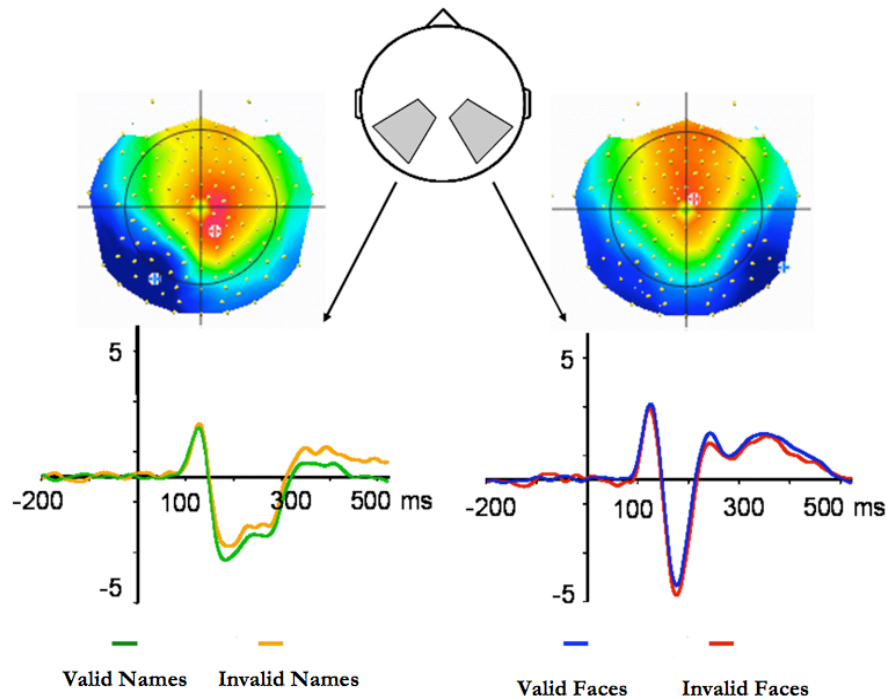


Figure 4. Attentional modulations on the face- and word-related N170. The display presents the location of the electrodes used for the voltage analyses, as well as the topographies for face and word processing during the N170 time-window.

Discussion

The present study investigated whether expectations about different perceptual categories were able to influence the perceptual stages of stimulus visual processing, by focusing specifically on the attentional modulation of the category-specific N170. Although category expectations had been previously studied (Esterman & Yantis, 2009; Puri & Wojciulik, 2008; Puri et al., 2009), the current investigation was the first to assess the topic from an electrophysiological approach to explore whether these

expectations modulate perceptual or post-perceptual stages of visual processing. We selected faces and words on the basis of the existence of a reliably index of categorical perceptual processing for these categories (although see Dering et al., 2009; Thierry et al., 2007). As attention was focused on perceptual categories, we hypothesized that the N170 would be a pertinent perceptual potential to be modulated by the attentional expectations.

Our behavioural results showed shorter RTs for valid as compared to invalid trials for both faces and words. These findings suggest that participants could use the symbolic cues to efficiently prepare for the appearance of stimuli belonging to the expected category. These findings are at odds with a previous study by Puri and Wojciulik (2008), which failed to show such a category expectation effect on behavioural measures. This study explored the effects of expectations about categories and specific exemplars but the results revealed a behavioural benefit exclusively on the latter case, which led the authors to conclude that category expectations were not able to induce a facilitation of stimulus processing. In contrast, two recent neuroimaging studies have provided divergent results (Esterman & Yantis, 2009; Puri et al., 2009) by showing that house and face expectations influenced behavioural indexes of performance. In addition, brain activation analysis revealed that these expectations led to a strong activation of category-specific visual areas prior to stimulus presentation (FFA for faces and PPA for houses). Taken together, these findings are in line with our results, which have confirmed that expectations regarding complex perceptual description of stimuli are able to influence target stimulus processing.

The results of the topographical analysis of our data showed that both categories shared a similar P1 topography. However, by 150 ms we observed that faces and words were processed by separable neural generators. The significantly different maps corresponded to the category-specific N170 component (e.g. Bentin et al., 1996; Bentin et al., 1999), which fit nice with previous correlational studies on neural and electrophysiological indexes of categorical processing (e.g. Brem et al., 2005; Henson et al., 2003; Herrmann et al., 2005; Itier et al., 2006). These topographies showed a

bilateral but slightly right lateralized negativity for faces and a left lateralized negativity for words on posterior sites. From 200 to 300 ms, face and word processing still revealed differential topographies. Nevertheless, the maps for both categories were again indistinguishable after 300 ms, which may represent common stages of response decision-making and motor preparation.

Voltage analyses were carried out on the P1, N170 and P3 to investigate the attentional effect along different stages of stimulus visual processing. The results revealed that category expectations did not modulate the P1 amplitude. Crucially, we found an attentional modulation of the N170 for both categories. This finding lends further support to the susceptibility of the face and word N170 potentials to top-down modulations. But crucially, it shows for the first time that category expectations influence the perceptual stages of stimulus processing. In addition, the N170 attentional modulation revealed a category-specific pattern. In first place, the attentional effect on the face N170 was exclusively significant on the right hemisphere, while the word N170 modulation was observed on both hemispheres: statistically and marginally significant on the left and right regions of the scalp, respectively. But crucially, the category-specific pattern was not restricted to laterality, but showed an opposed attentional effect on the N170 as a function of Target category. In response to faces, invalid trials elicited an enhanced negative peak than valid trials, while in response to words, valid trials evoked a larger negativity as compared to invalid trials, in spite of a comparable behavioural outcome for both categories.

Previous literature has claimed the automatic nature and cognitive impenetrability of initial face processing (e.g. Carmel & Bentin, 2002; Cauquil et al., 2000; Lueschow et al., 2004; Thierry et al., 2007). Nevertheless, our results lend support to recent findings that have reported top-down effects on this specific electrophysiological potential. Most of those findings arise from working memory research (Gazzaley et al., 2005; Morgan et al., 2008; Sreenivasan & Jha, 2007) or attentional paradigms, where visual perception is compromised by spatial attention (Crist et al., 2008; Holmes et al., 2003) or deprived stimulus presentation (Sreenivasan

et al., 2009). It is important to note that these studies share a particular characteristic: an experimental situation with high cognitive or perceptual demands. By contrast, lower demands, just as those frequently observed in selective attention paradigms, lead to no differences in the N170 for attended and unattended faces (e.g. Carmel & Bentin, 2002; Cauquil et al., 2000). To our knowledge, the present study provides novel and interesting data about the way that initial face processing can be modulated by attention under normal perceptual conditions. Nevertheless, we found a reversed pattern of the attentional modulation, as usually valid trials induced larger N170 amplitudes than invalid trials (Crist et al., 2008; Holmes et al., 2003; Sreenivasan et al., 2009). A closer examination of this effect suggested that this discrepancy might be only apparent. We hypothesized that face valid trials within the simple design used here did not benefit from the attentional orienting, just as it has been previously reported on traditional studies. However, we propose that the unexpected appearance of a face on invalid trials might required the reallocation of attentional resources, which would have induced a greater N170 potential as compared to valid trials. Note that this result closely resembles the face inversion effect, which is characterized by a larger N170 in response to inverted stimulus presentation (e.g. Bentin et al., 1996; Itier et al., 2006; Itier & Taylor, 2004; Jacques & Rossion, 2007; Rossion et al., 2000), although delayed latencies were not identified on our current data. Crucially, the N170 effect to inverted face-stimuli has been explained in terms of effortful processing (e.g. Haxby et al., 1999; Rossion et al., 1999).

The attentional modulation found for the word N170 potential is in accordance with previous findings (Ruz & Nobre, 2008), which showed an enhanced negativity to orthography task instructions compared to phonology or semantic instructions. Previous studies investigating the effects of attention on language perception had failed to find a similar effect on early stages of processing (Bentin, Kutas, & Hillyard, 1995; Cristescu & Nobre, 2008; Holcomb, 1993; e.g. Nobre et al., 1998). Nevertheless, our results extend Ruz and Nobre's by revealing a word N170 modulation as a result of focusing attention on the general configuration of linguistic stimuli rather than on their

orthographic features (like in Ruz and Nobre's study), which suggest that both tasks tap into a same analysis process of "word form" perception. Interestingly, the category-specific attentional modulation of the N170 suggests profound differences in the nature of word and face visual processing, despite of the previously remarked similarity in speed and accuracy behavioural indices.

It is not clear, however, to what extent spatial attention may have contributed to our findings. Faces and words in our experiment had a different spatial arrangement and hence, it could be argued that the reported effects are partially due to an adjustment of the focus of spatial attention. However, there are several factors that make this hypothesis unlikely. If this were the case, we would expect to find a validity effect on the P1 potential, which is known to be modulated in conditions of focused spatial attention (see Luck, Woodman, & Vogel, 2000 for a review). In addition, an explanation in terms of spatial attention would leave unexplained the reverted attentional effect found for faces, as the studies that have actually manipulated spatial attention to faces have found larger amplitude for valid than invalid stimuli (Crist et al., 2008; Holmes et al., 2003). Finally, fMRI findings show that category-expectations induce a selective activation on specialized areas, which suggest that anticipatory states rely on category-related information rather than on the spatial configuration of stimuli (Esterman & Yantis, 2009; Puri et al., 2009). Hence, although our current data cannot completely rule out the potential contribution of spatial attention, they suggest that additional factors are at play. Further studies will be needed to clarify this issue.

We also found later attentional modulations for faces and words. The P3 showed an increased positivity for valid in contrast to invalid stimuli for both type of stimuli, which have been observed in previous studies (e.g. Donchin, 1981; Hopfinger & Mangun, 1998; Lueschow et al., 2004; McCarthy & Nobre, 1993). This probably reflects post-lexical evaluation and decision-making processes related to the responses (e.g. Kramer & Strayer, 1988). It is important to note that both categories present the same topographical distribution during the P3 time window, which suggest that

attention modulates response-related processes through similar neural generators for both categories.

In conclusion, our results indicate that expectations about different perceptual categories are able to modulate both perceptual and later stages related to stimulus processing. Crucially, we show that face and word expectations influence the N170 in a category-specific fashion, during the time interval corresponding with differential topographies for both types of stimuli. These novel findings extend attention research by showing that endogenous attention can be focused on complex perceptual categories, and that this influences initial stages of categorical processing. Further research would be desired to clarify which specific stimulus representation is the target of attention in this paradigm, to disentangle the role of space-based and identity-based information. Thus, additional studies could explore whether specific items belonging to the same category, which share a common spatial arrangement, could also be modulated by top-down attention.

Clara Aranda
Daniel Sanabria
Pío Tudela,
María Ruz.

Manuscript in preparation

Equal but not the same:

Electrophysiological evidence of a dissociable
attentional modulation induced by face familiarity

Abstract

Previous research on the field of attention has shown that category expectancies elicited by predictive symbolic cues are able to modulate the processing of stimuli belonging to these categories. However, the study of expectations regarding particular stimuli within a category has received less attention by researchers. Here, we investigated whether expectations about particular faces differentially modulate visual face processing as a function of stimulus familiarity. We used a central cuing paradigm to direct participants' attention towards the appearance of either a familiar face (the king of the Spain) or an unfamiliar face. Behavioural results showed a comparable validity effect for both faces, whereas the ERP data revealed critical differences on the attentional modulation of face visual processing. We observed dissociable topographies for the unfamiliar and familiar face on the N170 interval, which suggest that different neural areas are recruited during face categorical encoding. In addition, voltage analyses showed a differential attentional modulation of the P1 and N170 potentials: the unfamiliar face displayed the classic attentional effect, with larger amplitudes for valid than for invalid trials, while the familiar face exhibited a reversed pattern, with larger amplitudes for invalid than for valid trials. Taken together, our results confirm that attention can be directed to particular items within a stimulus category, modulates early stages of stimulus processing and exerts a differential effect depending on the degree of familiarity of the item. This last finding supports the idea that familiar and unfamiliar faces rely on different perceptual representations.

Introduction

Undoubtedly, faces are stimuli with a special status for social interactions. Humans possess a highly qualified ability to discriminate between different facial identities and emotional expressions, which are essential requirements to achieve a successful communication with other people. Several investigations have highlighted the existence of face recognition processes that seem to be distinct from the recognition of other objects (e.g. Itier & Taylor, 2004). In fact, visual face perception is thought to rely on a configural processing that focuses on the relation between facial features as a whole, which leads to a faster and more accurate identification of face stimuli as compared to other non-face stimuli (e.g. Tanaka & Farah, 1993; Wilson, Maxwell Drain, & Tanaka, 1995). However, this advantage disappears when faces are inverted, while object recognition in other categories is less impaired after such inversion (e.g. Rhodes, Brake, & Atkinson, 1993; Yin, 1969).

Within the study of visual face processing, a large body of research has tried to determine whether familiar faces are processed in a different way as compared to unfamiliar ones (see Johnston & Edmonds, 2009 for a review). Face familiarity speeds up judgements in identification tasks, such as recognition and identity matching (e.g. Balas et al., 2007; Bruce et al., 2001; Bruck et al., 1991; Hancock et al., 2000), but crucially, it also influences performance on identity-independent perceptual tasks, such as the identification of race, gender, age, orientation and change detection (Balas et al., 2007; Bruyer et al., 1991; Bruyer et al., 2004; Buttle & Raymond, 2003; O'Donnell & Bruce, 2001; Rossion, 2002). In addition, variations in viewpoint, expression, lighting, and context are particularly detrimental to the recognition of unfamiliar faces, but not to familiar ones (e.g. Bruce, 1982; Davies & Milne, 1982; Eger, Schweinberger, Dolan, & Henson, 2005; Hill, Schyns, & Akamatsu, 1997; Troje & Kersten, 1999). On that basis, it has been suggested that familiar and unfamiliar faces subserved different perceptual representations. According to Bruce and Young's model (1986), the visual recognition of familiar and unfamiliar faces is achieved by accessing different codes: unfamiliar

faces rely on *pictorial codes*, which are literal/invariant descriptions of a face's appearance, while familiar faces rely on *structural codes*, which consist of a more flexible and abstract memory representation. According to Tong and Nakayama (1999), over-learned faces are more robustly represented than less familiar ones. However, whether this particular distinction relies on quantitative or qualitative differences is still a matter of debate (c.f. Johnston & Edmonds, 2009).

Event-related potentials (ERPs) technique provides a useful tool to identify discrete stages, from perceptual processes to response selection, along stimulus visual processing. Therefore, ERPs recordings are a suitable way to selectively focus on the early perceptual differences that might emerge between familiar and unfamiliar visual face processing. Electrophysiological studies have identified a negative potential that shows a specific pattern associated to the presentation of face stimuli: the N170 (e.g. Aranda, Tudela, Madrid, & Ruz, under review; Bentin et al., 1996; Eimer, 2000b). This specific N170 has been associated with face structural encoding (e.g. Sagiv & Bentin, 2001) and was initially thought to be insensitive to particular identities (e.g. Bentin & Deouell, 2000; Eimer, 2000b). However, it has been recently shown that the N170 amplitude can be modulated by face familiarity (e.g. Caharel, Fiori, Bernard, Lalonde, & Rebaï, 2006; Caharel et al., 2002; Heisz, Watter, & Shedden, 2006; Jemel, Pisani, Calabria, Marc Crommelinck, & Raymond Bruyer, 2003). Several investigations have reported a significantly larger N170 potential for well-known faces than for novel faces (e.g. Caharel et al., 2002). But, most importantly, other studies have uncovered dissociable effects on perceptual potentials when the same manipulation was performed either on familiar or unfamiliar face stimuli (priming effects: Begleiter, Porjesz, & Wang, 1995; Jemel et al., 2003; caricaturing effects: Kaufmann & Schweinberger, 2008; eye displacement effects: Caharel et al., 2006). These findings have been taken as an evidence of qualitatively different representations for familiar and unfamiliar faces (c.f. Caharel et al., 2006).

The current study investigates whether attention differentially influences visual face processing as a function of stimulus familiarity. To this aim, we used symbolic cues to generate expectations about the nature of the upcoming stimulus that could be

either a familiar or an unfamiliar face. It is now well established that the generation of an expectative about an upcoming target is able to optimize its posterior processing, by modulating different stages of visual perception, speeding reaction times and improving response accuracy (e.g. Correa et al., 2006; Cristescu & Nobre, 2008; Müller et al., 2006; Posner, 1980; Ruz & Nobre, 2008; Vossel, Weidner, Thiel, & Fink, 2009). Recent studies have highlighted that such optimization can also be observed after expectations referring to complex descriptions of the stimuli, as different perceptual categories (Aranda et al.; Esterman & Yantis, 2009; Puri et al., 2009). Thus, preparing participants for the appearance of either a face or a word has been shown to influence stimulus perceptual processing by modulating the category-specific N170 potential (Aranda et al. under review).

By contrast, expectations about particular stimuli within a perceptual category, what we call idiosyncratic expectations, have been scarcely investigated so far. The few existing studies have used expectations about well-known faces, which have shown to exert the expected enhancement on stimulus processing (e.g. Faulkner et al., 2002; Puri & Wojciulik, 2008). Within this context, the goal of the present study was twofold. In first place, we investigated the temporal course of the effects triggered by idiosyncratic expectations, as previous studies have exclusively reported behavioural data. In addition, we were interested in investigating the differences that might emerge on the attentional modulation of familiar and unfamiliar face processing.

We used a modified version of the Posner attentional paradigm, with central predictive cueing, to induce expectations about the subsequent appearance of either a perceptually familiar face (the king of Spain) or a novel face. As we were interested in the neural correlates of the attentional modulation, we measured participant's brain activity by means of high-density electrophysiological recordings. In the first place, we explored whether orienting endogenous attention to these stimuli was able to induce a behavioural advantage for valid compared to invalid trials. In addition, given that previous research has shown dissociable effects on perceptual stages for familiar and unfamiliar faces (e.g. Caharel et al., 2006; Kaufmann & Schweinberger, 2008), we explored the electrophysiological effects that attention exerted on this type of stimuli.

On the basis of previous results (Aranda et al., under review), we hypothesized that idiosyncratic expectations would be able to modulate perceptual stages of processing as indexed by the P1 and N170 potentials. In addition, we predicted a differential effect on the attentional modulation for familiar and unfamiliar faces. In our view, this finding would provide further support to the idea that these faces rely on different perceptual representations (e.g. Bruce & Young, 1986; Tong & Nakayama, 1999).

Methods

Participants. Twenty participants (11 females; mean age: 21; age range: 17-35) from the University of Granada took part in the experiment. All participants reported normal or corrected to normal vision and had no history of neurological disorders. They all signed a consent form approved by the Ethics committee of the University of Granada prior to the start of the experimental session and received course credits in exchange of their participation.

Apparatus and stimuli. The stimuli consisted of a fixation point sustaining 1.5°, a coloured cue (red or blue star) sustaining 3.84° and a target face, framed in an area of 230*307 pixels.

The target stimuli were two colour images representing a familiar face, the king of Spain, and an unknown face (see figure 3). Prior to the start of the experiment participants completed a Likert-scale of familiarity (1 not familiar at all - 5 highly familiar) to make sure that the selected faces differed in their degree of familiarity. The results confirmed that the face of the king of Spain was highly familiar to the participants as compared to the other face (Average ratings for the familiar face = 5; Average ratings for the unfamiliar face = 1,6). When asked, all participants correctly recognized the identity of the familiar face as the king of Spain. Images were extracted from the original picture, disposed on a black background and had their left or right ear

removed with Adobe Photoshop software. We selected a novel face that approximately matched the familiar face on perspective (front view), age, direction of gaze and neutral expression to compel participants to focus their attention on more detailed, identity-specific features in order to prepare for their appearance.

The stimuli were displayed at the centre of a 17-inch Dell monitor located at approximately 50 cm from the participants. The E-Prime V2.0 software (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation and response collection.

Design and Procedure. A within-subjects design was used with the factors of Target identity (familiar vs. unfamiliar face) and Validity (valid vs. invalid trials).

A trial consisted of the presentation of a fixation point (with a random duration between 300-700 ms), a coloured cue star (200 ms) and a blank inter-stimulus-interval (ISI of 1300 ms) followed by a face-target stimulus, which was displayed on the screen for 1200 ms. Figure 1 shows the temporal course of a single trial. The cue predicted the nature of the target on 80% of the trials (valid trials). The association cue colour-target identity was counterbalanced across subjects. Half of the participants expected the king's face after the red star and the novel face after the blue start, while the reverse assignment was used for the remaining half of the participants. The task consisted of indicating which ear had been removed from the face, by pressing the "z" key for left side and the "m" key for right side. Participants were instructed to respond as fast as possible while trying to avoid errors. The experiment consisted of a practice block of 40 trials followed by six experimental blocks of 80 trials each (480 experimental trials in total). The familiar and unfamiliar face had the same probability of appearance, 50%, within each block of trials. Participants were informed in advance about the colour-target face associations, and were told to use the cue to expect the upcoming face in order to improve their task performance. Short rests were allowed between blocks.

Prior to the beginning of the experiment, participants performed a recognition block of 80 trials (50% familiar and 50% unfamiliar stimuli). The purpose of this block

of trials was twofold: to briefly introduce participants to the novel face and to ensure that they correctly discriminated between the two faces. In this block of trials, participants were asked to press a key only in response to the king's face (Go/No go task).

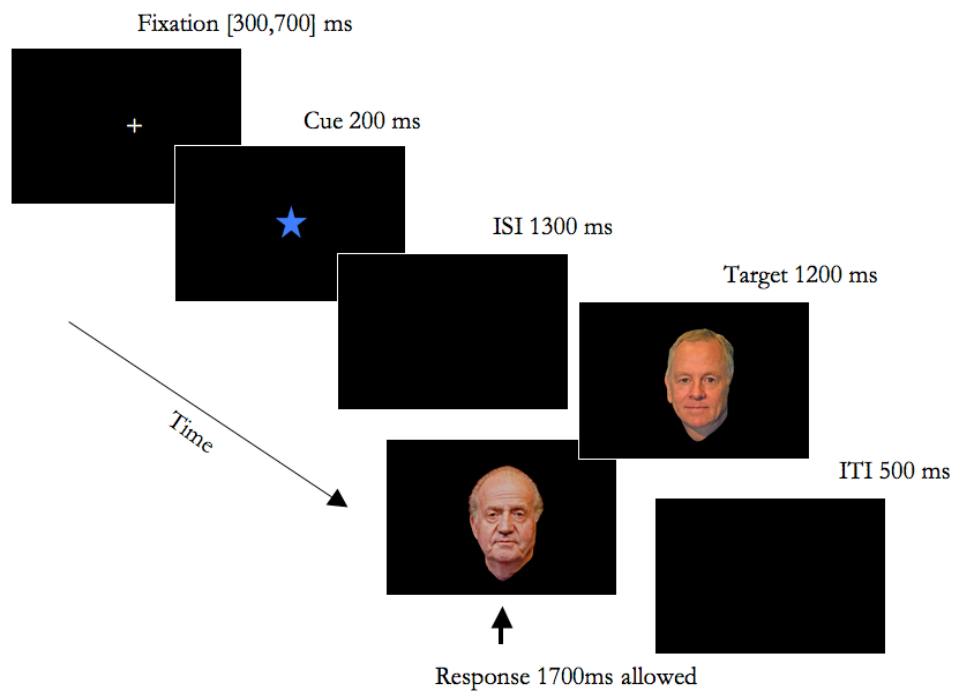


Figure 1. Sequence of events in a trial.

Participants sat in a dimly illuminated and electrically shielded room. EEG was collected with a high-density EEG system [Geodesics Sensor Net with 128 electrodes from *Electrical Geodesics, Inc. (EGI)*], referenced to the vertex channel. The electrodes located above, beneath and to the left and right of the external canthi of the eyes were used as electrooculograph leads to detect eye movements. The EEG net was connected to an AC-coupled, high-input impedance amplifier (200 M Ω); impedances were kept below 50k Ω , as recommended for the Electrical Geodesics high-input impedance

amplifiers. The signal was amplified (0.1 to 100-Hz band pass) and digitized at a sampling rate of 250 Hz (16 bits A/D converter). Data were filtered off-line with a 30 Hz low-pass filter.

The EEG continuous recording was segmented into epochs, 200 ms before and 1000 ms after target onset, and subsequently submitted to software processing for identification of artefacts. Epochs showing an excessively noisy EEG ($\pm 100 \mu\text{V}$ from one sample to the next), eye-movements artefacts (blinks or saccades: $\pm 70 \mu\text{V}$ on EOG channels) or incorrect behavioural responses were rejected. Data from individual channels that were consistently bad for a specific subject ($> 20\%$ of trials) were replaced using a spherical interpolation algorithm (Perrin et al., 1989). Trials with reaction times (RTs) faster than 300 ms or slower than 1100 ms were regarded as anticipations or late responses, and were also excluded from the analyses. Finally, we established a minimum criterion of 30 artefact-free trials per subject and condition to maintain an acceptable signal-to-noise ratio.

Four group-averaged ERPs waveforms were constructed according to the Target Identity (familiar, unfamiliar) and Validity (valid, invalid). ERPs were re-referenced to the average to eliminate the effects of reference-site activity and to generate an accurate estimation of the scalp topography of the recorded electrical fields (Dien, 1998; Tucker et al., 1994). The 200-msec pre-stimulus epoch served as baseline. The whole EEG recording session lasted about 60 minutes.

Electrophysiological analysis

Topographical analyses were performed on the ERP data to identify the sequence of topographical maps that was associated to each experimental condition over time. These maps represent stable periods of electrical field patterns that correspond to dissociable functional states of the brain, which usually match identifiable ERPs on the grand-averaged waveforms (see Pascual-Marqui et al., 1995). We performed this analysis to explore whether different conditions involved differential brain states evolving over time. In addition, it helped to select optimal spatio-temporal windows for posterior voltage comparisons on specific ERP components. A *Segmentation-into-*

microstates procedure was carried out to obtain the topographical maps on a group-average level (Cartool software developed by Denis Brunet: <http://brainmapping.unige.ch/Cartool.php>). In our case, this procedure was applied with several constraints: the maps had to remain stable for 20 ms and the maximum correlation between different topographies should not exceed 92%. Once differential maps had been identified on a group-average level, a *Fitting procedure* was used to test the statistical reliability of these findings. This procedure provides information about the percentage of times that the different maps are found in the data from individual participants. These values, when submitted to a multifactorial ANOVA, verified the existence of distinct neural configurations on the stimulus processing associated to each experimental condition (Brandeis et al., 1995; Lehmann & Skrandies, 1980; see Murray et al., 2004 for a detailed description of these procedures).

Voltage analyses were then performed on specific ERP potentials to study the effect of cue validity on the processing of target faces. A visual inspection of the grand averaged waveforms guided the selection of the spatio-temporal windows where the components were maximal. We made sure that each spatio-temporal window was selected within the temporal interval associated to the corresponding ERP topography. We tested the factors Target Identity (familiar, unfamiliar), Validity (valid, invalid), and Hemisphere where relevant (right, left). The mean amplitude values were computed with reference to the 200 ms pre-stimulus baseline.

Results

Behavioural results.

Reaction times shorter than 300 ms and longer than 1100 ms (2,98%) and errors (1,69%) were excluded from the analysis. We also discarded the data from one of the participants as a result of a computer error during the behavioural recording.

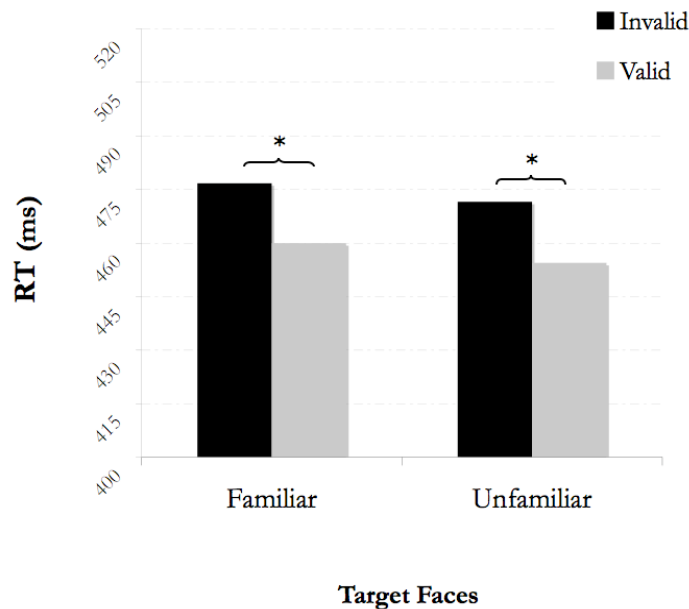


Figure 2. Validity effects on mean RTs for familiar and unfamiliar faces.

The ANOVA on participants' RTs showed that participants were faster on valid (457 ms) than on invalid targets (474 ms) overall, which led to a significant main effect of Validity, $F(1,18)=14.2$, $p=.001$. The interaction between Target identity and Validity did not reach statistical significance, $F<1$.

ERP results

After data pre-processing, the average number of trials retained for target analyses was 140 in both valid conditions (out of a possible maximum of 180) and 47 in

both invalid conditions (out of a possible maximum of 60). ERP data were filtered in order to level the signal-to-noise ratio³.

Topographical analyses. The segmentation analysis yielded fifteen different maps explaining 95.5% of the variance of the ERP data during 600 ms after stimulus-onset. Figure 3 displays five of these maps, which included the topographical configuration of the particular ERPs of interest as the P1 (Map 1), N170 (Map 2 and 3) and P3 (Map 5). Notably, the analysis suggested that different topographies were associated to the processing of the familiar and unfamiliar face from 156 to 188 ms. The topography of the familiar face revealed greater negative values on the left temporal region of the scalp and an enhanced positivity that extends towards the frontal pole as compared to the unfamiliar face topography, while both maps showed bilateral negative voltages on occipito-temporal sites. A *fitting procedure* was carried out on these two maps to test the differences at a statistical level (temporal interval: 156 to 188 ms). The ANOVA revealed a significant Map x Target identity interaction, $F(1,37)=8.35$, $p < .01$, which supported a significant predominance of each map on their corresponding experimental condition. The time period of these topographical maps corresponds to the face-specific N170 potential, which suggests that the perceptual encoding of familiar and unfamiliar faces involved different neural regions.

³ A supplementary analysis showed that similar results were achieved when using only a random subset of valid trials to match trial numbers across conditions.

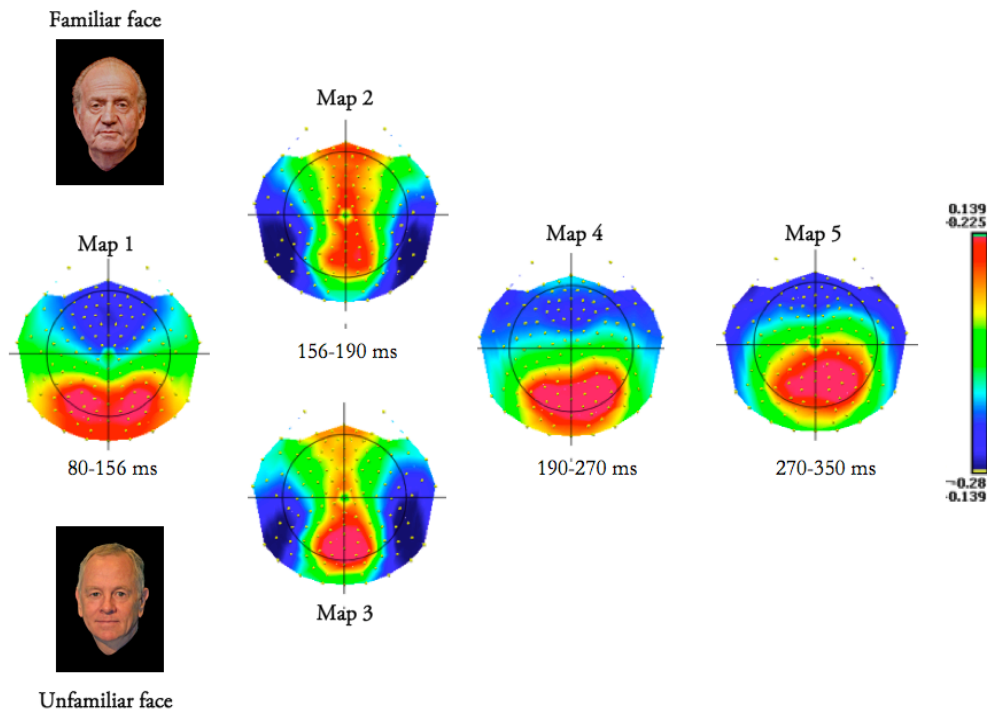


Figure 3. Topographical analyses of familiar and unfamiliar face processing (Maps 1-5). Target processing differs on maps 2 and 3 as a function of face familiarity.

Voltage analyses. Voltages comparisons were performed on three temporal windows, corresponding to the P1, N170 and P3 potentials. Spatio-temporal windows for specific ERPs were determined within the time period of their corresponding topographical maps by visual inspection to capture their peak component. Mean amplitude voltages for every temporal window on the selected electrodes were submitted to a repeated-measures ANOVA with the factors of Target Identity (familiar, unfamiliar), Validity (valid, invalid), and Hemisphere (left, right).

The first ANOVA was performed on the peak of the P1 potential, measured on the mean amplitudes of the window from 112 to 128 ms, over 22 occipito-parietal electrodes from both hemispheres in which this potential was most prominent. The

analysis only yielded a significant three-way interaction between Target identity, Validity and Hemisphere factors, $F(1,18)=6.46$, $p=.02$. Further analysis revealed that the P1 was differentially modulated by cue validity for the familiar and unfamiliar face on the right hemisphere, $F(1,18)=5.15$, $p=.03$, while we did not observe a significant validity effect for any target face on the left hemisphere, both $F_s < 1$. In the right hemisphere, the unfamiliar face showed a larger P1 for valid than for invalid trials (4.8 μV vs. 4.3 μV , respectively), although this difference only approached significance, $F(1,18)=3.59$, $p=.07$. In contrast, the familiar face showed the opposite modulation: the P1 amplitude was larger for invalid than for valid trials (4.8 μV vs. 4.3 μV), $F(1,18)=4.3$, $p=.05$ as can be seen in Figure 4.

The N170 peak was analysed in a temporal window from 166 to 180 ms over 12 electrodes that covered occipito-temporal areas in both hemispheres. The ANOVA revealed a significant main effect of Target identity, $F(1,18)=17.3$, $p < .001$, with a larger N170 for the familiar than for the unfamiliar face (-1.32 μV and -0.69 μV , respectively). Crucially, the interaction between Target identity, Validity, and Hemisphere also reached significance, $F(1,18)=8.32$, $p < .01$. A further exploration revealed that Target identity interacted with Validity exclusively on the left hemisphere, $F(1,18)=5.27$, $p=.03$, but not on the right hemisphere, $F(1,18)=2$, $p=.17$. This result indicated that familiar and unfamiliar faces were differentially modulated on the left region of the scalp: The N170 amplitude was larger for valid compared to invalid trials for the unfamiliar face (-0.88 μV vs. -0.49 μV , $F(1,18)=3.69$, $p=.07$), while invalid trials elicited an increased N170 compared to valid trials for the familiar faces (-1.47 μV vs. -1.17 μV ; $F(1,18)=3.48$, $p=.07$). Figure 5 illustrates this differential effect.

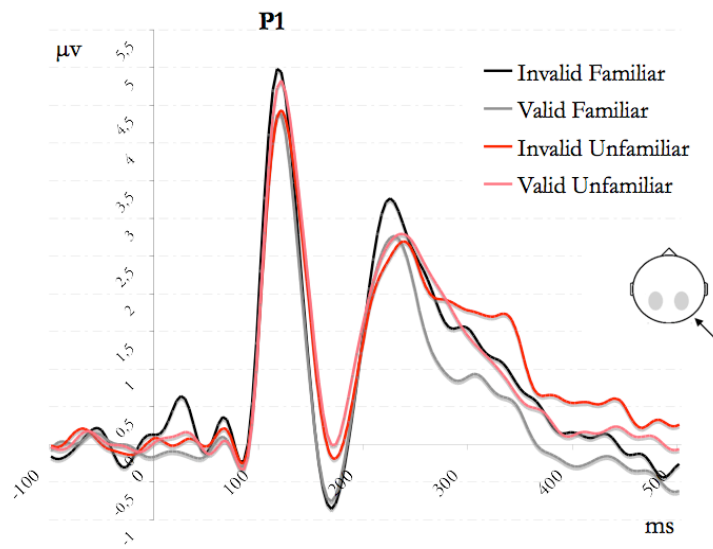


Figure 4. Validity effects on the P1 potential on channel 83 (Righ Hemisphere)

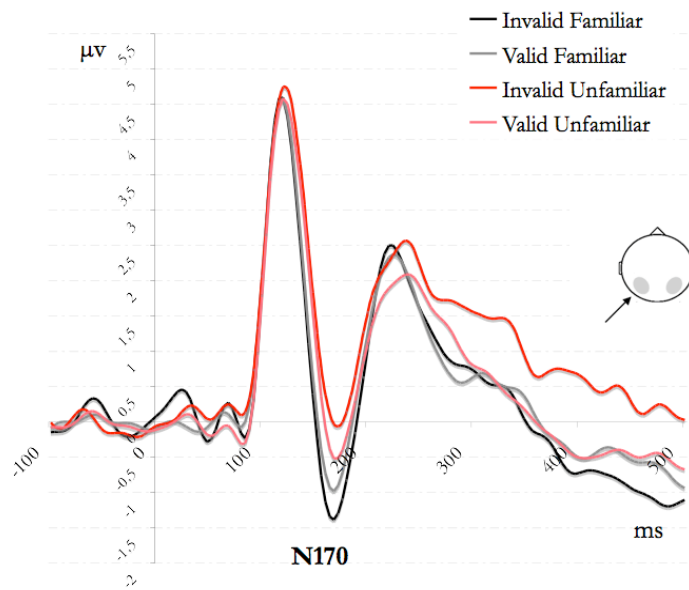


Figure 5. Validity effects on the N170 potential on channel 70 (Left Hemisphere).

For the P3 potential, we analysed 12 electrodes from the central region of the scalp during a temporal window from 292 to 308 ms. The ANOVA revealed a significant main effect of Target identity, $F(1,18)=7.87$, $p=.01$, with a more positive P3 for the familiar than for the unfamiliar face. The main effect of Validity was also significant. $F(1,18)=11.4$, $p<.01$, with a larger P3 for valid trials than for invalid trials. None of the rest of the terms in the analysis reached statistical significance.

Discussion

The main goal of the present study was to investigate whether expectations about particular items within a single category were able to influence perceptual stages of visual processing and whether they exerted a differential effect as a function of stimulus familiarity. The selection of faces as the target category allowed us to explore specifically the differences that could emerge between familiar and unfamiliar faces as a result of the attentional orienting. Our hypothesis was based on evidence that suggests that familiar faces, when compared to unfamiliar faces, involve different neural mechanisms (e.g. Taylor et al., 2009), rely on different internal representations (e.g. Tong & Nakayama, 1999) and seem to induce differential effects under single experimental manipulations (e.g. Caharel et al., 2006; Jemel et al., 2003; Kaufmann & Schweinberger, 2008).

The behavioural results confirmed that participants were able to form idiosyncratic expectations about familiar and unfamiliar faces, as RTs to valid trials were faster than to invalid trials. These results replicate previous findings on expectations about simple attributes (e.g. Cristescu & Nobre, 2008; Griffin, Miniussi, & Nobre, 2001; Krauzlis & Adler, 2001; Vierck & Miller, 2008; Vossel et al., 2009), category expectations (Aranda et al. under review; Esterman & Yantis, 2009; Puri et al., 2009) and idiosyncratic expectations about well-known stimuli (Faulkner et al., 2002; Puri & Wojciulik, 2008). As the validity effect was not modulated by Target identity at a behavioural level, one might have concluded that the attentional effect was

comparable for the familiar and unfamiliar face. However, as previous studies on this topic have shown (e.g. Aranda et al. under review; Begleiter et al., 1995), behavioural indexes may fail to capture subtle differences along the different stages of stimulus processing.

In fact, the ERP data revealed critical differences in visual face processing as a function of familiarity. Topographical analyses revealed that familiar and unfamiliar faces generated dissociable topographical distributions during the temporal window of the N170 potential, which supports the claim that familiar and unfamiliar faces recruit dissociable neural generators during initial perceptual stages of categorical analysis. Voltage analyses showed a larger N170 potential for the familiar as compared to the unfamiliar face, which was in line with previous findings (e.g. Caharel et al., 2006; Caharel et al., 2002).

Most importantly, we observed a dissociable attentional effect on the familiar and unfamiliar face on early perceptual stages of processing, in spite of identical outcomes on RTs measures. The unfamiliar face showed a typical attentional modulation, as the P1 and N170 amplitudes were larger for valid than for invalid trials (e.g. Eimer, 1994b; Hopf & Mangun, 2000; Luck et al., 1994; Martínez et al., 2001; Taylor, 2002). However, we observed a reversed pattern for the familiar face, characterized by a more pronounced P1 and N170 for invalid than for valid trials.

It is important to note at this point that in the present study expectations about a particular exemplar within a given category seem to influence earlier stages of processing (i.e., modulation of the P1 component), in comparison to Aranda et al.'s study (under review) who cued participants to expect a category and not a particular item. These findings are novel in the literature since, to our knowledge, this is the first study that investigates the neural correlates of idiosyncratic expectations. In addition, the results revealed interesting differences on the attentional modulation on visual face processing as a function of familiarity.

With regards to the inverted attentional pattern found for the familiar face, we have to make an a-priori distinction between the P1 and N170 potentials, as the N170 has shown this attentional effect on several occasions (e.g. Aranda et al. under review;

Fu, Fan, Chen, & Zhuo, 2001; Hopfinger & Ries, 2005). By contrast, the inversed effect of the P1 is much more rare and has been reported exclusively in spatial attention paradigms (Eimer, 1994a; Hopfinger & Mangun, 1998). The explanations offered for this reversed validity effect on the P1 are varied and not clear enough. Some authors suggest this pattern might be a reminiscent of inhibition of return (e.g. Hopfinger & Mangun, 1998). However, this explanation is not valid in the present context since we did not manipulate the spatial configuration or presentation of the stimuli. Instead, we think that the reported inversion of the validity effect for the familiar face might reflect a stronger recruitment of bottom-up attention by the unexpected appearance of a familiar stimulus, which would lead to an enhancement of both the P1 and N170 on invalid trials. In relation to this, Barret and colleagues (1988) reported that the N170 was larger for mismatching than for matching familiar faces, while the effect was absent for unfamiliar faces. In addition, is it also possible that, in our study, the initial processing of the familiar face had reached an optimal level of configural analysis that was not longer sensitive to the facilitation induced by valid symbolic cues (c.f. Kaufmann & Schweinberger, 2008). In any case, further research will be needed to fully explain this inversion of the validity effect on perceptual potentials.

Previous ERP studies have reported differential effects on perceptual potentials as a function of face familiarity (e.g. Begleiter et al., 1995; Caharel et al., 2006; Jemel et al., 2003; Kaufmann & Schweinberger, 2008). However, those differences were based on the absence of the effect for one of these faces. By contrast, we have revealed that attention appears to influence the processing of both familiar and unfamiliar faces, although in an opposite direction. In our view, this finding lends a clearer support to the idea that familiar and unfamiliar faces rely on qualitatively different perceptual representations. Interestingly, our results provide a novel finding within the related ERP literature, as there seems to be only an fMRI study that shows a similar dissociation between familiar and unfamiliar faces (Henson, Shallice, & Dolan, 2000). This study reports a differential effect of priming that revealed a decreased activity for familiar faces (*repetition suppression*) and an enhanced activity for unfamiliar faces (*repetition enhancement*) on the right fusiform area, in spite of an analogous effect on behavioural

measures. These authors suggested that the decreased response could reflect a sharpening of the existing representation for familiar faces, while the enhanced response could reflect a better encoding of the relevant features during the strengthening of a new representation for unfamiliar faces.

The attentional dissociation for the familiar and unfamiliar face on early ERPs in our study disappeared on later stages of processing, as the same typical validity effect (i.e., larger amplitudes for valid than for invalid trials) was found for both faces in the P3. The P3 has been related to response selection processes and is thought to index the allocation of cognitive resources (e.g. Kramer & Strayer, 1988; Kramer, Strayer, & Buckley, 1991; Watter, Geffen, & Geffen, 2001; Wickens, Kramer, Vanasse, & Donchin, 1983). Therefore, the similar validity effect in the P3 for both faces probably constitutes the neural correlate of the comparable behavioural effect on RTs.

In summary, the present study shows that participants can use symbolic cues to anticipate the appearance of particular faces, independently of their degree of familiarity. Although behavioural effects were comparable for the familiar and unfamiliar face, the ERP data revealed the existence of electrophysiological dissociations between these stimuli. In first place, we identified dissociable neural topographies on the temporal stage associated to the N170, which suggests the recruitment of different neural areas. In addition, we observed that expectations induced a reversed modulation as a result of face familiarity on the same perceptual stages of processing, indexed by the P1 and N170. In our view, these results taken together add further support to the idea of a qualitatively distinct processing for familiar and unfamiliar faces, as opposed to the existence of simple quantitative differences between them. Regarding the novel nature of our findings, further research will be desired to replicate the present results and to explore whether this differential attentional modulation for familiar stimuli extended to other stimulus categories or remains exclusive to visual face processing.

Clara Aranda

María Ruz.

Pío Tudela,

Daniel Sanabria

Attention, Perception & Psychophysics, *in press*

Focusing on the bodily self :

The influence of endogenous attention on visual
body processing

Abstract

The present study explores whether endogenous attention can modulate body perception. A modified version of the Posner paradigm was used to direct participants' attention towards the appearance of distinct body images, which differed merely in detailed idiosyncratic features: Own and Other's hands. Hand stimuli were preceded by symbolic cues that predicted their identity with high probability, which made it possible to compare the processing of expected (valid) and unexpected (invalid) targets. Results revealed that endogenous attention influenced the processing of participants' own hands by speeding participants' responses to valid in contrast to invalid trials. Crucially, no validity effect was found for other's hands. These findings cannot be explained in terms of perceptual familiarity, since an optimization of the processing for both familiar and unfamiliar faces by symbolic cues was observed. In light of these results, it is suggested that participants are able to anticipate particular stimuli within the same perceptual category as long as these stimuli appear to be remarkably distinct to them, which is probably the case of particular faces and their own body in contrast to other people's bodies.

Introduction

Over recent decades, the notion of *self* has become a central issue in experimental psychology and cognitive neuroscience (Gillihan & Farah, 2005; Northoff et al., 2006). Despite its complexity and multiple dimensions (Damasio, 2003, 1999; Gallagher, 2000; James, 1890; Neisser, 1988), it is undisputed that the self constitutes a unique phenomenological experience. But, can we capture this subjective *uniqueness* with objective measures? Experimental evidence provides a positive answer to this question, since self-related information seems to be processed in a distinct and special way in contrast to non self-related information (e.g. Kircher et al., 2000; see Gillihan & Farah, 2005 for a review).

The experience of a normal self includes the feeling of residing within the limits of one's body (Blanke & Arzy, 2005). In fact, the body is considered a seminal stage of the emergence of the self (Damasio, 1999; Gallagher, 2000; James, 1890), since the perception of intero- and exteroceptive stimuli and their linkage to a particular subjectivity is thought to be at the basis of one's own awareness. This *bodily self* seems to sustain a special status for visual perception (cf. Daprati, Wriessnegger, & Lacquaniti, 2007b; Frassinetti et al., 2008; Knoblich & Flach, 2003).

The visual processing of our own body comprises two dissociable aspects – motion and physical appearance – that have been approached by different areas of research (see Frassinetti et al., 2009). In the literature on body motion perception, several studies have shown that self-generated movements are processed differently from someone else's movements and that the former are closely related to motor cognition (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Daprati & Sirigu, 2002; Knoblich & Flach, 2003). This different processing typically leads to a better discrimination of the kinematic parameters of our own movements compared to others' movements, which takes place within awareness (explicit self-recognition: Daprati, Wriessnegger, & Lacquaniti, 2007a; Jokisch, Daum, & Troje, 2006; Loula,

Prasad, Harber, & Shiffrar, 2005) and outside it (enhanced perceptual performance: Daprati et al., 2007b; Knoblich & Flach, 2003).

Research on static images or self-appearance has mainly focused on face recognition. Behavioural studies have shown that the recognition of one's own face is consistently faster than the recognition of a stranger's face either in typical (upright, front, three-quarters) or atypical (upside-down, profile) views, even after hundreds of presentations (Tong & Nakayama, 1999). However, the main goal of this line of research has been to determine the different neural underpinnings of perceiving our own face as compared to other faces, which has highlighted a specific neural network for self-face stimuli (Kircher et al., 2000; Sugiura et al., 2000, 2006, 2005). The visual recognition of headless bodies or other different body parts has evoked considerably less interest in researchers. However, these few studies have revealed some interesting findings that resemble the previously mentioned results in body motion perception (see Daprati et al., 2007b). For instance, Frassinetti et al. (2008) identified a "*self-advantage effect*" that led to a faster and more accurate match-to-sample performance for participants' own vs. extraneous body images (hands and feet: Frassinetti et al., 2009; Frassinetti et al., 2008). In addition, recent fMRI studies have also revealed the neural specificity of self-body processing (Headless bodies: Hodzic et al., 2009; Hodzic et al., 2009; Hands: Myers & Sowden, 2008).

Taken together, the findings described above suggest that our own body receives a *special* processing, which fulfils the criteria of functional independence and anatomical specificity proposed by Gilliam and Farah (2005). Nevertheless, it is important to note that the abovementioned studies have emphasized the distinctiveness of body visual perception by means of stimulus-driven effects. That is, all these studies have identified a self-specific pattern of data that emerged from the direct presentation of one's own and someone else's body displays (e.g. Frassinetti et al., 2008; Hodzic et al., 2009; Hodzic et al., 2009; Myers & Sowden, 2008). Here, a novel approach is proposed to assess this issue: How do expectations about one's own or someone else's body influence their subsequent processing?

Endogenous attention is understood as the ability to voluntarily focus cognitive resources on a specific attribute of a stimulus. This form of attention has mainly been studied using symbolic cues, whose interpretation enables participants to intentionally direct their attention to the cued attribute (e.g. Posner, 1980). The preparatory state triggered by the symbolic cue can be referred to various dimensions of the upcoming stimulus such as its spatial location, temporal occurrence, colour, direction of motion or even the semantic meaning of linguistic stimuli. This preparatory state or expectation is known to optimize the subsequent processing of the target (e.g. Correa et al., 2006; Griffin et al., 2001; Krauzlis & Adler, 2001; Ruz & Nobre, 2008; Vierck & Miller, 2008; Vossel et al., 2009), probably by providing a competitive bias that favours task-relevant representations over competing representations (Bar, 2003; Stokes et al., 2009).

The present study explores whether symbolic cues that prepare participants to process a visual image of their own hands or someone else's hands can enhance the processing of expected (valid) as compared to unexpected (invalid) hand images. Thus, the rationale of the study differs from previous research on body perception, since it explores the effects on visual body processing of orienting attention to different body images, which goes beyond mere visual presentation.

The present study also represents interesting progress in research on attention, since the effect of preparatory states regarding the perceptual appearance of specific objects remained unexplored until recently (see Lauwereyns, 1998). Few studies have assessed whether expectations about different categories (e.g. faces, houses, or words) can optimize the processing of upcoming stimuli belonging to these categories (Aranda et al. under review; Esterman & Yantis, 2009; Puri et al., 2009). However, the authors of the present study are only aware of two studies that have explored whether endogenous attention can be devoted to particular stimuli within a perceptual category (Faulkner et al., 2002; Puri & Wojciulik, 2008). These studies showed that cues that anticipate the specific identity of stimuli are able to optimize the visual processing of their corresponding images. The present study extends these findings, given that the two expected items that belong to the same perceptual category differ exclusively in very fine-grained features.

Therefore, the present study had a double objective. One objective was to assess the special quality of the bodily self from an innovative perspective, testing whether one's own/others' expectations exert a different influence on visual body processing (hand images). The second objective was to explore whether endogenous attention can be focused on idiosyncratic stimuli that belong to a single perceptual category.

A modified version of the Posner attentional paradigm with symbolic predictive cues was used to induce expectations about the subsequent appearance of either one's own or someone else's hands. Cues were predicted to enhance the processing of one's own and others' hands stimuli in valid compared to invalid trials. In addition, given that previous research has shown that our own body holds a distinctive status (e.g. Frassinetti et al., 2008), it was hypothesized that attention might have a greater effect on participants' own hands compared to others' hands.

Experiment 1

The aim of Experiment 1 was to study whether expectations about one's own and others' hands can modulate their subsequent visual processing.

Methods

Participants. Twenty-four participants (14 females; mean age: 26 years; age range: 21-32 years) from the University of Granada took part in Experiment 1. All of them had normal or corrected to normal vision, provided informed consent prior to participation in the experiment, and received course credits in exchange.

Apparatus and stimuli. Stimuli consisted of a fixation point (+), a coloured cue (a red or blue star) sustaining 3.8° of angular size, and a target hand, framed in an area of 450*601 pixels.

Target stimuli consisted of colour images of left and right hands presented in an upright position (egocentric perspective) on a black background. The hands of each

participant were photographed with a digital camera in a session prior to the experiment. This session took place in a controlled environment with constant artificial light and a fixed distance between the camera lens and the hands (40 cm), which were always photographed in the same horizontal position. Subsequently, photographs were modified with Adobe Photoshop software: they were cut from the original picture, pasted on a black background and reoriented into a vertical position. Others' hands were selected from this database as the best match for size, skin colour, age, and gender as compared to each participant's hands. The size of the hands was compared on the pictures. The selected pair belonging to the participant (own hands) or to the other person (other hands) differed on average ± 89 mm and ± 58 mm in length and width, respectively. In addition, the age of the participants whose hands were matched ranged from 0 to 4 years. This criterion was adopted to prevent participants from using holistic features to orient attention, and to favour expectations based on the stimulus idiosyncrasy instead. In each session, target stimuli consisted of two pairs of hands (left and right) obtained from the corresponding participant and an unidentified single subject (Own and Other's hands).

All stimuli were presented centrally on a 17-inch Dell screen controlled by E-Prime V2.0 software (Psychology Software Tools, Pittsburgh, PA). The PC screen was approximately 50 cm from the participants.

Design and Procedure. The experiment used a within-participant design with the factors Target identity (own vs. other's hands) and Validity (valid vs. invalid trials).

Every trial involved presenting a fixation point of a random duration between 300 and 700 ms, followed by a coloured star for 200 ms. After an inter-stimulus-interval (ISI) of 1300 ms, the target appeared for 1200 ms. Figure 1 shows the temporal course of a single trial. The coloured cue predicted the nature of the target on 80% of the trials (valid trials). For half of the participants, the red cue predicted the appearance of their own hand and the blue cue predicted the appearance of the other's hand. The reverse was true for the remaining twelve participants. Once the target hand was shown, participants had to discriminate whether it was a left or right hand. Participants

responded to left hand stimuli pressing the “z” key on the keyboard with their left index finger and to right hand stimuli pressing the “m” key with their right index finger. This specific stimulus-response correspondence was kept for all participants to avoid Simon interference effects. Participants were instructed to respond as fast as possible while trying to avoid errors. The experiment consisted of a practice block of 40 trials followed by six experimental blocks of 40 trials each (240 experimental trials in total). Within each block of trials, half of the stimuli were participants’ own hands and the other half were others’ hands. Participants were informed in advance about colour-target hand associations (cue validity), but not about the presence of invalid trials in the design. They were explicitly asked to maintain their gaze on the centre of the screen and to avoid looking at their hands during the whole length of the experimental session. Short breaks were allowed between blocks.

Prior to the beginning of the experiment, subjects performed a recognition block of 80 trials (50% own and 50% someone else’s stimuli). Its purpose was to expose participants to their own and someone else’s hands, to ensure that they were able to discriminate between them and to facilitate the subsequent attentional orienting to specific hand stimuli in the testing session. Participants were asked to press a key only in response to own hand stimuli (Go/No-go task). Those who did not reach an 80% accuracy in this block (5 out of 72 subjects across the three experiments reported in this paper, 5.5% of the entire sample) were exempted from participating. The whole experimental session lasted about 30 min.

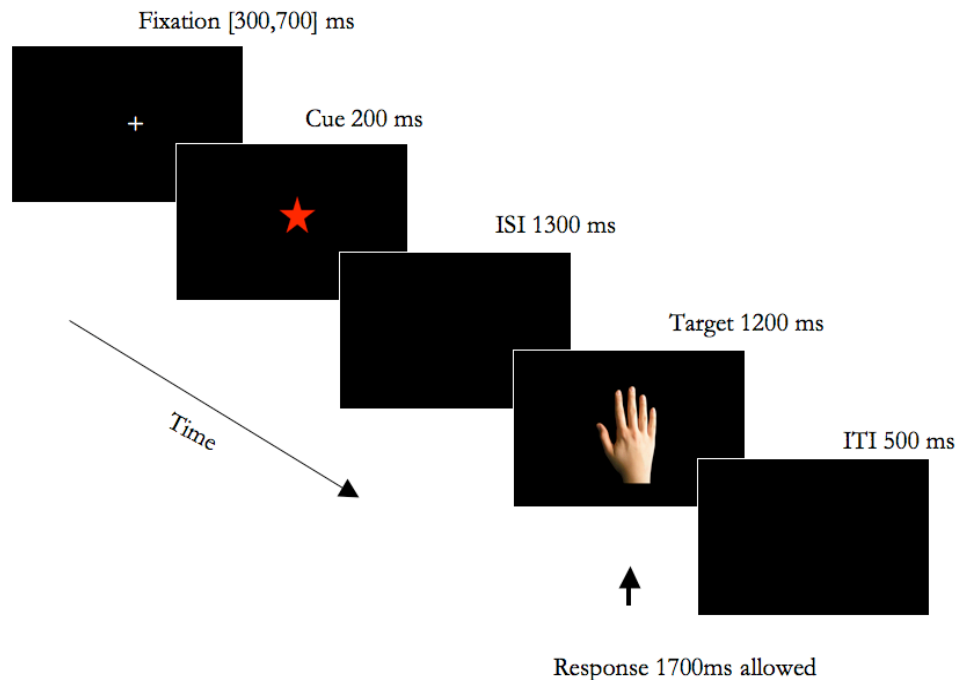


Figure 1. Sequence of events in a trial.

Results and Discussion

Reaction times shorter than 100 ms and longer than 1200 ms, data from practice trials, and errors were excluded from the analysis (see Table 1).

A repeated-measures analysis of variance (ANOVA) was conducted on the participants' mean RTs. The ANOVA only revealed a significant interaction between Target identity and Validity, $F(1,23)=7.46$, $MSE=436$, $p=.012$. Subsequent *a priori* comparisons revealed that participants responded faster to valid than to invalid trials exclusively for their own hands (521 ms vs. 539 ms, $MSE=423$, $p=.004$), whereas the difference in RT between valid and invalid trials for others' hands was not statistically significant (531 ms vs. 527 ms, $F < 1$; see Figure 2). The same two-factor ANOVA on participants' error ratings did not reveal any significant effects.

The results of Experiment 1 showed that endogenous attention can influence the visual processing of body images (hands). Crucially, endogenous orienting did not improve the processing of every expected stimulus. Attention influenced the processing of participants' own hands, whereas no validity effect was found for others' hands. In any case, this finding suggests that attention, at least under certain circumstances, can be oriented to particular items on the basis of detailed idiosyncratic features. However, it should be noted that this differential effect for own and others' stimuli admits other interpretations.

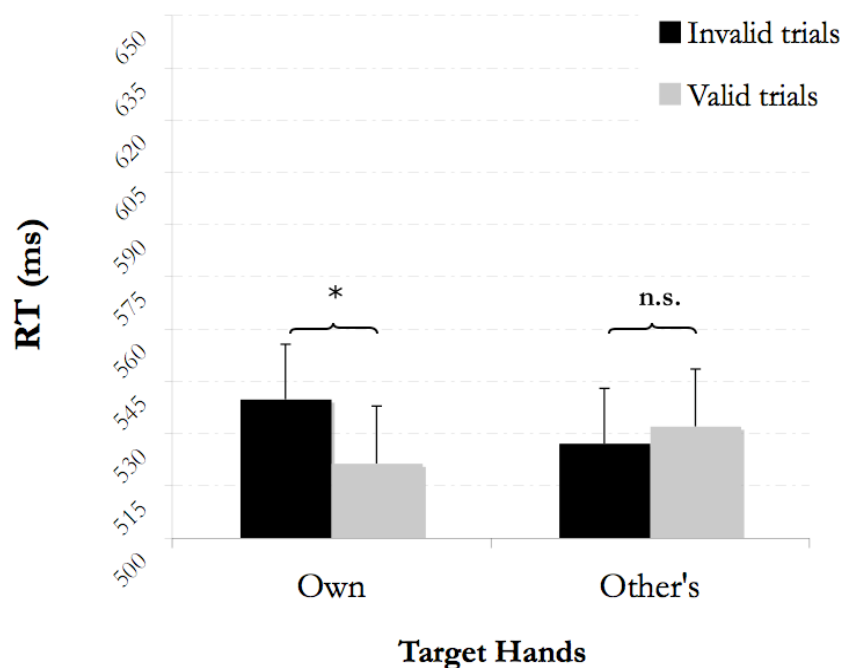


Figure 2. Validity effects on mean RTs for own and other's hands in Experiment 1 (manual response).

The results of Experiment 1 could be explained by an essential distinctiveness between one's own and someone else's hands. It seems plausible that one's own hand stimuli sustain a more robust internal representation in contrast to someone else's hand

stimuli (see Tong & Nakayama, 1999), which would have induced a greater attentional effect on target processing. Thus, the present results might reflect the existence of critical differences between one's own and others' hands, which influence the capacity of endogenous attention to optimize their subsequent visual processing.

Alternatively, these results could be explained in terms of pure manual response facilitation, rather than an optimization of processing triggered by endogenous attention. The manual response facilitation could have emerged as a result of the direct match between expectation (own-coloured star), stimulus (own hand) and response (performed by the same own hand just perceived) present in valid own trials. This match could have lead to a significant difference between valid and invalid trials exclusively for own hand stimuli, since the same full stimulus-response congruency is not present for others' hand stimuli. Before drawing any firm conclusion, a second experiment was performed to test this alternative account.

Experiment 2

In Experiment 2, the manual response was replaced by a vocal response to test whether the results of Experiment 1 were due to the influence of endogenous attention on target processing or, alternatively, to response-facilitation processes.

Methods

Participants. Twenty-four participants (12 females; mean age: 25 years; age range: 18-32 years) from the University of Granada took part in Experiment 2. All of them had normal or corrected to normal vision, provided informed consent prior to participation, and received course credits in exchange.

Apparatus, stimuli, design, and procedure. They were the same as in Experiment 1 except for the following: Participants were required to give a vocal response for left-right judgements using a microphone connected to the PC. They kept their hands on

their knees, under the black desk that supported the PC screen and the microphone. During the experimental session, the examiner stayed inside the room but out of sight of participants to code the accuracy of responses.

Results and Discussion

The same exclusion parameters were applied as in Experiment 1: only reaction times between 100 and 1200 ms and correct responses from the six experimental blocks were considered for statistical analysis (see Table 1 for percentage of trials excluded).

The ANOVA on RT data only revealed a significant interaction between Target identity and Validity, $F(1,23)=6.53$, $MSE= 373$, $p=.019$ (see Figure 3). Further analyses showed a significant difference between valid and invalid trials for own hand targets (588 ms vs. 608 ms, respectively, $MSE= 554$, $p=.007$) while no effect was obtained for others' hand targets (603 ms for valid trials vs. 603 ms for invalid trials, $F < 1$). The analysis of error data did not reveal statistically significant results.

The results of Experiment 2 suggest that the response facilitation hypothesis does not account for the results obtained in Experiment 1. Thus, these results support the hypothesis of a differential modulation of the processing of own hands with respect to others' hands as a result of endogenous orienting. However, there is an aspect in the design of Experiments 1 and 2 that might be crucial to explain the present results. In both experiments, participants performed a recognition block prior to the experimental procedure where they had to respond only to their own hands. Therefore, an arbitrary bias to self-stimuli may have been established as a result of these explicit instructions. To test this new alternative hypothesis, participants responded exclusively to others' hands in the recognition block of Experiment 3. If the dissociation found in Experiments 1 and 2 is caused by an arbitrary bias to self-stimuli, Experiment 3 should show an attentional modulation restricted to others' stimuli. However, if the effect is due to an essential distinctiveness of participants' own hands, the results reported previously should be replicated.

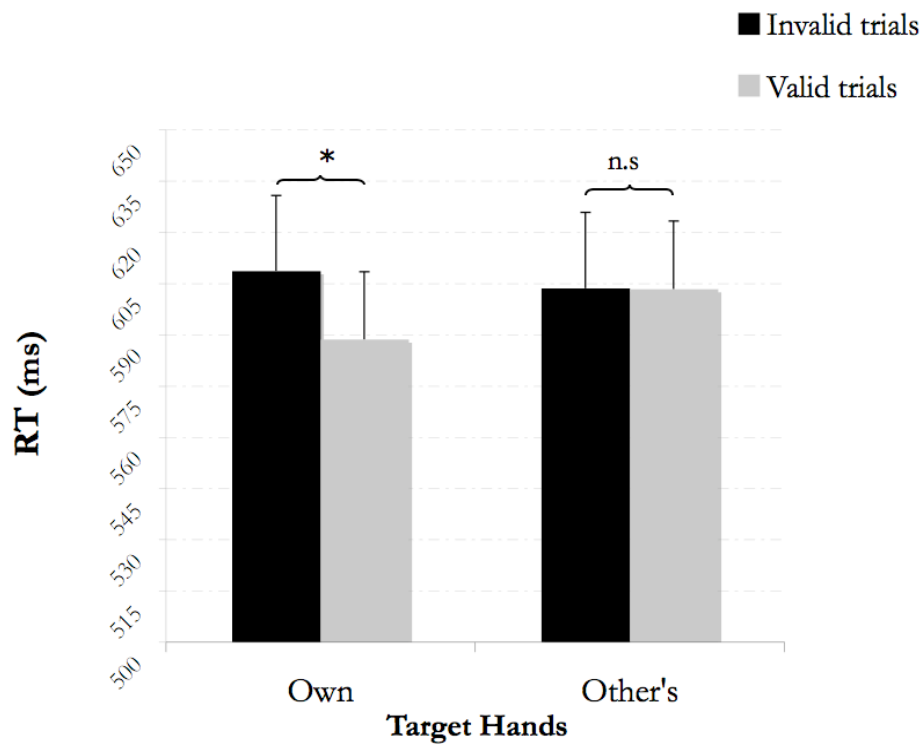


Figure 3. Validity effects on mean RTs for own and other's hands in Experiment 2 (vocal response).

Experiment 3

Experiment 3 tested a different explanation of the self-specific attentional effect reported in the Experiments 1 and 2. To rule out the presence of an induced bias to self-stimuli, the recognition Go/No-go task was modified to require participants to respond only to someone else's hands.

Methods

Participants. Twenty-four participants (20 females; mean age: 21 years; age range: 19-29 years) from the University of Granada took part in Experiment 3. All of them had normal or corrected to normal vision, provided informed consent prior to participation, and received course credits in exchange.

Apparatus, stimuli, design, and procedure. These were the same as in Experiment 1 except for the following: In the recognition block, participants were required to discriminate between the stimuli by responding exclusively to others' hands.

Results and Discussion

The criteria used for data exclusion were the same as in Experiments 1 and 2: only reaction times between 100 and 1200 ms and correct responses from the six experimental blocks were included in the statistical analysis (see Table 1 for percentage of trials excluded).

The ANOVA of the participants' mean RT revealed a significant main effect of Validity $F(1,23)=8.33$, $MSE=293$, $p<.01$. Crucially, this validity effect was modulated by Target identity as revealed by the significant interaction between the two factors, $F(1,23)=4.47$, $MSE=463$, $p<.05$ (see Figure 4). Subsequent *a priori* comparisons replicated the findings of Experiments 1 and 2: Endogenous orienting to self-stimuli speeded participants' responses in valid trials as compared to invalid trials for their own hands (512 ms vs. 532 ms, $MSE=312$, $p<.001$). In contrast, no significant RT differences were obtained between valid and invalid trials for others' hands (523 ms for valid trials vs. 523 ms for invalid trials, $F<1$). Error ratings did not show any significant difference across variables.

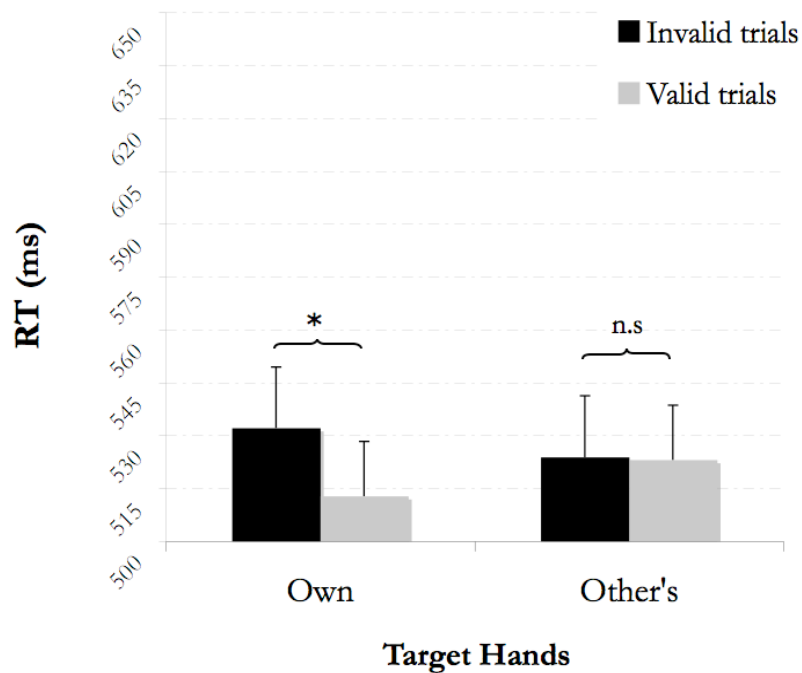


Figure 4. Validity effects on mean RTs for own and other's hands in Experiment 3 (reversed recognition block).

A further between-experiment ANOVA was carried out to compare participants' performance among the three experiments. The factor Target type (right vs. left hand) was also included to explore whether participants were expecting a specific hand image (right or left) within identities. Thus, the analysis was performed with the factors Experiment, Validity, Target identity and Target type. This ANOVA revealed a significant main effect of Experiment, $F(2,69) = 5.62$, $MSE = 31867$, $p < .01$, showing a longer mean RT in Experiment 2 (vocal response) when compared to Experiments 1 and 3 (manual response). These RT differences between manual and vocal responses have been repeatedly shown in previous research (e.g. Baron & Journey, 1989; Doose & Feyereisen, 2001; Nebes, 1978; Wells, 1924) and response modality does not seem to alter the experimental findings (e.g. Borkenau, Paelecke, & Yu, 2010). The main effect

of Validity and the interaction between Validity and Target Identity also reached statistical significance (MSE= 573, $p=.002$ and MSE= 424, $p<.001$, respectively). Once again, subsequent comparisons revealed that validity effects were confined to processing of participants' own hands ($F(1,69)=31$, MSE= 429, $p<.001$ vs. $F<1$ in others' hands). Crucially, the significant interaction between Target identity and Validity was not modulated by the Experiment factor, $F<1$. In addition, none of the interactions involving Validity and Target type reached statistical significance (Validity x Target type: $F(1,69)= 0.01$, $p=.91$; Target identity x Validity x Target type: $F(1,69)=0.001$, $p=.97$; Experiment x Target identity x Validity x Target type: $F(2,69)= 0.2$, $p= .75$), suggesting that expectations were not biased towards a left or right image of the hands.

The results of Experiment 3 seem to confirm that the self-specific attentional effect is independent of arbitrary biases caused by the previous Go/No-go task. The self-advantage may thus be based on the particular distinctiveness of own hand stimuli. Nevertheless, it is necessary to consider a further alternative explanation related to the two types of stimuli used in the current set of experiments. Our own hands are highly familiar compared to the hands of a stranger. Therefore, the identified effect may be related to the perceptual familiarity of stimuli rather than a special distinctiveness of self-related stimuli. To assess this issue, a further experiment was performed to test the influence of perceptual familiarity or prior experience with the target stimulus in the generation of idiosyncratic expectancies and their subsequent effect on visual processing.

Experiment 4

Experiment 4 tested whether the identified self-specific attentional effect reported in Experiments 1-3 may be due to the high perceptual familiarity of one's own hands compared to someone else's hand stimuli. To clarify self-reference and

familiarity factors, a highly familiar face that was not personally related to the participants was chosen (the king of Spain) as well as a matched unknown face, which was perceptually similar in terms of hair colour, age, front view, direct gaze and neutral emotional expression (see Figure 5). Face stimuli were selected because they belong to a body category (like hand stimuli) and they are highly discriminable in terms of perceptual familiarity. In addition, previous research has shown that participants can create expectations about faces, both as a general category and as particular stimuli belonging to famous people (e.g. Aranda et al. under review; Faulkner et al., 2002; Puri & Wojciulik, 2008).

Methods

Participants. Twenty-four participants (15 females; mean age: 21 years; age range: 17-24 years) from the University of Granada took part in Experiment 4. All of them had normal or corrected to normal vision, provided informed consent prior to participation, and received course credits in exchange.

Apparatus, stimuli, design, and procedure. They were the same as in Experiment 1 except for the stimuli used and the task that had to be performed on the targets. Two coloured faces were used (see Figure 5 for a black and white display of the faces), with one of their ears removed (left or right). Participants were asked to respond to the side in which the ear was missing by pressing “z” for left absence and “m” for right absence. This task was selected because of its similarity with the left-right decision performed on the hands on the previous experiments. Participants completed a Likert scale of familiarity ratings (1 - not familiar at all; 5 - highly familiar) with both faces prior to the beginning of the experiment (Average ratings for the familiar face = 5; Average ratings for the unfamiliar face = 1.6). All participants explicitly recognized the familiar face’s identity as the king of Spain.

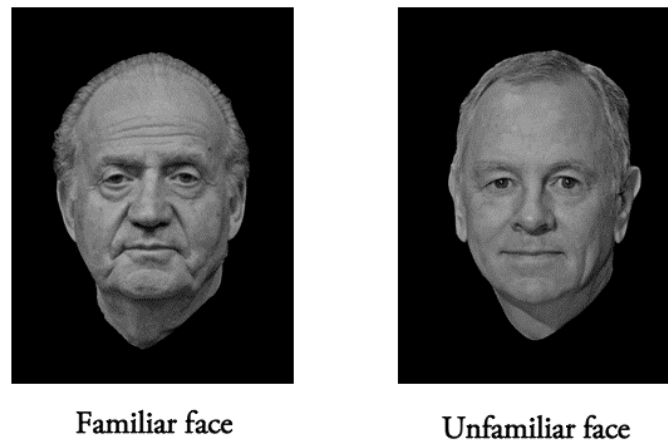


Figure 5. Familiar and Unfamiliar face displays.

Results and Discussion

The criteria used for data exclusion were the same as in Experiments 1 to 3: only reaction times between 100 and 1200 ms and correct responses from the six experimental blocks were included in the statistical analysis (see Table 1 for percentage of trials excluded). Data from one of the participants were also excluded due to a computer error recording her responses.

The ANOVA only revealed a significant main effect of Validity, $F(1,22) = 10,35$, $MSE = 647$, $p < .01$. Crucially, no interaction was observed between Validity and Target Identity factors, $F(1,22) = 1,52$, $MSE = 175$, $p = .2$, which stands in sharp contrast to the previously reported experiments. Subsequent *a priori* comparisons showed that attentional expectations influenced both familiar and unfamiliar faces, which was reflected on faster RTs to valid than to invalid trials (familiar face: 454 vs. 468 ms, $p < .05$; unfamiliar face: 447 vs. 467, $p < .01$).

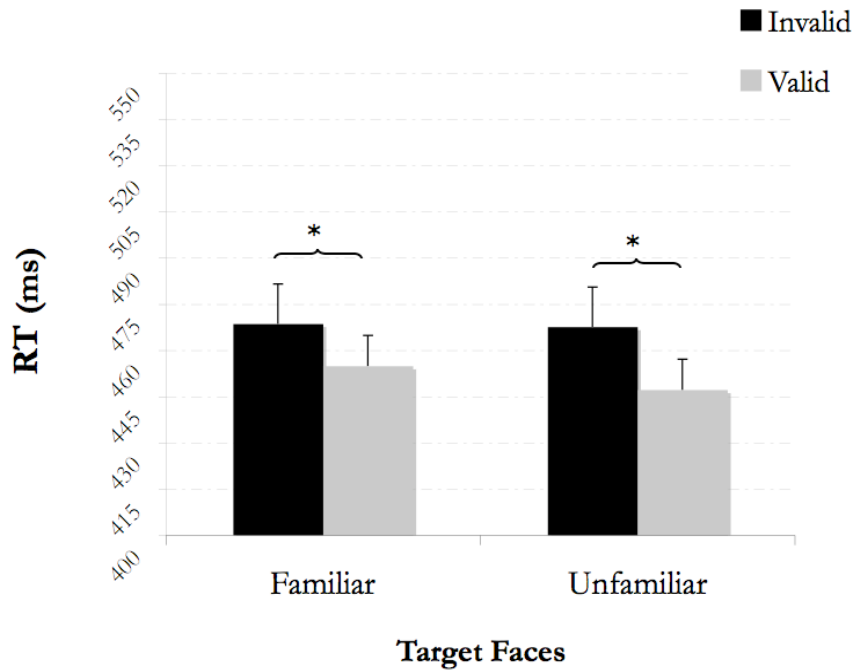


Figure 6. Validity effects on mean RTs for familiar and unfamiliar faces in Experiment 4 (perceptual familiarity).

Results of Experiment 4 showed that participants were able to generate endogenous expectations about particular well-known faces (as previously shown by Faulkner et al., 2002; Puri & Wojciulik, 2008) and unknown faces. Responses were faster for valid as compared to invalid trials, and, importantly, this effect did not depend on the degree of familiarity of the faces. This result indicates that mere differences in the perceptual familiarity of the targets cannot account for the divergence between the validity effects for own and other hands reported in Experiments 1-3.

Discussion

The set of experiments reported in this manuscript explored for the first time whether symbolic cues that predict the appearance of our own hand or another person's hand can optimize the processing of these stimuli. Results showed that participants could prepare in advance to see their own hands, since cue validity influenced their performance by speeding up RTs with expected as compared to unexpected own hand stimuli. Interestingly, no attentional effect was observed for the hands of other people, which suggests that participants could not use the cue to generate an expectation for those specific stimuli. Experiments 2 and 3 tested alternative hypotheses to explain these findings, which ruled out explanations in terms of manual response facilitation and an arbitrary bias to own hand stimuli, respectively. Crucially, the results of Experiments 2 and 3 replicated those of Experiment 1. Finally, Experiment 4 tested whether this selective attentional effect could be due to the higher perceptual familiarity of one's own hands with respect to other people's hands by replacing the stimuli with a highly familiar face (the king of Spain) and a non-familiar face. Results showed that participants could use the cues to anticipate the appearance of both faces, since a behavioural advantage was observed for all valid face stimuli regardless of their degree of familiarity. Therefore, the results of Experiments 1-3 cannot be explained in terms of mere perceptual familiarity.

A key question arising from such results is why no attentional effect was observed with someone else's hands. Previous research has shown that devoting attention to general stimulus attributes can optimize target processing regardless of stimulus type (Esterman & Yantis, 2009; Griffin et al., 2001; Krauzlis & Adler, 2001; Puri et al., 2009; Ruz & Nobre, 2008; Vierck & Miller, 2008; Vossel et al., 2009; Aranda et al. under review). This can lead to expecting validity effects for non-self stimuli in the present paradigm. However, the vast majority of previous studies did not require participants to expect *particular* items within a single category (e.g. participants

were required to attend to a spatial location). This crucial difference between the present experiments and previous studies may explain the divergence of findings.

Regarding expectations about particular stimuli, recent studies have revealed that attention influences task performance on expected items when using well-known stimuli (famous faces and buildings; Faulkner et al., 2002; Puri & Wojciulik, 2008). Given that Experiment 4 showed that non-familiar face stimuli also benefit from this specific orienting, it is considered plausible to explain these findings in terms of *stimulus distinctiveness*. Idiosyncratic expectations are based on very subtle perceptual differences that need to be available to the participants prior to the presentation of stimuli. It is suggested that participants are able to create idiosyncratic expectations only when these are referred to stimuli that appear clearly distinct to them. Thus, no attentional effect was observed with the processing of other's hands because their perceptual appearance might not be distinctive enough for participants and they cannot prepare in advance for their presentation. This does not seem to be the case for either familiar or unfamiliar faces, since research has shown that we are experts in processing, recognizing, and retrieving face stimuli (e.g. Bruce & Humphreys, 1994; Le Grand, Mondloch, Maurer, & Brent, 2003). Importantly, our own hands also seem to appear highly distinct to us as compared to the hands of other people.

Existing literature on body perception suggests that our own body subserves a *special* processing in contrast to others' bodies, regarding both motion and static appearance displays. As previously mentioned, these studies have reported that when our own body is compared to someone else's body, self-stimuli show a perceptual advantage (Daprati et al., 2007a; Frassinetti et al., 2008; Knoblich & Flach, 2003) and recruit specific underlying neural substrates (Calvo-Merino et al., 2006; Hodzic et al., 2009; Myers & Sowden, 2008). These findings seem to indicate that our body sustains a distinct internal representation as compared to others' bodies. Along the same lines, the self-specific advantage for endogenous attention reported here may emerge from a more distinctive and robust representation of our body in contrast to someone else's body (see Tong & Nakayama, 1999).

Previous neuroimaging results have shown that attentional expectations activate category-specific areas on the visual ventral stream prior to stimulus presentation, which have been interpreted in the context of mental imagery and perceptual representations (Esterman & Yantis, 2009; see also Kosslyn & Thompson, 2003). In addition, recent fMRI studies using pattern-decoding methods have revealed that attentional mechanisms can activate target-specific neural subpopulations in the visual cortex when stimuli are not concurrently in view. The activation pattern observed in the latter studies closely resembles the neural activity triggered by stimulus-driven input; its level of specificity discriminates between different letters and grating orientations (Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009; Stokes, Thompson, Cusack, & Duncan, 2009; Stokes et al., 2009). Based on this, it has been claimed that attentional biases are mediated via preparatory activation of relevant perceptual representations in the visual cortex with a high degree of specificity (Stokes et al., 2009).

In light of these findings, it is proposed that the expectations about specific hand stimuli may imply the activation of their corresponding perceptual representations, which would help participants to anticipate the target stimulus. Since the representation of our own hands is more distinct and robust than the representation of someone else's hands (see Tong & Nakayama, 1999), the reported differential validity effect is observed on one's own and others' hands. In addition, the analysis of hand type (right vs. left) did not yield any significant difference in the present study. This suggests that participants did not focus on a particular feature of one of their hands (or the other person's hands) and that they used the cue to represent the personal features that define both the left and right hands as belonging to a particular identity.

In conclusion, our present results show that attention can be devoted to the specific features that define particular stimuli within a same perceptual category when those particular stimuli are remarkable distinctive for the participants. It is suggested that one's own hands sustain a distinct and more robust perceptual representation as compared to someone else's hands. This might have led to the emergence of an attentional effect only on self-stimuli. Nevertheless, further research on several respects

would be desirable. First, it would be relevant to test whether the observed self-specific attentional effect holds for non-bodily items when they belong or not to the participants. In addition, it would be interesting to explore how idiosyncratic attentional expectations modulate the different levels of target processing by means of electrophysiological recordings. Finally, further research would be crucial to better characterize the distinctiveness arising from the internal representation we hold about our own body and other people's bodies.

Clara Aranda

María Ruz

Pío Tudela

Daniel Sanabria

Manuscript in preparation

Were those my hands?

Attention modulates perceptual stages of visual own
body processing

Abstract

In a recent study, Aranda et al. (Aranda, Ruz, Tudela, & Sanabria, in press) reported that attentional expectations could modulate the visual processing of certain body parts (hand stimuli) depending on ownership. The results showed that expectations only influenced the processing of own hand stimuli, as measured by behavioural indexes of performance. The goal of the current study was to investigate the neural correlates of this differential effect of attention by means of a high-density electroencephalographic recording system. In line with Aranda et al.'s previous findings, the present results revealed that attention modulated the visual processing of own and someone else's hands differentially. Expectations influenced early perceptual components, such as the P1 and N170 potentials, exclusively for own hands stimuli. However, both target hands showed analogous attentional modulations on later potentials. In light of these findings, we suggest that own hand's representation would sustain a higher level of perceptual definition than other hand's representation, enabling attention to influence the perceptual stages of stimulus processing exclusively on self-stimuli. Therefore, we interpret these results as a further evidence that own and others' body stimuli rely on different perceptual representations

Introduction

Our own body is a unique object for perception. It possesses a multimodal quality, which can be experienced from the outside through vision, audition, olfaction, taste and touch, as other common objects around us, but it can also be felt from the inside through tactile sensation, kinaesthesia, proprioception and interoception. This way, our body seems to constitute a gate to the conscious experience of the world and, at the same time, of ourselves as individual entities.

Traditionally, the study of body perception has focused on the interaction between sensory and motor signals originated within our body and lead to a subjective experience of ownership (*it is my body*) and agency (*I can control it*) (e.g. Tsakiris, Schütz-Bosbach, & Gallagher, 2007). However, this form of experience cannot be confronted with the perception of other objects, as we usually do not feel someone else's body from the inside. Ownership and agency breakdowns are exclusively observed under experimentally induced illusions ("rubber hand illusion" e.g. Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005) and neurological or psychiatric syndromes (alien hand syndrome, e.g. Della Sala, Marchetti, & Spinnler, 1991; delusions of control, e.g. Frith, 1987). Nevertheless, we can perceive our own body through other sensory channels allowing a direct comparison with other objects' perception. Vision seems to be the most suitable channel to study the differences that might emerge between the perception of our own and other bodies. In that context, a main question arises: Does our body subservise a special processing compared to other's people bodies?

Extensive evidence has highlighted the fact that self-referential information is processed in a distinct way in contrast to non self-related information (e.g. Craik et al., 1999; Fischler et al., 1987; Gilboa, 2004; Graham et al., 2003; Kelley et al., 2002; Miyakoshi, Nomura, & Ohira, 2007; Zhao et al., 2009). These findings have led to the idea that the representation of the self might be *special*, that is, that "it emerges from systems that are physically and functionally distinct from those used for more general purpose cognitive processing" (in Gillihan & Farah, 2005).

Research on the visual perception of the own body as compared to other persons' bodies has shown that self-generated movements are processed faster and more accurately than someone else's movements (Daprati et al., 2007b; Jokisch et al., 2006; Knoblich & Flach, 2003; Loula et al., 2005). These differences might emerge from own-movements being closely related to motor cognition, as suggested by fMRI findings (e.g. Calvo-Merino et al., 2006) and behavioural effects (e.g. Daprati & Sirigu, 2002). On the other hand, static images of self-appearance elicit a similar "*self-advantage effect*", which leads to a faster and more accurate recognition of our own face compared to other faces, either in typical or atypical views (Tong & Nakayama, 1999), and to a better match-to-sample performance for our own than extraneous body images (hands and feet: Frassinetti et al., 2008; Frassinetti et al., 2009). Right brain damage patients seem to be specifically impaired in matching own compared to other's bodies or different stimulus categories, which suggest that self-body processing relies on a specific neural substrate that involves areas of the right hemisphere (Frassinetti et al., 2009; Frassinetti et al., 2008). This neural specificity has also been explored in recent fMRI studies, which have revealed dissociable neural activations for own and someone else's bodies or body parts (headless bodies: Hodzic et al., 2009; Hodzic et al., 2009; hands: Myers & Sowden, 2008).

A recent study by Aranda et al. (in press) has revealed that attentional expectations to hands modulate participants' RT performance as a function of ownership. A modified version of the Posner cuing paradigm was used to prepare participants to see images of either their own hands or someone else's hands. The results showed that expectations modulate exclusively own hand's processing, by speeding up RTs on valid as compared to invalid trials. Crucially, the attentional modulation was absent for other hand's stimuli. This effect was replicated over three different experiments, which were performed to rule out explanations in terms of motor facilitation, arbitrary biases or mere stimulus familiarity. These findings were interpreted as reflecting underlying differences between the perceptual representations that we hold regarding our own hands and other people's hands. The authors suggested that the perceptual distinctiveness of an internal representation might be an essential

requirement to observe the effects of expectations about particular stimuli. As a result, they proposed that own hand's representation sustains a higher perceptual distinctiveness compared to other hands.

The present study was designed to investigate the neural correlates of the differential effect triggered by attentional expectations on own and other person's hand visual processing reported by Aranda et al (in press). To this aim, we adapted Aranda et al's paradigm to measure participants' brain activity by means of a high-density electrophysiological recording system.

Methods

Participants. Twenty right-handed students (6 males; mean age: 20; age range: 19-30) were recruited from the University of Granada. Volunteers provided written informed consent to participate in the study in accordance with the Ethics committee of the University of Granada. All of the participants had normal or corrected to normal vision and no neurological or psychiatric disorders, and received course credits in exchange of their participation.

Apparatus and stimuli. The stimuli consisted of a fixation point (+), a coloured cue (red or blue star) sustaining 3.8°, and a target hand, framed in an area of 230*307 pixels.

Target hands belonged either to the participant (own hands) or to another single unidentified participant (someone else's hands). Photographs of left and right hands were taken from all participants in a session prior to the experiment, within a controlled environment with artificial constant luminance, a fixed distance between the camera lens and the hand stimulus (40 cm), and an invariant horizontal position of the hand. Hands were modified by means of Adobe Photoshop software to present them in an upright position on a uniform black background. Someone else's hand stimuli, belonging from a single participant, were selected from this database as the best match for size, skin colour, age and gender as compared to each participant's hands. The size of the hands was compared on a 450*601 pixels scale and the selected pair belonging to the

participant (own hands) or to the other person (other hands) differed on average ± 92 mm and ± 61 mm in the vertical and horizontal axis, respectively. This matching was conducted to induce participants to focus on the characteristics that define each stimulus idiosyncrasy (own vs. someone else's), while preparing for a particular hand.

Stimuli were presented centrally in a 17'' Dell monitor, located at approximately 50 cm from the participants. The E-Prime V2.0 software (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation and response collection.

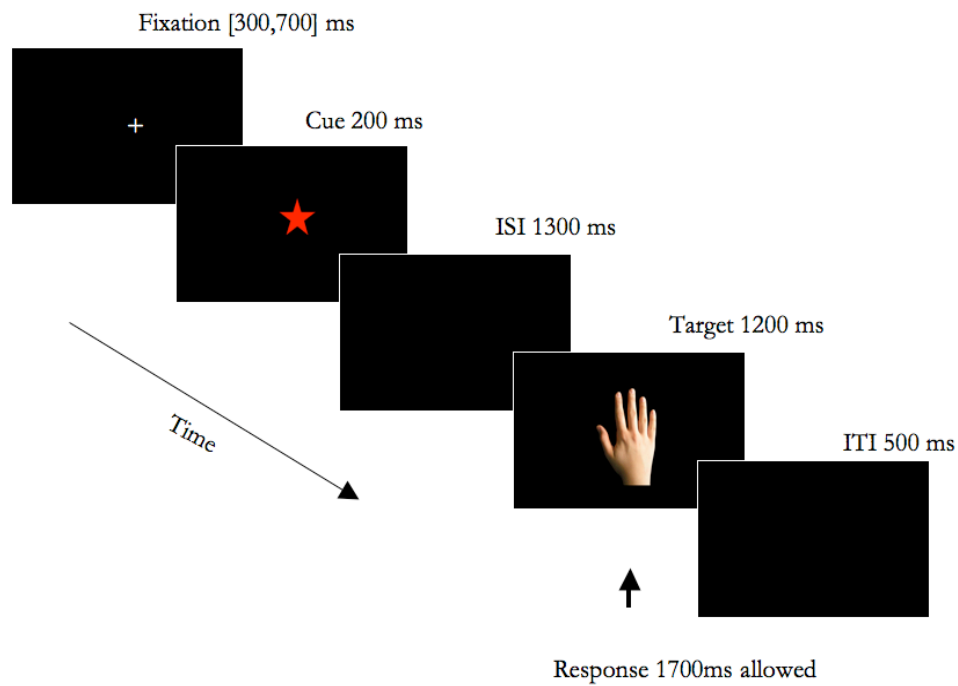


Figure 1. Sequence of events in a trial.

Design and Procedure. A modified Posner paradigm was used to direct participants' attention towards the appearance of own or other's hands, leading to a within-subjects design with the factors of Target identity (own vs. other's hands) and Validity (valid vs. invalid trials).

After electrode placement, participants sat in an electrically shielded and dimly lighted room. They were carefully instructed to maintain their eyes fixated on the centre of the screen and to avoid blinks and eye movements during stimulus presentation. Each trial began with a fixation point of a random duration between 300-700 ms. After this, the cue was flashed for 200 ms, which was followed by a blank interstimulus interval of 1300 ms. The target hand was then presented for 1200 ms. The coloured cue predicted the target identity on 75% of the trials (valid trials). Colour-Hand identity associations were counterbalanced between participants: the red star predicted own hands and the blue star predicted other's hands for half of the participants while the reverse was true for the remaining half. Participants were required to perform a laterality judgement by pressing the "z" key for left hands and the "m" key for right hands with the corresponding index. RT and response accuracy were measure for each trial. The temporal sequence of a trial is displayed in Figure 1.

The experiment started with a practice block of 80 trials, followed by six experimental blocks of the same length. Own and Other's hands presentation was equated within each block (50%). Participants were allowed to pause for a brief rest between blocks. The EEG recording session comprised a total of 480 experimental trials and lasted for about 50 min.

As a prior condition to begin the experiment, subjects performed a recognition block of 100 trials to ensure that they were able to distinguish between own and other's hand images. Participants were asked to press two different keys in response to own and other's hands. A minimum of 80% of accuracy was required to continue with the experiment proper.

EEG Acquisition and Analysis. Electrophysiological activity was recorded from 128 surface electrodes [*Electrical Geodesics, Inc. (EGI)*], referenced to the vertex channel

(Impedances < 50 k Ω , 250 Hz digitization, band pass filtered 0.1-100 Hz). Electrodes located above, beneath and to the left and right of the external canthi of the eyes were used to detect horizontal and vertical eye movements. Continuous data was filtered off-line with a 30 Hz low-pass filter.

Epochs of EEG from -200 ms to 1000 ms post-target onset were submitted to software off-line processing for artefact detection. Trials containing non-ocular artefacts (± 100 μ V from one sample to the next), blinks or saccades (± 70 μ V on horizontal and vertical EOG channels) and incorrect behavioural responses were rejected. In addition, trials with reaction times exceeding a time interval between 300 and 1100 ms were regarded as anticipations or errors and excluded from further analyses (3% trials were discarded). Individual channels that showed a consistently noisy recording for a specific subject (>20% trials) were replaced using a spherical interpolation algorithm (Perrin, Pernier, Bertrand, & Echallier, 1989). A minimum criterion of 30 artefact-free trials per subject per condition was established in order to maintain an acceptable signal-to-noise ratio.

Epochs were recalculated to the average reference to eliminate the effects of reference-site activity and generate an accurate estimation of scalp topographies (Dien, 1998; Tucker et al., 1994). The grand mean calculation gave rise to four separated waveforms according to Target identity (Own vs. Other's hands) and Validity (valid vs. invalid trials) and the 200-msec pre-stimulus epoch served as baseline. ERP analyses were based on voltage amplitudes and topographical maps examinations.

Topographical analyses search for the spatial variations of the voltage distribution over time, identifying stable map topographies that represent functional microstates of the brain during information processing. The finding of different maps for the contrasted experimental conditions is associated to dissociable neural generators. In addition, these topographies usually match identifiable ERPs on the grand-average waveforms (Murray et al., 2004; Thierry et al., 2007), which optimize the posterior selection of spatio-temporal windows for subsequent amplitude analyses. Own vs. Other's hands segments were submitted to a *Segmentation-into-microstates* procedure (Cartool Software: <http://brainmapping.unige.ch/Cartool.php>). This software tool uses a

spatial cluster analysis to identify the dominant map topographies on a group-averaged level across experimental conditions over time (e.g. Blanke & Arzy, 2005; Ducommun et al., 2002; Itier & Taylor, 2004). The optimal number of these template maps is determined by a modified cross-validation criterion, which was applied with several constraints: maps had to remain stable for 20 ms and the maximum correlation between different topographies should not exceed 92% (Pascual-Marqui et al., 1995). The presence of a given map at a group-averaged level can be statistically tested at an individual level by a *fitting* procedure. Obtaining of a significant interaction Map x Condition suggests that dissociable neural configurations account for the different conditions (Brandeis et al., 1995; Lehmann & Skrandies, 1980).

Once the topographical distributions were obtained, multifactorial analyses of variance (ANOVA) were performed on the critical ERP voltages. We used a combination of the topographies' temporal constraints and a visual inspection of the grand-average waveforms to determine the most optimal spatio-temporal window for each evoked potential. Five components were clearly identified: the occipito-temporal P1 and N170, a more anterior P2, a posterior N2 and the centro-parietal P3. Mean amplitude values were computed with reference to the 200 ms pre-stimulus baseline.

Results

Behavioural results.

Reaction times shorter than 300 ms and longer than 1100 ms (3%) and errors (2,8%) were excluded from the analysis.

Participants' mean RTs were submitted to a repeated-measures ANOVA with Target identity and Validity as factors. The results revealed a significant main effect of Target Identity, $F(1,19)=7.1$, $p=.01$, with faster RTs to own hands (511 ms) than to other's hands (519 ms). We also observed a significant main effect of Validity, $F(1,19)=9.8$, $p<.01$, while the interaction between Target Identity and Validity did not reach statistical significance, $F<1$. Planned comparisons showed that the validity effect

was present for both hands, although it was only marginally significant for other's hands (own hands: $p=.01$; other's hands: $p=.06$; see Figure 2). This result contrasts with our previous findings (Aranda et al., in press) that failed to find a significant attentional effect for other people's hands. A crucial difference between the two paradigms relied on the total number of trials. Whereas the experiments in Aranda et al. (in press) consisted in 240 trials, the current experiment had 480 trials, which were needed to acquire an adequate signal to noise ratio for ERP analyses. To explore this further, we carried out an analysis to observe whether the validity effect for other hands developed progressively throughout the experiment. The whole session was divided in two parts (Phase 1-2) that were introduced as a new factor in the ANOVA. The results revealed a significant three-way interaction involving Phase x Target Identity x Validity, $F(1,19)=5.1$, $p=.03$ (see Figure 3).

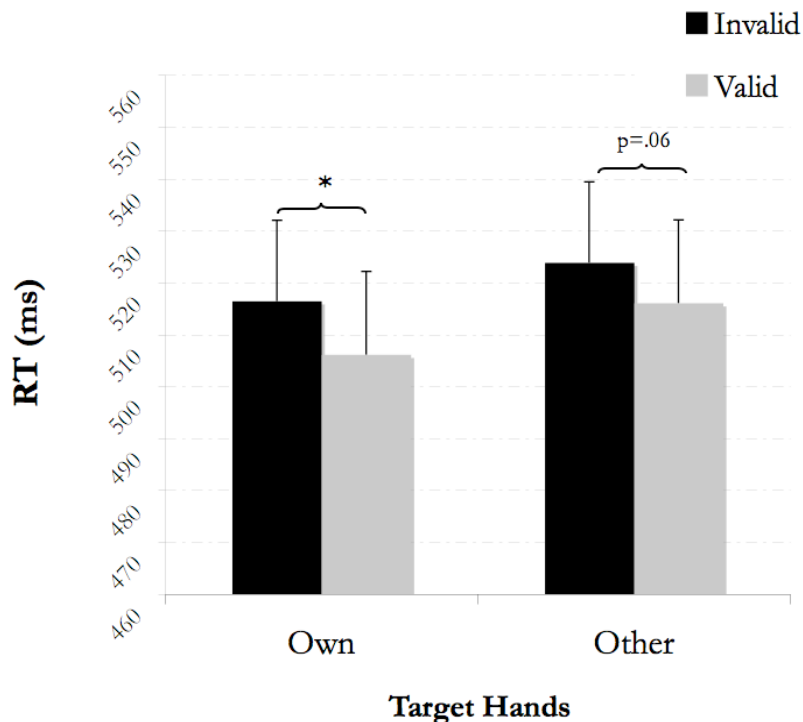


Figure 2. Validity effects on mean RTs for own and other target hands.

A break down of the analysis by Phase revealed a significant Target Identity x Validity interaction, $F(1,19)=7.11$, $p=.01$, in the first phase of the experiment. This interaction was due to a significant effect of validity for own hands, $F(1,19)= 7.6$, $p=.01$, but not for other hand stimuli, $F<1$. However, the same Target Identity x Validity interaction did not reach statistical significance during the second phase of the experiment, $F<1$. These findings suggest that the validity effect for other's hands emerged gradually in the course of the experiment. A similar ANOVA on participants' accuracy data did not reveal any significant term.

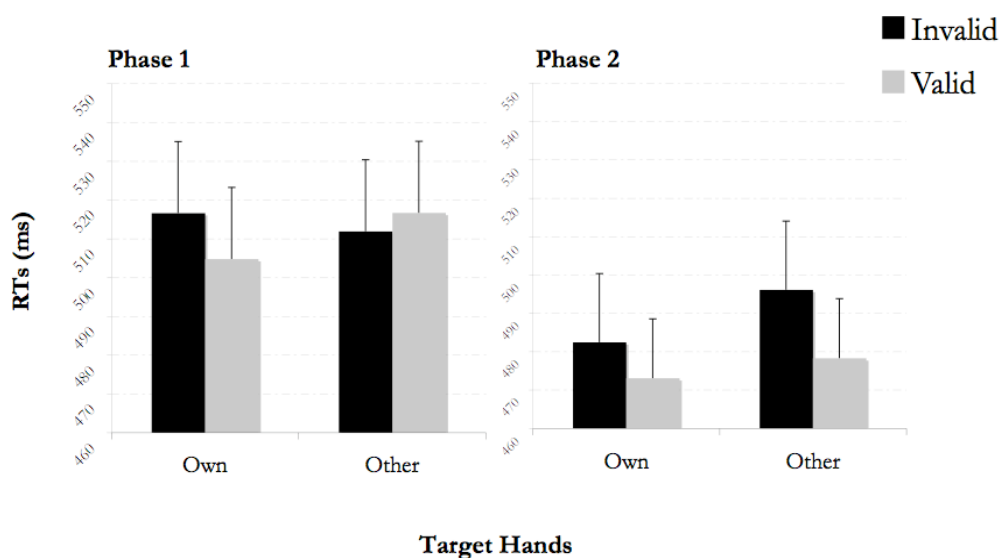


Figure 3. Differential validity effects observed in the phase 1 and 2 of the experiment.

Electrophysiological results.

Topographical analyses identified a sequence of 11 different distributions over the scalp surface during the processing of own and other hand stimuli, along a 1.000 ms

interval locked to target onset. However, the spatial cluster analysis did not reveal any different map between conditions, which suggests that the visual processing of own and other's hand stimuli relies on similar neural networks. Figure 4a displays five topographical maps that guided the selection of relevant spatio-temporal windows for posterior analyses.

Voltage analyses were performed on the P1, N170, P2, N2 and P3 evoked potentials. The factors tested were Target identity (own vs. other hands), Validity (valid vs. invalid trials), and Hemisphere (right vs. left) where relevant.⁴

The analysis of the P1 comprised 16 electrodes located on the parieto-occipital regions of both hemispheres (peak time window: 108-120 ms). The results revealed a significant three-way interaction involving Target identity, Validity and Hemisphere, $F(1,19)=5.83$, $p=.026$. To further investigate this interaction we broke down the analysis as a function of Target identity. The ANOVA on own hand's data revealed a significant Validity x Hemisphere interaction, $F(1,19)=4.08$, $p=.05$. This two-way interaction showed that attention influenced the P1 amplitude exclusively for own hands on the right hemisphere (validity effect for the left hemisphere, $F<1$), where invalid trials evoked significantly larger amplitudes than valid trials (2.22 μV vs. 1.88 μV , $F(1,19)=4.8$, $p<.05$). By contrast, no validity effects were obtained for other hands stimuli, $F<1$, as can be seen in Figure 4a.

The N170 was most pronounced on a group of 14 electrodes located over occipito-temporal sites on both hemispheres (peak time window: 174-186 ms). The ANOVA yielded a significant main effect of Target identity, $F(1,19)=5.13$, $p=.03$, and a significant two-way interaction between Target identity and Validity, $F(1,19)=4.74$, $p<.05$. The Target identity effect was observed in larger N170 amplitudes for own hands as compared to someone else's hands. A closer examination of the two-way interaction revealed that the N170 was exclusively modulated by attention to own hand stimuli, $F(1,19)= 5.31$, $p=.03$, (validity effect for other hands, $F<1$), showing larger

⁴ Although separated voltage analyses for Phase 1 and 2 would have been of interest, the number of trials within these two levels did not reach the minimum number needed to obtain a clearly defined waveform on each experimental condition.

amplitudes for invalid as compared to valid trials (-2.2 μv and -1.9 μv , respectively; see Figure 4b).

The ANOVA on the P2 potential was carried on 14 electrodes located over parieto-temporal sites in both hemispheres (peak time window: 204-220 ms). In contrast to previous analyses, the P2 showed a significant main effect of Validity, $F(1,19)=6.65$, $p=.018$, that was not modulated by Target Identity, $F<1$. This latter result suggested that attention influenced P2 amplitude to both target hands. The main effect of validity was modulated by Hemisphere, $F(1,19)=4.4$, $p<.05$, showing larger amplitudes for valid as compared to invalid trials exclusively on the left hemisphere, $F(1,19)=9.56$, $p=.005$ (validity effect for the right hemisphere, $F<1$].

The N2 potential was analysed on 22 occipito-temporal electrodes from both hemispheres (peak time window: 280-296 ms). The ANOVA revealed a significant main effect of Validity, $F(1,19)=6.95$, $p=.016$, which was not modulated by either Target identity, $F(1,19)=2.48$, $p=.13$, or Hemisphere, $F<1$. The significant main effect resulted from larger amplitudes for invalid as compared to valid trials (-0.1 μv vs. 0.2 μv).

The P3 potential was maximal on a single spatial window comprising 9 centroparietal electrodes (peak time window: 412-428 ms). The ANOVA yielded a significant main effect of Target identity, $F(1,19)=16$, $p=.001$, and Validity, $F(1,19)=13.96$, $p=.001$. Once again, the validity effect was not modulated by Target identity, $F<1$. The significant effects showed that own hands elicited a larger positive peak than other's hands, while both target hands showed an increased amplitude for valid as compared to invalid trials (see Figura 4c).

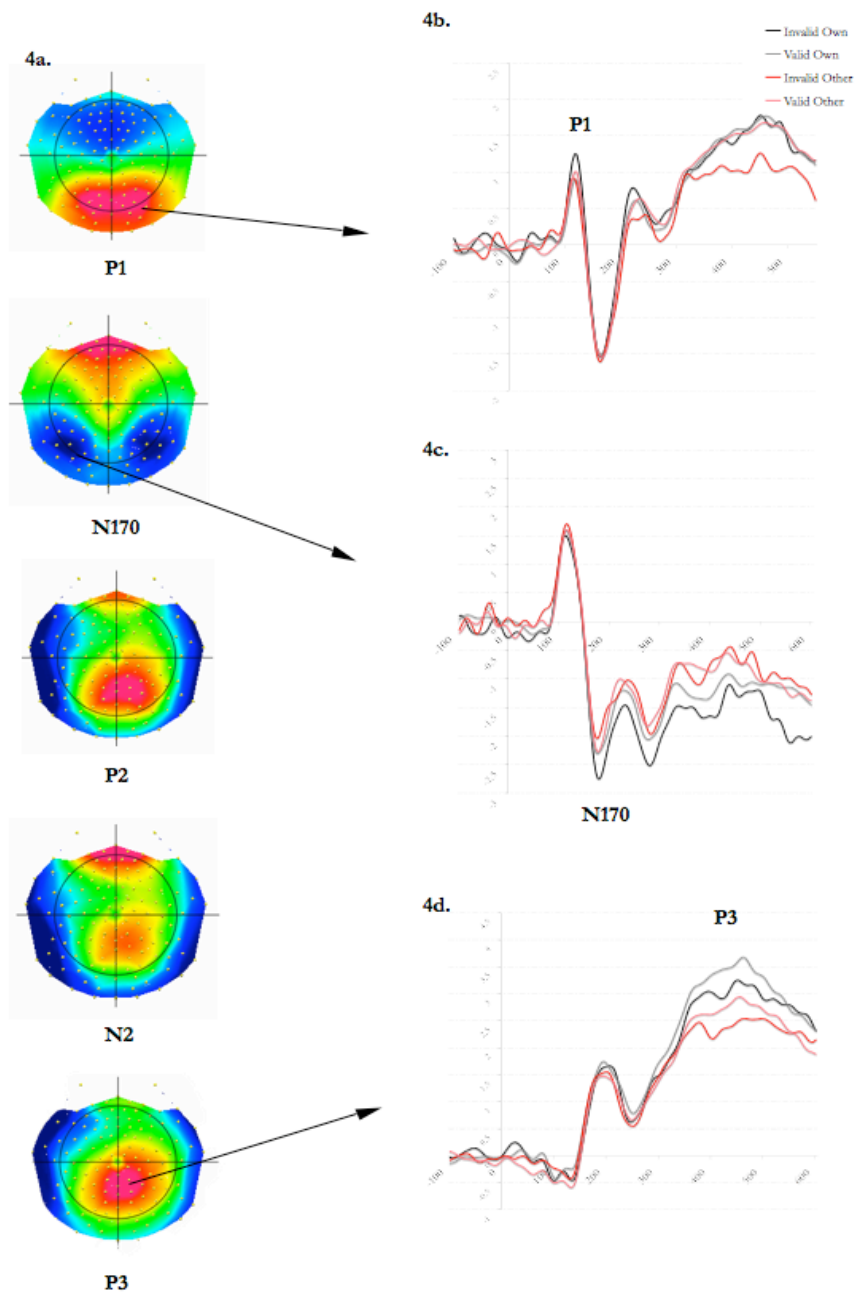


Figure 4. **4a.** Topographical analyses of hands visual processing, showing the relevant maps associated to P1, N170, P2, N2 and P3 potentials. **4b.** Attentional modulation of the P1 displayed on a right hemisphere channel. **4c.** Attentional modulation of the N170 displayed on a left hemisphere channel. **4d.** Attentional modulation of the P3 displayed on a central channel.

Discussion

The main goal of the present study was to investigate the neural correlates of the attentional modulation that expectations could exert on the visual processing of own and someone else's hands. Our behavioural results revealed that attentional expectations induced a processing optimization for own and other hand stimuli, as responses were faster for valid compared to invalid trials. Although these results seemed to be at odds with previous findings by Aranda et al. (in press), who did not show a validity effect on other people's hands, we observed that in the first phase of the experiment the cueing effect was indeed modulated by the target identity. By contrast, this interaction was not longer significant in the second phase, as cue validity seemed to influence the processing of both target hands. In light of these results, one might argue that an increasing visual experience facilitates the emergence of an attentional effect for extraneous hands at least on RT performance. In any case, the crucial results in our study revealed that attention differentially modulates the visual processing of own and other hands stimuli.

Electrophysiological results revealed a differential attentional modulation for target hands on perceptual stages of processing, indexed by the occipito-temporal P1 and N170 potentials. We found that attention exclusively modulated the P1 and N170 on self-stimuli, which showed larger amplitudes on invalid than valid trials. In contrast, no significant effects emerged for other hands stimuli. This differential attentional modulation between own and other hands supports the behavioural dissociation reported on Aranda et al's study (in press).

The attentional modulation of P1 and N170 for own hands revealed a reversion of the classical effect of attention. Traditional paradigms of spatial attention have repeatedly showed that P1 and N170 amplitudes are larger on valid than invalid trials (see e.g. Eimer, 1994b; Luck et al., 1994). However, we did not manipulate spatial attention in the present study since we used symbolic cues to prepare participants to see a particular item within a category. Under this attentional manipulation, we observed

that invalid trials elicited a larger P1 and N170 than valid trials for own hand stimuli. Previous studies have shown that the N1 can be reduced to valid as compared to invalid trials in certain occasions (e.g. Aranda et al., under review; Fu et al., 2001; Hopfinger & Ries, 2005). However, such a modulation of the P1 has been scarcely reported and it has been exclusively described within the spatial attention literature (Eimer, 1994a; Hopfinger & Mangun, 1998). Interestingly, a recent study has reported an analogous attentional modulation of the P1 and N170 to familiar faces as a result of idiosyncratic expectations (Aranda, Sanabria, Tudela, & Ruz, in preparation). This study used a central cueing paradigm to direct participants's attention towards a face, which could be either familiar or unfamiliar. The results revealed that invalid trials evoked larger amplitudes than valid trials on perceptual components (P1 and N170) exclusively to the familiar face, while the unfamiliar face showed the classic attentional effect (i.e., larger amplitudes for valid than for invalid trials).

In light of the findings reported by Aranda et al. (in preparation), we propose that the reversed pattern of validity on perceptual components showed in the present study reflects the effect of idiosyncratic expectations when deployed to perceptually familiar stimuli (either a familiar face or own hands). The increase of P1 and N170 to invalid in contrast to valid trials might be due as a result of exogenous attention, that is, the automatic capture of attention triggered by the unexpected appearance of a familiar stimulus (c.f. Aranda et al., in preparation). Interestingly, the few reported inversions of the P1 have been described as an effect of exogenous spatial attention. In addition, our interpretation of the present data can be applied to other experimental results like the face inversion effect, which induces larger amplitudes on the P1 (e.g. Itier & Taylor, 2002; Vizioli, Foreman, Rousselet, & Caldara, 2010) and the N170 (e.g. Bentin et al., 1996; Jacques & Rossion, 2007), as the presentation of up-side down faces can be considered an unexpected situation involving a highly familiar stimulus that captures attention in an automatic way. In any case, it is important to highlight that the validity effect on the P1 and N170 components was only observed for own hand stimuli. As it has been shown that expectations about particular unfamiliar items also influence

perceptual components (an unfamiliar face; Aranda et al., in preparation), the absence of an attentional effect on the P1 and N170 for other hands cannot be explained in terms of mere familiarity. Instead, we suggest that there must be another factor mediating the reported attentional dissociation between own and someone else's body parts. Again, one might argue that this result could reflect differences in the perceptual distinctiveness of own and other hands' internal representations.

On later stages of stimulus processing, own and other's hand stimuli revealed an analogous attentional modulation. The parietal P2 and the centro-parietal P3 showed more positive values for valid vs. invalid hand stimuli, while the parieto-temporal N2 revealed larger amplitudes for invalid than for valid trials, independently of their specific identity. The P2 is thought to reflect automatic stimulus processing, which is affected by attention or orienting processes (e.g. Luck et al., 1994; Näätänen & Picton, 1987). The N2 component seems to reflect the identification of deviant stimuli, as it has been related to a mismatch negativity in response to low-probability stimuli (e.g. Harter & Aine, 1984; Näätänen & Gaillard, 1983). Crucially, both target hands showed a larger N2 to invalid as compared to valid trials. However, the findings on the P3 potential, which showed larger amplitudes for own vs. other hands as well as for valid vs. invalid trials, are critical as previous research has shown that the P3 reliably discriminates attended and self-related stimuli from their corresponding counterparts (Attention effects: see Coles, Smid, Scheffers, & Otten, 1995 for a review; Self-related effects: Berlad & Pratt, 1995; Gray, Ambady, Lowenthal, & Deldin, 2004; Perrin, García-Larrea, Mauguère, & Bastuji, 1999). In addition, it seems probably that the reported behavioural effects were related to the attentional modulation of the P3 amplitude.

Taken together, our results revealed that idiosyncratic expectations exert a differential effect on visual body processing (at least on hand stimuli) as a function of ownership. We propose that the reported differences between own and other hands' processing might rely on the distinctiveness of their perceptual representations, as an hypothesis in terms of mere familiarity has been previously discarded (Aranda et al. in press; Aranda et al. in preparation). Our behavioural results suggest that an extensive

visual practice can improve the perceptual distinctiveness of a stimulus, which led to the emergence of a validity effect for other hands in the second phase of our experiment. However, the electrophysiological results revealed a dissociable attentional effect on perceptual components for own and other hands. We hypothesize that the level of perceptual definition in own hand representation is highly detailed as compared to other hands, which would allow attention to influence early perceptual processes exclusively on self-stimuli. By contrast, expectations exert a similar influence on posterior stages of processing for both hands, which might be related to higher cognitive processes as conscious detection of deviant stimuli, semantic analysis and response selection. Further research would be desired to explore whether these identified differences remain after a more extended visual training with other hand stimuli. Interestingly, Tong and Nakayama (1999) showed that the processing advantages associated to the own face as compared to a different face persisted even after hundreds of presentations. Nevertheless, it is still a matter of debate whether an own-body distinct processing might reflect the influence of an extremely high visual familiarity, as it may be beyond reach to fully disentangle both factors.

Discusión General

1. Atención endógena centrada en el objeto

Este proyecto doctoral profundiza en el estudio de la orientación atencional endógena o voluntaria. Como comentábamos previamente, el debate actual no debería establecerse en torno a qué dimensión prima en la selección atencional de información (espacial vs. no espacial). Por el contrario, nuestros esfuerzos deberían encaminarse a explorar el potencial de la atención y su capacidad para optimizar el procesamiento cuando ésta se focaliza en los múltiples aspectos no-espaciales que configuran nuestro entorno sensorial. En esta línea de pensamiento, decidimos estudiar si la atención endógena, entendida como expectativa atencional, podía dirigirse hacia un objeto en base a su categoría o identidad idiosincrásica (véase Lauwereyns, 1998) y modular el procesamiento visual de ese estímulo desde sus etapas perceptivas.

Nuestro primer estudio investigó el efecto que ejerce la atención dirigida mediante señales simbólicas que anticipaban una categoría específica sobre el procesamiento de un estímulo. Estas señales predecían con una alta probabilidad la aparición de una cara o una palabra. La medición de ERPs nos permitió explorar aquellas etapas del procesamiento visual moduladas por la atención endógena. El resultado más relevante mostró un efecto atencional en el componente N170, el cual es considerado un índice de procesamiento perceptivo categorial tanto para caras (e.g. Bentin et al., 1996; Eimer, 2000c; Lueschow et al., 2004; Watanabe et al., 1999) como para palabras (e.g. Bentin et al., 1999; Maurer et al., 2005; Tarkiainen et al., 1999). De forma crucial, esta modulación atencional mostró un patrón categorial específico: para las palabras, los ensayos válidos revelaron un N170 de mayor amplitud que los ensayos inválidos, mientras que para las caras, los ensayos inválidos mostraron una mayor amplitud que los ensayos válidos.

El segundo estudio de la serie investigó el efecto de dirigir la atención a estímulos particulares dentro de una misma categoría, utilizando para ese fin una cara familiar y una cara no familiar. Nuestros resultados mostraron que las expectativas idiosincrásicas lograban modular componentes perceptivos más tempranos (el P1), que

aquellos modulados por expectativas categoriales (el N170). La modulación atencional del P1 y el N170 reveló un patrón diferencial en función de la familiaridad: la cara no familiar mostró más amplitud de voltaje en ensayos válidos que en inválidos, mientras que la cara familiar mostró una mayor amplitud en ensayos inválidos en comparación con los válidos.

Finalmente, el tercer y cuarto estudio exploraron el efecto de expectativas acerca de estímulos específicos, uno de los cuales no sólo era familiar, sino que pertenecía al propio sujeto. Los estímulos seleccionados fueron las propias manos del participante y las manos de una persona desconocida. El estudio 3 investigó la posibilidad de dirigir la atención a estos estímulos corporales mediante medidas conductuales de TR. Los resultados mostraron que la atención optimizaba el tiempo de ejecución exclusivamente en aquellos ensayos que mostraban imágenes de las propias manos. Este efecto diferencial no pudo explicarse mediante una preparación motora, un sesgo arbitrario o la familiaridad de los estímulos.

El estudio 4 se llevó a cabo para examinar los correlatos neuronales del efecto diferencial de la atención en función de la identidad propia y ajena del estímulo mediante ERPs. En claro contraste con el estudio 3, los resultados conductuales revelaron un efecto de la atención tanto para manos propias como ajenas. El número de ensayos en el experimento de ERPs era dos veces superior al del experimento conductual, por lo que este resultado divergente mostró que una práctica extendida con manos ajenas permitía el desarrollo de un efecto atencional para estos estímulos. Sin embargo, el análisis de los datos electrofisiológicos reveló una disociación entre estímulos propios y ajenos en la modulación atencional: el P1 y el N170 eran modulados por la atención *exclusivamente* en manos propias, exhibiendo una mayor amplitud para ensayos inválidos en comparación con ensayos válidos.

El siguiente apartado propone un marco teórico que permite explicar nuestros resultados y sugiere qué puede estar ocurriendo cuando pedimos a los participantes que focalicen su atención sobre una categoría o un ítem en particular.

2. El vínculo entre la expectativa y la representación analógica

[...] *la imagen mental emerge cuando la percepción de un objeto o una escena se anticipa tan vívidamente que una representación descriptiva del objeto es creada en el córtex visual* [...]

(Kosslyn & Thompson, 2003)

La investigación sobre imaginación visual, como previamente exponíamos en la introducción, demuestra la existencia de representaciones mentales de naturaleza analógico/visual. Sin embargo, podrían derivarse conclusiones muy similares a partir de otras áreas de investigación, como el estudio de las expectativas (Bar, 2003; Chawla, Rees, & Friston, 1999; Esterman & Yantis, 2009; Puri et al., 2009; Shulman et al., 1999; Summerfield et al., 2006) o la memoria de trabajo (Curtis & D'Esposito, 2003; Johnson, Mitchell, Raye, D'Esposito, & Johnson, 2007; Postle, Druzgal, & D'Esposito, 2003; Ranganath & D'Esposito, 2005; Ranganath, DeGutis, & D'Esposito, 2004; Ruchkin, Grafman, Cameron, & Berndt, 2003). Probablemente, uno de los obstáculos que ha mantenido estas áreas de investigación en ámbitos independientes es el uso de distintas terminologías para conceptos que hacen referencia a una realidad muy semejante. Sin ir demasiado lejos, traer a la mente una representación que anticipe la aparición de un estímulo se ha denominado de formas tan dispares como expectativa (Bar, 2003), código predictivo (predictive code; Summerfield et al., 2006), modelo interno (Internal template; Summerfield et al., 2006), Set perceptivo (Corbetta & Shulman, 2002; Summerfield et al., 2006) o conjetura inicial (Initial guess; Bar, 2003).

Desde algunas perspectivas teóricas se deriva la idea de que las expectativas facilitan el reconocimiento de un objeto mediante la restricción del número de *representaciones perceptivas* que se activan y compiten entre sí en *áreas visuales* (Bar, 2003). El control sobre la activación o inhibición de distintas representaciones perceptivas se implementaría mediante una modulación *top-down* de áreas posteriores de análisis visual. Los estudios de Summerfield y colaboradores, entre otros, ofrecen un apoyo empírico a este modelo ya que muestran que las expectativas sobre caras (mantener una expectativa general o identificar erróneamente un estímulo difuso),

inducen un incremento en la FFA (Summerfield et al., 2006; Summerfield, Egner, Mangels, & Hirsch, 2006). Sin embargo, es importante tener en cuenta que este modelo describe qué puede estar ocurriendo *durante* el reconocimiento de un estímulo. ¿Qué ocurriría en el caso de que las expectativas se crearan antes de la aparición del estímulo objetivo?

Los estudios sobre este tipo de expectativas muestran activación en regiones especializadas asociadas al procesamiento visual de la categoría atendida (FFA para caras y el giro Parahipocampal para edificios), *antes* de la presentación del estímulo objetivo (Esterman & Yantis, 2009; Puri et al., 2009). Estos resultados sugieren que la señal atencional logra modificar la actividad neural en función del contenido de la expectativa y en ausencia del estímulo, mostrando una clara equivalencia entre anticipar una categoría perceptiva, recuperar una imagen mental asociada a esa categoría (Ishai et al., 2000; O'Craven & Kanwisher, 2000) o mantener en la memoria de trabajo una representación de esa categoría (e.g. Lepsien & Nobre, 2007).

Finalmente, estudios muy recientes han demostrado una estrecha semejanza entre las expectativas y la activación o el mantenimiento de determinadas representaciones mentales sobre *estímulos específicos*. Estos estudios revelan que el circuito neural activado por la presentación visual de un estímulo particular es equiparable al observado durante la generación interna, en ausencia de estimulación, de una expectativa (Stokes et al., 2009), de una imagen mental (Stokes et al., 2009) o el mantenimiento de una representación en la memoria de trabajo de ese mismo estímulo (Harrison & Tong, 2009). El nivel de especificidad del análisis *MVPA* permite discriminar entre patrones asociados a distintas letras (X ó O) o a distintas orientaciones de un enrejado (/// ó \\\).

En conjunto, estos hallazgos sugieren que crear una expectativa, generar una imagen mental o mantener una representación en la memoria de trabajo pueden aludir, bajo ciertas circunstancias, a un mismo estado mental: la activación de una representación visual del estímulo. Esta representación se corresponde con su correlato perceptivo tanto a nivel categorial, asociado a áreas especializadas (e.g. FFA -caras-, VWFA -palabras-, Giro Parahipocampal -edificios-) como a nivel idiosincrásico,

asociado a la activación de subpoblaciones neurales específicas que codifican un ejemplar particular. Estos datos apoyan la hipótesis de que ciertas representaciones del conocimiento se almacenan en forma de símbolos perceptivos sobre el mismo substrato neural asociado al procesamiento visual (véase Barsalou, 1999).

Nuestros resultados muestran que dirigir la atención endógena a categorías o ejemplares idiosincrásicos, logra modular etapas perceptivas del procesamiento visual del estímulo objetivo. Teniendo en cuenta que las expectativas pueden inducir activación en áreas visuales (Esterman & Yantis, 2009; Puri et al., 2009; Stokes et al., 2009) y que la unidad atendida parece determinar la etapa de procesamiento modulada (e.g. Cristescu & Nobre, 2008; Ruz & Nobre, 2008b), resulta probable que estas expectativas estén activando una *representación perceptiva* del estímulo esperado. A pesar de que esta hipótesis tan sólo podría confirmarse mediante la adaptación de nuestro diseño a la técnica de fMRI, consideramos que nuestro planteamiento se fundamenta en un sólido cuerpo de evidencia empírica. Por esta razón, nos permitimos interpretar nuestros resultados en el contexto de las representaciones mentales perceptivas.

3. Atención a representaciones perceptivas del objeto

El primer estudio de la serie que conforma este proyecto muestra que las expectativas categoriales logran modular etapas perceptivas del procesamiento visual de un estímulo. De manera crucial, el primer componente modulado es el N170, el cual se ha identificado como un índice de procesamiento perceptivo categorial. Este dato ratifica la hipótesis de que la atención actúa principalmente sobre aquellas etapas relacionadas con la representación atendida (e.g. Cristescu & Nobre, 2008; Ruz & Nobre, 2008). En este caso, la representación atendida incluye información visual a un nivel medio de especificidad, el cual permite distinguir entre categorías pero no discrimina entre estímulos particulares pertenecientes a una misma categoría, facilitando el procesamiento de todos ellos. En contraste, las expectativas

idiosincrásicas facilitan el procesamiento de un estímulo determinado y modulan componentes perceptivos más tempranos que el N170. Según el planteamiento de Kosslyn y Thompson (2003), las imágenes mentales con un alto nivel de definición logran inducir activación en áreas extraestriadas de la corteza visual. En nuestro caso, las expectativas idiosincrásicas podrían estar mediadas por la generación de una imagen mental detallada sobre el estímulo particular, lo cual explicaría la observación de una modulación atencional en el P1, tanto en el estudio 2 como en el 4.

Por otra parte, a lo largo de nuestros estudios hemos observado que la atención ejerce su efecto en una dirección o en otra en función del estímulo esperado, incrementando la amplitud en ensayos válidos o en ensayos inválidos. En el primer estudio, las caras muestran un patrón atencional invertido: los ensayos inválidos inducen una mayor amplitud que los ensayos válidos. Según nuestra hipótesis, la atención no influiría en la amplitud del N170 en ensayos válidos debido a una máxima optimización de su procesamiento en situaciones de baja demanda perceptiva (e.g. Carmel & Bentin, 2002; Cauquil et al., 2000; Lueschow et al., 2004). No obstante, la aparición inesperada de una cara atraería la atención de forma automática, induciendo una mayor amplitud del N170 en ensayos inválidos en comparación a los válidos. En el segundo y en el cuarto estudio, este patrón atencional invertido emerge en estímulos familiares (cara familiar y manos propias). Esta modulación podría explicarse de forma similar, entendiendo esta inversión como un efecto de la atención exógena provocada por la aparición inesperada de un estímulo muy conocido en ensayos inválidos, cuyo procesamiento no se ve afectado en ensayos válidos.

Sin embargo, existe un dato entre nuestros resultados que parece contradecir estas hipótesis. En el estudio 1 argumentamos que el procesamiento de caras no es susceptible de una mayor optimización en etapas perceptivas, pero en el estudio 2 las caras no familiares muestran un efecto atencional clásico: los ensayos válidos inducen un mayor P1 y N170 que los ensayos inválidos. Esta contradicción es tan sólo aparente, ya que anticipar la aparición de un estímulo específico (*expectativa idiosincrásica*) probablemente aumente las demandas perceptivas y/o cognitivas de la situación

experimental, permitiendo la emergencia de esta modulación atencional en etapas iniciales del procesamiento (véase Sreenivasan et al., 2009).

Finalmente, pero no por ello menos importante, nuestros datos muestran la existencia de un efecto diferencial de la atención en función de la familiaridad e identidad del estímulo. Tanto la cara familiar como la cara no familiar muestran un efecto atencional en etapas perceptivas tempranas, lo cual nos permite sugerir que el participante logra recuperar una imagen detallada de la apariencia de ambos rostros (representaciones distintivas). Sin embargo, el efecto atencional se manifiesta en dirección opuesta. Según nuestro punto de vista, este dato apoyaría la idea de que caras familiares y no familiares poseen representaciones internas distintas (c.f. Bruce & Young, 1986; Tong & Nakayama, 1999). Las caras familiares estarían representadas de forma más estable y robusta, permitiendo un procesamiento visual óptimo no susceptible a una facilitación atencional en etapas perceptivas (efecto invertido). En cambio, las caras no familiares estarían representadas más frágilmente, beneficiándose de la orientación atencional en su procesamiento visual (efecto clásico).

En relación al efecto diferencial observado en función de la identidad de los estímulos, nuestros datos sugieren que el participante posee una representación más detallada de sus manos que de las manos de otra persona. Esta conclusión resulta obvia, pero no puede explicarse simplemente mediante la familiaridad de los estímulos, ya que las caras no familiares muestran un efecto conductual desde un primer momento (estudio 3) y su procesamiento es modulado desde etapas perceptivas (estudio 2). Por lo tanto, existe una diferencia básica entre la representación que poseemos de nuestro cuerpo y la representación que poseemos del cuerpo de otras personas: la *distintividad*. Los datos conductuales del estudio 4 sugieren que la práctica con manos ajenas permite la creación de una representación interna cada vez más definida para estos estímulos. Sin embargo, la atención endógena no logra modular etapas perceptivas del procesamiento en este tipo de estímulos, lo cual sugiere que su representación aún no alcanza un nivel óptimo de detalle. En su conjunto, estos resultados apoyan la hipótesis

de que la representación corporal propia difiere de la representación de otros cuerpos (c.f. Frassinetti et al., 2008; Myers & Sowden, 2008) en términos de distintividad.

¿Se mantendrían estas diferencias tras una práctica visual más extendida? Ciertos estudios han revelado que las ventajas perceptivas asociadas al procesamiento de la propia cara en contraste a caras de otras personas se mantienen después de cientos de repeticiones (Tong & Nakayama, 1999). Sin embargo, resulta una tarea compleja diferenciar los efectos de la identidad y la familiaridad en la constitución de una representación distintiva interna de nuestro propio cuerpo en relación al cuerpo de otras personas.

4. Conclusiones finales... ¿una propuesta de futuro?

Este proyecto doctoral profundiza en el estudio del efecto de la atención endógena dirigida a una unidad atencional escasamente estudiada hasta el momento: la representación categorial e idiosincrásica del estímulo. En esta línea de actuación, nuestros resultados revelan que las expectativas acerca del objeto logran modular el procesamiento en sus etapas perceptivas más tempranas.

Nuestros datos corroboran que las señales simbólicas no espaciales son capaces de modular el procesamiento visual desde componentes perceptivos como el P1 y el N170. Basándonos en la literatura expuesta en la Introducción, nuestro planteamiento defiende que el *objeto de la atención* parece ser un factor determinante en la observación o no de estos efectos en etapas perceptivas. De esta manera, nuestros hallazgos apoyarían la idea de que el objeto de la atención en nuestros estudios es una *representación perceptiva/ analógica* del estímulo esperado (c.f. Esterman & Yantis, 2009; Puri et al., 2009; Stokes et al., 2009). De forma coherente a nuestras hipótesis, nuestros resultados revelan que, a medida que la *expectativa se hace más específica*, la modulación atencional se observa en *componentes más tempranos* de análisis visual (c.f. Kosslyn & Thompson, 2003). Finalmente, nuestros datos revelan un efecto diferencial de la atención en función de la familiaridad e identidad de los estímulos,

sugiriendo que los estímulos familiares vs. no familiares, y los estímulos propios vs. ajenos podrían poseer *representaciones internas distintas*, apoyando resultados previos en ambas líneas de investigación (e.g. Bruce & Young, 1986; Frassinetti et al., 2009; Frassinetti et al., 2008; Tong & Nakayama, 1999)

Sin embargo, estos estudios esbozan un horizonte de preguntas por responder. ¿Estas expectativas realmente activan una representación visual de los estímulos esperados? ¿Qué efectos encontraríamos dirigiendo la atención a estímulos específicos *no corporales*? ¿Y si éstos fueran familiares? ¿o pertenecientes al propio sujeto? ¿Es posible disociar completamente los efectos de identidad de los efectos de familiaridad? Entre las múltiples trayectorias que emergen de este proyecto, señalaremos tres posibles caminos.

En primer lugar, consideramos de gran importancia llevar a cabo un experimento que compare de forma directa el efecto de la atención sobre el procesamiento de un estímulo propio y un estímulo familiar. Nuestros resultados muestran que el efecto de la identidad surge al contrastar manos del propio sujeto con manos de una persona ajena. Sin embargo, la modulación atencional observada en el P1 y el N170 para manos propias es análoga a la identificada en caras familiares. Por tanto, el próximo experimento lógico de esta línea de investigación debería contrastar el efecto de la atención utilizando la cara del propio participante y la de una persona familiar. Según nuestro planteamiento, esperaríamos encontrar un efecto de la atención invertido para ambos estímulos en componentes perceptivos tempranos pero, probablemente, de mayor magnitud en el caso de nuestro propio rostro.

En segundo lugar, resultaría de gran interés estudiar cómo la atención modula el procesamiento de distintos objetos dentro de una misma categoría no-biológica. Basándonos en el conjunto de estímulos utilizado por Miyakoshi y colaboradores (2007), podríamos investigar el efecto de expectativas que anticiparan distintos objetos cotidianos dentro de una misma categoría: uno perteneciente al sujeto (e.g. taza de desayuno personal), un estímulo familiar (e.g. taza dispensable de un solo uso) y un estímulo perteneciente a otra persona (e.g. taza de desayuno de otro participante). Basándonos en estos resultados y en nuestros propios datos, esperaríamos observar un

efecto atencional clásico para objetos de otra persona y un efecto atencional invertido para objetos familiares y propios, este último probablemente de mayor magnitud.

Finalmente, resultaría decisivo adaptar estos estudios a la técnica de fMRI. Esta técnica nos permitiría explorar de forma directa si las expectativas inducen realmente una activación de la representación perceptiva del estímulo esperado en áreas del córtex visual y si éstas difieren entre sí en función de la familiaridad o la identidad del estímulo. Para lograr una identificación adecuada de las sutiles diferencias entre representaciones idiosincrásicas, utilizaríamos la técnica multi-voxel de descodificación de patrones previamente descrita (véase Norman et al., 2006).

En vista de estas nuevas ideas, resulta obvio que finalizar un proyecto de tesis no conlleva necesariamente finalizar una línea de investigación. Las preguntas surgen unas de otras, marcando un camino que se pierde en la distancia... Así, confiamos que esta tesis y el punto que le pone fin marquen un prometedor principio para futuros proyectos.

Summary

1. Endogenous object-based attention

The present project investigates the endogenous orienting of attention. As we noted in the Introduction, the debate about the primary object of attentional selection (spatial vs. non spatial information) should be overcome to free researchers to investigate the focusing of attention on the non-spatial aspects that conform our sensorial environment. Within this line of thought, we decided to study whether endogenous attention would optimize stimulus visual processing when focused on the category or idiosyncratic identity of an upcoming object (see Lauwereyns, 1998).

Our first study investigated, by means of ERPs, whether endogenous attention driven by symbolic cues that predicted the most probable category of the target stimulus, either a face or a word, could influence its visual processing. Category expectations modulated the N170 component, which is thought to be an appropriate index of perceptual categorical processing for both faces (e.g. Bentin et al., 1996; Eimer, 2000c; Lueschow et al., 2004; Watanabe et al., 1999) and words (e.g. Bentin et al., 1999; Maurer et al., 2005; Tarkiainen et al., 1999). Crucially, the attentional modulation revealed a category-specific pattern: words showed larger N170 amplitudes for valid as compared to invalid trials, while faces elicited a larger amplitude for invalid than for valid trials.

The second study of the series investigated whether attention could be deployed to specific items belonging to the same perceptual category. To this aim, symbolic cues were used to direct participants' attention to the appearance of a highly familiar face or an unfamiliar face. The results showed that idiosyncratic expectations were able to modulate earlier perceptual components (P1) than category expectations did (N170). The attentional modulation of the P1 and N170 revealed a differential pattern as a function of stimulus familiarity: the unfamiliar face elicited larger amplitudes for valid in contrast to invalid trials, whereas the familiar face showed larger potentials for invalid than for valid trials.

Finally, the third and fourth studies investigated whether attention could be focused on a particular stimulus that was not only familiar, but also belonged to the participant (self-owned), in order to study the differences that might emerge when it was compared to a stimulus belonging to a different person (other-owned). The selected stimuli were the participants' own hands and the hands of an unknown person. The third study explored the effect of orienting attention to these bodily stimuli by means of behavioural indexes of performance (RTs). Our results showed that attention optimized stimulus processing exclusively for own hands' stimuli. This differential effect could not be explained by a manual preparation, an arbitrary bias or by stimulus familiarity.

The fourth study was carried out to investigate the neural correlates of the identified differential effect of attention as a function of stimulus identity (own vs. other hands). In order to obtain an appropriate number of trials for experimental condition, the number of trials in this study was doubled as compared to the previous behavioural study. The behavioural results showed that attention influenced task performance for both own and other hand stimuli, which contrasts with the outcome of our third study. This result suggested that an extensive practice with other hands was able to induce a progressive development of the attentional effect for these stimuli. However, the ERP analyses uncovered an attentional dissociation as a function of identity: the P1 and the N170 were modulated by attention *exclusively* for own hands, which elicited larger amplitudes for invalid as compared to valid trials.

The following section proposes a theoretical framework that enables us to explain our results and hypothesize about the processes that might be taking place when we ask participants to focus their attention on the category or the idiosyncratic identity of an upcoming stimulus.

2. The link between expectations and visual representations

[...] *mental images arise when one anticipates perceiving an object or scene so strongly that a depictive representation of the stimulus is created in early visual cortex [...]*

(Kosslyn & Thompson, 2003)

Research on visual mental imagery has revealed that certain mental representations can be stored in an analogical or modality-specific fashion. The critical data that finally bear out the existence of *mental images* was the finding that an internal representation could activate the same visual areas that undertake the perceptual processing of the imagined object (e.g. Ishai et al., 2000; O'Craven & Kanwisher, 2000). Nevertheless, research on attentional expectations research (Bar, 2003; Chawla et al., 1999; Esterman & Yantis, 2009; Puri et al., 2009; Shulman et al., 1999; Summerfield et al., 2006) or working memory processes (Curtis & D'Esposito, 2003; Johnson et al., 2007; Postle et al., 2003; Ranganath & D'Esposito, 2005; Ranganath et al., 2004; Ruchkin et al., 2003) seem to offer valid evidence to achieve a similar set of conclusions. These different lines of research have been kept independent, despite they have probably been using different terms to describe equivalent mental states. The present discussion tries to highlight the link between visual imagery, working memory processes and attentional expectations.

Certain theories have proposed that top-down expectations can facilitate object recognition by limiting the number of *representations* that are currently active within the *visual cortex* during the perceptual processing of a stimulus (Bar, 2003). Several studies have supported these hypotheses by revealing that internal expectations indeed influence the activity of specific visual areas. For example, both maintaining a face expectation during a block of trials and mistaking a blurred stimulus for a face enhance the activation of the FFA (Summerfield et al., 2006; Summerfield et al., 2006). However, it is important to note that this type of expectations *modulates* the activity of

visual areas *during* stimulus perceptual processing. What would we observe as a result of expectations that are generated prior to the appearance of the target stimulus?

Research has shown that such expectations induce activity within the visual cortex *prior* to target presentation (Esterman & Yantis, 2009; Puri et al., 2009). Crucially, these studies revealed that attentional cues evoked increased activity in category-specific visual areas depending of the content of expectations: expecting a face enhances FFA activity, while expecting a house enhances parahippocampal gyrus activity. These findings suggest an equivalence between expecting a category and retrieving a mental image of a specific category (Ishai et al., 2000; O'Craven & Kanwisher, 2000).

Finally, recent fMRI investigations using a fine-grained pattern analysis (*Multi-Voxel Pattern Analysis*; see Norman et al., 2006) have revealed that generating an internal image (Stokes et al., 2009), maintaining a representation in working memory (Harrison & Tong, 2009) or expecting the appearance of a *specific stimulus* (Stokes et al., 2009), induce the selective activation of target-specific neural subpopulations within the visual cortex. The high-level specificity of this analysis allows the discrimination between different letters (X or O) or different oriented gratings (/// or \\\\) within a single neural population. This finding reveals a clear analogy between the perceptual processing of a stimulus and its internal visual representation.

Taking together, these results suggest that an attentional expectation, a mental image or the maintenance of a stimulus representation in WM might be related, under certain circumstances, to a common mental state. That is, the activation of a perceptual representation of a category or a particular item. Our results have revealed that both category and idiosyncratic expectations are able to modulate perceptual stages of stimulus processing. We hypothesize that expectations in our studies might be activating a perceptual representation of the upcoming stimulus given that expectations can induce activation within the visual cortex (Esterman & Yantis, 2009; Puri et al., 2009; Stokes et al., 2009) and that the “object of attention” seems to play a crucial role determining the stage that is modulated by attention (e.g. Cristescu & Nobre, 2008; Ruz & Nobre, 2008b). Although this hypothesis could only be tested by neuroimaging

techniques, we considered that our discourse is solidly grounded on empirical evidence. Therefore, we will allow ourselves to discuss the present data within the theoretical context of perceptual representations.

3. Orienting attention to perceptual object representations

Our first study revealed that category expectations were able to modulate perceptual stages of processing: the N170. Crucially, this evoked potential is considered a perceptual index of *categorical processing*. This result supports the hypothesis that attention primarily operates on those stages related to the attended representation of the stimulus (e.g. Cristescu & Nobre, 2008; Ruz & Nobre, 2008). In this particular case, the attended representation might comprise visual information at a medium level of specificity, which is able to distinguish between categories but not between different exemplars within a category. By contrast, idiosyncratic expectations revealed an attentional modulation in an earlier perceptual component: the P1. According to Kosslyn and Thompson (2003), the generation of a highly detailed mental image leads to the activation of the extrastriate visual cortex. The observation of an earlier attentional effect by idiosyncratic as compared to category expectations would support that deploying attention to a particular item activates a detailed perceptual representation of the specific stimulus.

On the other hand, it appears from our results that attention exerts an influence on stimulus visual processing in one or the opposite direction depending on the cued category or particular item. In the first study, faces revealed an inverted attentional modulation, as invalid trials elicited a more negative N170 than valid ones. In our view, attention might not be able to influence the N170 in valid trials due to a maximized optimization of face perceptual processing under situations of low perceptual or cognitive load (e.g. Carmel & Bentin, 2002; Cauquil et al., 2000; Lueschow et al., 2004). However, the unexpected appearance of a face might have captured exogenous attention, inducing a larger amplitude for invalid in contrast to valid trials. Study 2 and

4 showed a reversed attentional pattern for familiar stimuli (the familiar face and own hands) that could be explained in a similar way, as an effect of exogenous attention. However, one of our results seems to challenge this hypothesis. Although faces in study 1 do not show an optimization of perceptual processing in valid trials, the unfamiliar face in study 2 does benefit from the attentional orienting, revealing larger P1 and N170 amplitudes for valid as compared to invalid trials. This contradiction might be only apparent, as expecting a particular item rather than a general stimulus category probably increases the perceptual and/or cognitive demands of the experimental situation, which would lead to the emergence of an attentional modulation on perceptual stages of face processing (see Sreenivasan et al., 2009).

And last but not least, our results have revealed the existence of a differential effect of attention as a function of the familiarity (study 2) and identity (study 3 and 4) of the stimuli. The familiar and the unfamiliar faces showed an attentional modulation on perceptual stages of processing, which suggests that participants were able to retrieve a detailed mental representation of both faces (distinctive representations). However, the attentional effect emerged in opposite directions. In our view, this result would support the hypothesis that familiar and unfamiliar faces hold a different internal representation (c.f. Bruce & Young, 1986; Tong & Nakayama, 1999). Familiar faces may be represented in a more robust and stable way, leading to a maximal optimization of processing not susceptible of attentional modulation in perceptual stages on valid trials (inverted effect). By contrast, unfamiliar faces might be less robustly represented, which let them benefit from the attentional orienting from perceptual stages (classical effect).

In addition, stimulus' identity also seems to influence how endogenous attention modulates its visual processing. The results of our third and fourth studies suggest that participants hold a more distinctive representation of their own hands as compared to the hands of another person. Although this conclusion seems quite obvious, the effect cannot be merely explain by stimulus familiarity, as the unfamiliar face showed an attentional effect on behavioural measures from the first moment (study 3) and its visual processing was modulated by attention from perceptual stages (study 2). These findings

suggest that own hand representation differs from other hand representation in the degree of *distinctiveness*. In addition, although an increased practice allowed the emergence of an attentional effect for other hands on behavioural measures, its internal representation might still not be as distinctive as the own hands' representation, as attention did not influence its perceptual stages of processing (study 4). These results are in line with the hypothesis that own and other bodies hold different internal representations (c.f. Frassinetti et al., 2008; Myers & Sowden, 2008).

4. Final conclusions... A proposal for future research?

The present thesis aimed to advance the study of endogenous object-based attention. Our results revealed that expectations about an upcoming object were able to influence its perceptual stages of processing. Based on previous findings, we suggest that the *object of attention* determines the processing stages that are modulated by attention (e.g. Cristescu & Nobre, 2008; Ruz & Nobre, 2008). Therefore, our findings would support that the attended unit in our studies might be a *perceptual/analogic representation* of the expected stimulus (c.f. Esterman & Yantis, 2009; Puri et al., 2009; Stokes et al., 2009). In addition, our results revealed that as the *expectation referred to a more specific stimulus*, the attentional modulation was observed on *earlier stages* of visual processing (c.f. Kosslyn & Thompson, 2003). Finally, we identified a differential effect of endogenous attention as a function of stimulus *familiarity* and *identity*, which supports the hypothesis that familiar vs. unfamiliar stimuli, and own vs. other stimuli might hold *different internal representations* (e.g. Bruce & Young, 1986; Frassinetti et al., 2009; Frassinetti et al., 2008; Tong & Nakayama, 1999).

However, these findings bring about a panorama of multiple questions to answer. Do these expectations really activate a visual representation of the upcoming object? What would we observe if attention were focused on *non-bodily* stimuli? And what if those stimuli were familiar or self-owned? Is it possible to totally disentangle identity effects from familiarity effects? Between the numerous possibilities that could

emerge from the present project, we will highlight three possible pathways to follow in the future.

In the first place, we find interesting to directly compare the effects of endogenous attention focused on a familiar stimulus and a self-stimulus. Our results showed that the identity-differential effect emerges when own hands are compared to other hands. However, the attentional modulation of the P1 and N170 for own hands seems equivalent to the one observed for the familiar face. Therefore, a logical following study should contrast the effects of attention using the participant's own face and a highly familiar face. We would expect to find an inverted attentional effect for both stimuli and maybe, a larger attentional effect for own vs. the familiar face.

In the second place, we could carry out an experiment using the stimuli by Miyakoshi and colleagues (2007) to investigate the effect of orienting attention to different *non- bodily* objects: owned by the participant (e.g. her favourite cup), highly familiar to the participant (e.g. a disposal cup) or owned to another person (e.g. the favourite cup of a different participant). Based on our results, we might expect a classic attentional effect for other-owned objects and an inverted effect for familiar and self-owned objects, maybe the latter showing a larger effect in magnitude.

Finally, it would be highly desirable to adapt our design to fMRI in order to test whether expectations actually activate a perceptual representation of the expected stimulus within the visual cortex and whether those representations differ as a function of familiarity or identity. We would use the *Multi Voxel Pattern Analysis* technique to appropriately discriminate between idiosyncratic representations that might activate different patterns within a single neural population (see Norman et al., 2006; Stokes et al., 2009).

In light of these new ideas, it seems obvious that concluding a doctoral thesis does not necessarily involve finishing an experimental line of research. On the contrary, questions raise one from another...So, we trust that this thesis and its end point only signify a momentary breath, which precedes a promising beginning of new research projects.

Referencias - References

- Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998). An area within human ventral cortex sensitive to "building" stimuli: evidence and implications. *Neuron*, *21*(2), 373-383.
- Allison, McCarthy, Nobre, A., Puce, & Belger. (1994). Human extrastriate visual cortex and the perception of faces, words, numbers, and colors. *Cerebral Cortex (New York, N.Y.: 1991)*, *4*(5), 544-554.
- Andersen, S., Müller, & Hillyard, S. A. (2009). Color-selective attention need not be mediated by spatial attention. *Journal of Vision*, *9*(6), 2.1-7. doi:10.1167/9.6.2
- Anllo-Vento, & Hillyard, S. A. (1996). Selective Attention to the Color and Direction of Moving Stimuli: Electrophysiological Correlates of Hierarchical Feature Selection. *Perception and Psychophysics*, *58*(2), 191-206.
- Anllo-Vento, L., Luck, S. J., & Hillyard, S. A. (1998). Spatio-temporal dynamics of attention to color: evidence from human electrophysiology. *Human Brain Mapping*, *6*(4), 216-238.
- Aranda, C., Ruz, M., Tudela, P., & Sanabria, D., in press. Focusing on the bodily self: The influence of endogenous attention on visual body processing.
- Aranda, C., Sanabria, D., Tudela, P., & Ruz, M., in preparation. Equal but not the same: Electrophysiological evidence of a dissociable attentional modulation induced by face familiarity.
- Aranda, C., Tudela, P., Madrid, E., & Ruz, M., submitted. Category Expectations: A differential modulation of the N170 potential for faces and words.
- Baddeley, A. D., & Hitch, G. (1974). Working memory. En *The psychology of learning and motivation: Advances in research and theory* (Vol. 8, págs. 47-89). New York: Academic Press.
- Balas, B., Cox, D., & Conwell, E. (2007). The effect of real-world personal familiarity on the speed of face information processing. *PLoS One*, *2*(11), e1223. doi:10.1371/journal.pone.0001223
- Bar, M. (2003). A cortical mechanism for triggering top-down facilitation in visual object recognition. *Journal of Cognitive Neuroscience*, *15*(4), 600-609. doi:10.1162/089892903321662976
- Baron, A., & Journey, J. (1989). Age Differences in Manual Versus Vocal Reaction Times: Further Evidence. *The Journal of Gerontology*, *44*(5), 157-159.

- Barrett, S. E., Rugg, M. D., & Perrett, D. I. (1988). Event-related potentials and the matching of familiar and unfamiliar faces. *Neuropsychologia*, *26*(1), 105-117.
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, *22*(04). doi:10.1017/S0140525X99002149
- Begleiter, H., Porjesz, B., & Wang, W. (1995). Event-related brain potentials differentiate priming and recognition to familiar and unfamiliar faces. *Electroencephalography and Clinical Neurophysiology*, *94*(1), 41-49.
- Bentin, S., Allison, Puce, Perez, & McCarthy. (1996). Electrophysiological studies of face perception in humans. *J. Cognitive Neuroscience*, *8*(6), 551-565.
- Bentin, S., & Deouell, L. Y. .. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cognitive Neuropsychology*, *17*(1), 35. doi:10.1080/026432900380472
- Bentin, S., Kutas, & Hillyard, S. A. (1995). Semantic processing and memory for attended and unattended words in dichotic listening: behavioral and electrophysiological evidence. *Journal of Experimental Psychology. Human Perception and Performance*, *21*(1), 54-67.
- Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: time course and scalp distribution. *Journal of Cognitive Neuroscience*, *11*(3), 235-260.
- Berlad, I., & Pratt, H. (1995). P300 in response to the subject's own name. *Electroencephalography and Clinical Neurophysiology*, *96*(5), 472-474.
- Binder, J. R., & Mohr, J. P. (1992). The topography of callosal reading pathways: A case-control analysis. *Brain*, *115*(6), 1807.
- Blanke, O., & Arzy, S. (2005). The out-of-body experience: disturbed self-processing at the temporo-parietal junction. *The Neuroscientist: A Review Journal Bringing Neurobiology, Neurology and Psychiatry*, *11*(1), 16-24. doi:10.1177/1073858404270885
- Borkenau, P., Paelecke, M., & Yu, R. (2010). Personality and lexical decision times for evaluative words. *European Journal of Personality*, *24*(2), 123-136. doi:10.1002/per.747

- Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature*, *391*(6669), 756.
doi:10.1038/35784
- Brandeis, Lehmann, Michel, & Mingrone. (1995). Mapping event-related brain potential microstates to sentence endings. *Brain Topography*, *8*(2), 145-159.
- Brem, S., Lang-Dullenkopf, A., Maurer, U., Halder, P., Bucher, K., & Brandeis, D. (2005). Neurophysiological signs of rapidly emerging visual expertise for symbol strings. *Neuroreport*, *16*(1), 45-48.
- Broadbent, D. E. (1958). *Perception and communication*. Pergamon Press London.
- Bruce. (1982). Changing faces: visual and non-visual coding processes in face recognition. *British Journal of Psychology (London, England: 1953)*, *73*(Pt 1), 105-116.
- Bruce, Henderson, Z., Newman, C., & Burton, A. M. (2001). Matching identities of familiar and unfamiliar faces caught on CCTV images. *Journal of Experimental Psychology. Applied*, *7*(3), 207-218.
- Bruce, & Young, A. (1986). Understanding face recognition. *British Journal of Psychology (London, England: 1953)*, *77* (Pt 3), 305-327.
- Bruce, V., & Humphreys, G. W. (1994). Recognizing objects and faces. *Visual Cognition*, *1*(2), 141.
doi:10.1080/13506289408402299
- Bruck, M., Cavanagh, P., & Ceci, S. J. (1991). Fortysomething: recognizing faces at one's 25th reunion. *Memory & Cognition*, *19*(3), 221-228.
- Bruyer, Lafalize, A., & Distefano, M. (1991). Age decisions on familiar and unfamiliar faces. *Behavioural Processes*, *24*(1), 21-35. doi:10.1016/0376-6357(91)90084-D
- Bruyer, Leclere, S., & Quinet, P. (2004). Ethnic categorisation of faces is not independent of face identity. *Perception*, *33*(2), 169-179.
- Bush, Luu, & Posner. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, *4*(6), 215-222.
- Buttle, H., & Raymond, J. E. (2003). High familiarity enhances visual change detection for face stimuli. *Perception & Psychophysics*, *65*(8), 1296-1306.

- Caharel, S., Fiori, N., Bernard, C., Lalonde, R., & Rebaï, M. (2006). The effects of inversion and eye displacements of familiar and unknown faces on early and late-stage ERPs. *International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology*, 62(1), 141-151. doi:10.1016/j.ijpsycho.2006.03.002
- Caharel, S., Poiroux, S., Bernard, C., Thibaut, F., Lalonde, R., & Rebai, M. (2002). ERPs associated with familiarity and degree of familiarity during face recognition. *The International Journal of Neuroscience*, 112(12), 1499-1512.
- Callejas, A., Lupiáñez, J., & Tudela, P. (2004). The three attentional networks: on their independence and interactions. *Brain and Cognition*, 54(3), 225-227. doi:10.1016/j.bandc.2004.02.012
- Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or Doing? Influence of Visual and Motor Familiarity in Action Observation. *Current Biology*, 16(22), 2277. doi:10.1016/j.cub.2006.10.065
- Capitani, E., Laiacona, M., Mahon, B., & Caramazza, A. (2003). Why are the facts of semantic category-specific deficits? A critical review of the clinical evidence. *Cognitive Neuropsychology*, 20(3), 213. doi:10.1080/02643290244000266
- Carmel, & Bentin, S. (2002). Domain specificity versus expertise: factors influencing distinct processing of faces. *Cognition*, 83(1), 1-29.
- Cauquil, Edmonds, & Taylor. (2000). Is the face-sensitive N170 the only ERP not affected by selective attention? *Neuroreport*, 11(10), 2167-2171.
- Cave, & Pashler. (1995). Visual selection mediated by location: selecting successive visual objects. *Perception & Psychophysics*, 57(4), 421-432.
- Cave, K. R., & Bichot, N. P. (1999). Visuospatial attention: beyond a spotlight model. *Psychonomic Bulletin & Review*, 6(2), 204-223.
- Chao, Haxby, J. V., & Martin. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat Neurosci*, 2(10), 913-919. doi:10.1038/13217
- Chao, Martin, & Haxby, J. V. (1999). Are face-responsive regions selective only for faces? *Neuroreport*, 10(14), 2945-2950.

- Chawla, D., Rees, G., & Friston, K. J. (1999). The physiological basis of attentional modulation in extrastriate visual areas. *Nature Neuroscience*, *2*(7), 671-676. doi:10.1038/10230
- Chen, Kato, T., Zhu, X. H., Ogawa, S., Tank, D. W., & Ugurbil, K. (1998). Human primary visual cortex and lateral geniculate nucleus activation during visual imagery. *Neuroreport*, *9*(16), 3669-3674.
- Chica, A. B., & Lupiáñez, J. (2009). Effects of endogenous and exogenous attention on visual processing: An Inhibition of Return study. *Brain Research*, *1278*, 75-85. doi:10.1016/j.brainres.2009.04.011
- Ciaramitaro, V. M., Cameron, & Glimcher, P. W. (2001). Stimulus probability directs spatial attention: an enhancement of sensitivity in humans and monkeys. *Vision Research*, *41*(1), 57-75.
- Clark, V. P., & Hillyard, S. A. (1996). Spatial selective attention affects early extrastriate but not striate components of the visual evoked potential. *J. Cognitive Neuroscience*, *8*(5), 387-402.
- Clifton, R. K., Rochat, P., Litovsky, R. Y., & Perris, E. E. (1991). Object representation guides infants' reaching in the dark. *Journal of Experimental Psychology. Human Perception and Performance*, *17*(2), 323-329.
- Cohen, Dehaene, S., Naccache, L., Lehericy, S., Dehaene-Lambertz, G., Henaff, M., & Michel, F. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain*, *123*(2), 291-307. doi:10.1093/brain/123.2.291
- Coles, M., Smid, H., Scheffers, M., & Otten, L. (1995). Mental chronometry and the study of human information processing. En M. D. Rugg & M. Coles (Eds.), *Electrophysiology of mind: event-related brain potentials and cognition*. New York: Oxford University Press.
- Cooper, L., & Shepard, R. N. (1973). Chronometric studies of the rotation of mental images. En *Visual information processing*. London: Academic Press.
- Corbetta, M., Patel, G., & Shulman, G. L. (2008). The Reorienting System of the Human Brain: From Environment to Theory of Mind. *Neuron*, *58*(3), 306-324. doi:10.1016/j.neuron.2008.04.017
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews. Neuroscience*, *3*(3), 201-215. doi:10.1038/nrn755
- Correa, Á., Lupiáñez, J., Madrid, E., & Tudela, P. (2006). Temporal attention enhances early visual

- processing: A review and new evidence from event-related potentials. *Brain Research*, 1076(1), 116-128. doi:10.1016/j.brainres.2005.11.074
- Correa, Á., Sanabria, D., Spence, C., Tudela, P., & Lupiáñez, J. (2006). Selective temporal attention enhances the temporal resolution of visual perception: Evidence from a temporal order judgment task. *Brain Research*, 1070(1), 202-205. doi:10.1016/j.brainres.2005.11.094
- Coull, J. T., Frith, C. D., Frackowiak, R. S., & Grasby, P. M. (1996). A fronto-parietal network for rapid visual information processing: a PET study of sustained attention and working memory. *Neuropsychologia*, 34(11), 1085-1095.
- Craik, Moroz, T. M., Moscovitch, M., Stuss, D. T., Winocur, G., Tulving, E., & Kapur, S. (1999). In Search of the Self: A Positron Emission Tomography Study. *Psychological Science*, 10, 26-34. doi:10.1111/1467-9280.00102
- Crist, R. E., Wu, C., Karp, C., & Woldorff, M. G. (2008). Face Processing is Gated by Visual Spatial Attention. *Frontiers in Human Neuroscience*, 1. doi:10.3389/neuro.09.010.2007
- Cristescu, & Nobre, A. (2008). Differential modulation of word recognition by semantic and spatial orienting of attention. *J. Cognitive Neuroscience*, 20(5), 787-801.
- Cunningham, S. J., Turk, D. J., Macdonald, L. M., & Macrae, C. N. (2008). Yours or mine? Ownership and memory. *Consciousness and Cognition*, 17(1), 312-318. doi:10.1016/j.concog.2007.04.003
- Curtis, C. E., & D'Esposito, M. (2003). Persistent activity in the prefrontal cortex during working memory. *Trends in Cognitive Sciences*, 7(9), 415-423. doi:10.1016/S1364-6613(03)00197-9
- D'Esposito, M., Detre, J. A., Aguirre, G. K., Stallcup, M., Alsop, D. C., Tippet, L. J., & Farah, M. J. (1997). A functional MRI study of mental image generation. *Neuropsychologia*, 35(5), 725-730.
- Damasio, Damasio, & Van Hoesen. (1982). Prosopagnosia: Anatomic basis and behavioral mechanisms. *Neurology*, 32(4), 331.
- Damasio, A. (2003). Feelings of emotion and the self. *Ann NY Acad Sci*, 1001, 253-261.
- Damasio, A. R. (1999). *The feeling of what happens: Body and emotion in the making of consciousness*. Mariner Books.
- Daprati, & Sirigu, A. (2002). Laterality effects on motor awareness. *Neuropsychologia*, 40(8), 1379-

1386.

- Daprati, E., Wriessnegger, S., & Lacquaniti, F. (2007a). Kinematic cues and recognition of self-generated actions. *Experimental Brain Research*, *177*(1), 31-44. doi:10.1007/s00221-006-0646-9
- Daprati, E., Wriessnegger, S., & Lacquaniti, F. (2007b). Knowledge of one's kinematics improves perceptual discrimination. *Consciousness and Cognition*, *16*(1), 178-188. doi:10.1016/j.concog.2006.03.001
- Davies, & Milne. (1982). Recognizing faces in and out of context. *Current Psychology*, *2*(4), 235-246. doi:10.1007/BF02684516
- Dehaene, S., Le Clec'H, G., Poline, J., Le Bihan, D., & Cohen. (2002). The visual word form area: a prelexical representation of visual words in the fusiform gyrus. *Neuroreport*, *13*(3), 321-325.
- Della Sala, S., Marchetti, C., & Spinnler, H. (1991). Right-sided anarchic (alien) hand: a longitudinal study. *Neuropsychologia*, *29*(11), 1113-1127.
- Dering, B., Martin, C. D., & Thierry, G. (2009). Is the N170 peak of visual event-related brain potentials car-selective? *Neuroreport*, *20*(10), 902-906. doi:10.1097/WNR.0b013e328327201d
- Deutsch, & Deutsch. (1963). Some theoretical considerations. *Psychological Review*, *70*, 80-90.
- Dien, J. (1998). Issues in the application of the average reference: Review, critiques, and recommendations. *Behavior research methods, instruments & computers*, *30*(1), 34-43. doi:10.1033/10634269800007512347.0030
- Doallo, S., Lorenzo-López, L., Vizoso, C., Rodríguez Holguín, S., Amenedo, E., Bará, S., & Cadaveira, F. (2005). Modulations of the visual N1 component of event-related potentials by central and peripheral cueing. *Clinical Neurophysiology*, *116*(4), 807-820. doi:10.1016/j.clinph.2004.11.013
- Donchin, E. (1981). Surprise!...Surprise? *Psychophysiology*, *18*(5), 493-513. doi:10.1111/j.1469-8986.1981.tb01815.x
- Doose, G., & Feyereisen, P. (2001). Task Specificity in Age-Related Slowing Word Production Versus Conceptual Comparison. *The Journal of Gerontology*, *56*(2), 85-87. doi:10.1093/geronb/56.2.P85
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A Cortical Area Selective for Visual

- Processing of the Human Body. *Science*, 293(5539), 2470-2473. doi:10.1126/science.1063414
- Ducommun, C. Y., Murray, M. M., Thut, G., Bellmann, A., Viaud-Delmon, I., Clarke, S., & Michel, C. M. (2002). Segregated processing of auditory motion and auditory location: an ERP mapping study. *NeuroImage*, 16(1), 76-88. doi:10.1006/nimg.2002.1062
- Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General*, 113(4), 501-517.
- Eger, E., Schweinberger, S. R., Dolan, R. J., & Henson, R. N. (2005). Familiarity enhances invariance of face representations in human ventral visual cortex: fMRI evidence. *NeuroImage*, 26(4), 1128-1139. doi:10.1016/j.neuroimage.2005.03.010
- Egley, R., Driver, J., & Rafal, R. D. (1994). Shifting visual attention between objects and locations: evidence from normal and parietal lesion subjects. *Journal of Experimental Psychology: General*, 123(2), 161-177.
- Eimer, M. (1993). Spatial cueing, sensory gating and selective response preparation: an ERP study on visuo-spatial orienting. *Electroencephalography and Clinical Neurophysiology*, 88(5), 408-420.
- Eimer, M. (1994a). An ERP study on visual spatial priming with peripheral onsets. *Psychophysiology*, 31(2), 154-163. doi:10.1111/j.1469-8986.1994.tb01035.x
- Eimer, M. (1994b). "Sensory gating" as a mechanism for visuospatial orienting: electrophysiological evidence from trial-by-trial cuing experiments. *Perception & Psychophysics*, 55(6), 667-675.
- Eimer, M. (1997). An event-related potential (ERP) study of transient and sustained visual attention to color and form. *Biological Psychology*, 44(3), 143-160.
- Eimer, M. (2000a). Attentional Modulations of Event-Related Brain potentials sensitive to Faces. *Cognitive Neuropsychology*, 17(1), 103. doi:10.1080/026432900380517
- Eimer, M. (2000b). Effects of face inversion on the structural encoding and recognition of faces. Evidence from event-related brain potentials. *Brain Research. Cognitive Brain Research*, 10(1-2), 145-158.
- Eimer, M. (2000c). Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology: Official Journal of the International*

- Federation of Clinical Neurophysiology*, 111(4), 694-705.
- Eimer, M. (2000d). An ERP study of sustained spatial attention to stimulus eccentricity. *Biological Psychology*, 52(3), 205-220. doi:10.1016/S0301-0511(00)00028-4
- Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature*, 392(6676), 598-601. doi:10.1038/33402
- Eriksen, & Eriksen. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & Psychophysics*, 16(1), 143-149.
- Eriksen, & Hoffman. (1972). Temporal and spatial characteristics of selective encoding from visual displays. *Perception & Psychophysics*, 12, 201-204.
- Eriksen, C. W., & St James, J. D. (1986). Visual attention within and around the field of focal attention: a zoom lens model. *Perception & Psychophysics*, 40(4), 225-240.
- Esterman, M., & Yantis, S. (2009). Perceptual Expectation Evokes Category-Selective Cortical Activity. *Cereb. Cortex*, bhp188. doi:10.1093/cercor/bhp188
- Fan, McCandliss, B. D., Sommer, T., Raz, A., & Posner, M. I. (2002). Testing the efficiency and independence of attentional networks. *Journal of Cognitive Neuroscience*, 14(3), 340-347. doi:10.1162/089892902317361886
- Fan, McCandliss, B. D., Fossella, J., Flombaum, J. I., & Posner, M. I. (2005). The activation of attentional networks. *NeuroImage*, 26(2), 471-479. doi:10.1016/j.neuroimage.2005.02.004
- Farah, M. J. (1984). The neurological basis of mental imagery: a componential analysis. *Cognition*, 18(1-3), 245-272.
- Farah, M. J. (1995). *Visual Agnosia: Disorders of Object Recognition and What They Tell Us About Normal Vision* (New edition.). MIT Press.
- Faulkner, T. F., Rhodes, G., Palermo, R., Pellicano, E., & Ferguson, D. (2002). Recognizing the un-real McCoy: priming and the modularity of face recognition. *Psychonomic Bulletin & Review*, 9(2), 327-334.
- Fischler, I., Jin, Y. S., Boaz, T. L., Perry, N. W., & Childers, D. G. (1987). Brain potentials related to seeing one's own name. *Brain and Language*, 30(2), 245-262.

- Fodor, J. A. (1983). *The modularity of mind*. MIT Press.
- Frassinetti, Maini, M., Benassi, M., Avanzi, S., Cantagallo, A., & Farnè, A. (2009). Selective impairment of self body-parts processing in right brain-damaged patients. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*. doi:10.1016/j.cortex.2009.03.015
- Frassinetti, Maini, M., Romualdi, S., Galante, E., & Avanzi, S. (2008). Is it Mine? Hemispheric Asymmetries in Corporeal Self-recognition. *Journal of Cognitive Neuroscience*, 20(8), 1507-1516. doi:10.1162/jocn.2008.20067
- Frassinetti, Pavani, F., Zamagni, E., Fusaroli, G., Vescovi, M., Benassi, M., Avanzi, S., et al. (2009). Visual processing of moving and static self body-parts. *Neuropsychologia*, 47(8-9), 1988-1993. doi:10.1016/j.neuropsychologia.2009.03.012
- Frith, C. D. (1987). The positive and negative symptoms of schizophrenia reflect impairments in the perception and initiation of action. *Psychological Medicine*, 17(3), 631-648.
- Fu, S., Fan, Chen, & Zhuo, Y. (2001). The attentional effects of peripheral cueing as revealed by two event-related potential studies. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, 112(1), 172-185.
- Funes, M. J., Lupiáñez, J., & Milliken, B. (2007). Separate mechanisms recruited by exogenous and endogenous spatial cues: evidence from a spatial Stroop paradigm. *Journal of Experimental Psychology. Human Perception and Performance*, 33(2), 348-362. doi:10.1037/0096-1523.33.2.348
- Gallagher. (2000). Philosophical conceptions of the self: implications for cognitive science. *Trends in Cognitive Sciences*, 4(1), 14-21.
- Gauthier, I., Behrmann, M., & Tarr, M. J. (2004). Are Greebles like faces? Using the neuropsychological exception to test the rule. *Neuropsychologia*, 42(14), 1961-1970. doi:10.1016/j.neuropsychologia.2004.04.025
- Gauthier, I., & Tarr, M. J. (1997). Becoming a "Greeble" expert: exploring mechanisms for face recognition. *Vision Research*, 37(12), 1673-1682.
- Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005). Top-down

- enhancement and suppression of the magnitude and speed of neural activity. *Journal of Cognitive Neuroscience*, 17(3), 507-517. doi:10.1162/0898929053279522
- Gerlach, C. (2009). Category-specificity in visual object recognition. *Cognition*, 111(3), 281-301. doi:10.1016/j.cognition.2009.02.005
- Gilboa, A. (2004). Autobiographical and episodic memory--one and the same? Evidence from prefrontal activation in neuroimaging studies. *Neuropsychologia*, 42(10), 1336-1349. doi:10.1016/j.neuropsychologia.2004.02.014
- Gillihan, S. J., & Farah, M. J. (2005). Is Self Special? A Critical Review of Evidence From Experimental Psychology and Cognitive Neuroscience. *Psychological Bulletin*, 131(1), 76-97.
- Gómez, C. M., Clark, V. P., Fan, Luck, S. J., & Hillyard, S. A. (1994). Sources of attention-sensitive visual event-related potentials. *Brain Topography*, 7(1), 41-51.
- Graham, K. S., Lee, A. C. H., Brett, M., & Patterson, K. (2003). The neural basis of autobiographical and semantic memory: new evidence from three PET studies. *Cognitive, Affective & Behavioral Neuroscience*, 3(3), 234-254.
- Gray, H. M., Ambady, N., Lowenthal, W. T., & Deldin, P. (2004). P300 as an index of attention to self-relevant stimuli. *Journal of Experimental Social Psychology*, 40(2), 216-224. doi:10.1016/S0022-1031(03)00092-1
- Griffin, Miniussi, & Nobre, A. (2001). Orienting attention in time. *Frontiers in Bioscience: A Journal and Virtual Library*, 6, D660-671.
- Griffin, Miniussi, & Nobre, A. (2002). Multiple mechanisms of selective attention: differential modulation of stimulus processing by attention to space or time. *Neuropsychologia*, 40(13), 2325-2340.
- Hancock, P. J. B., Bruce, V., & Burton, A. M. (2000). Recognition of unfamiliar faces. *Trends in Cognitive Sciences*, 4(9), 330-337. doi:10.1016/S1364-6613(00)01519-9
- Handy, T. C. (2010). The object of my attention: An ERP study of self-relevant information processing. *Oral presentation in SEPEX (Granada); unpublished data.*
- Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early

- visual areas. *Nature*, 458(7238), 632-635. doi:10.1038/nature07832
- Harter, M. R., & Aine, C. J. (1984). Brain mechanisms of visual selective attention. *Varieties of attention*, 293-321.
- Haxby, J. V., Horwitz, B., Ungerleider, L., Maisog, J., Pietrini, P., & Grady, C. (1994). The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. *J. Neurosci.*, 14(11), 6336-6353.
- Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*, 22(1), 189-199.
- Head, & Holmes. (1911). Sensory disturbances from cerebral lesions. *Brain*, 34, 102-254.
- Heinze, H., Luck, S. J., Mangun, G., & Hillyard, S. A. (1990). Visual event-related potentials index focused attention within bilateral stimulus arrays. I. Evidence for early selection. *Electroencephalography and Clinical Neurophysiology*, 75(6), 511-527. doi:10.1016/0013-4694(90)90138-A
- Heisz, J. J., Watter, S., & Shedden, J. M. (2006). Automatic face identity encoding at the N170. *Vision Research*, 46(28), 4604-4614. doi:10.1016/j.visres.2006.09.026
- Henson, Goshen-Gottstein, Y., Ganel, T., Otten, L., Quayle, A., & Rugg, M. D. (2003). Electrophysiological and Haemodynamic Correlates of Face Perception, Recognition and Priming. *Cereb. Cortex*, 13(7), 793-805. doi:10.1093/cercor/13.7.793
- Henson, R., Shallice, T., & Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science (New York, N.Y.)*, 287(5456), 1269-1272.
- Herrmann, M. J., Ehlis, A., Muehlberger, A., & Fallgatter, A. J. (2005). Source localization of early stages of face processing. *Brain Topography*, 18(2), 77-85. doi:10.1007/s10548-005-0277-7
- Hill, H., Schyns, P. G., & Akamatsu, S. (1997). Information and viewpoint dependence in face recognition. *Cognition*, 62(2), 201-222.
- Hillyard, S. A., & Anllo-Vento. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences of the United States of America*,

95(3), 781-787.

- Hochberg, J., & Galper, R. R. (1967). Recognition of faces: an explanatory study. *Psychological Science*, 9, 619-620.
- Hodzic, A., Am, Kaas, A., Muckli, L., Stirn, A., & Singer, W. (2009). Distinct cortical networks for the detection and identification of human body. *NeuroImage*, 45(4), 1264-1271. doi:10.1016/j.neuroimage.2009.01.027
- Hodzic, A., Muckli, L., Singer, W., & Stirn, A. (2009). Cortical responses to self and others. *Human Brain Mapping*, 30(3), 951-962. doi:10.1002/hbm.20558
- Holcomb, P. J. (1993). Semantic priming and stimulus degradation: implications for the role of the N400 in language processing. *Psychophysiology*, 30(1), 47-61.
- Holmes, Vuilleumier, P., & Eimer, M. (2003). The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials. *Brain Research. Cognitive Brain Research*, 16(2), 174-184.
- Hopf, J. M., & Mangun, G. (2000). Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, 111(7), 1241-1257.
- Hopfinger, J. B., & Ries, A. J. (2005). Automatic versus contingent mechanisms of sensory-driven neural biasing and reflexive attention. *Journal of Cognitive Neuroscience*, 17(8), 1341-1352. doi:10.1162/0898929055002445
- Hopfinger, J. B., & Mangun, G. (1998). Reflexive Attention Modulates Processing of Visual Stimuli in Human Extrastriate Cortex. *Psychological Science*, 9(6), 441-447.
- Hopfinger, J. B., & West, V. M. (2006). Interactions between endogenous and exogenous attention on cortical visual processing. *NeuroImage*, 31(2), 774-789. doi:10.1016/j.neuroimage.2005.12.049
- Hume, D. (1739). *A Treatise of Human Nature*. Oxford: Clarendon Press.
- Ishai, Ungerleider, Martin, Schouten, & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences of the United States of America*, 96(16), 9379-9384.

- Ishai, A., Ungerleider, L. G., & Haxby, J. V. (2000). Distributed neural systems for the generation of visual images. *Neuron*, *28*(3), 979-990.
- Itier, R. J., & Taylor, M. J. (2002). Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: a repetition study using ERPs. *NeuroImage*, *15*(2), 353-372. doi:10.1006/nimg.2001.0982
- Itier, R. J., Herdman, A. T., George, N., Cheyne, D., & Taylor, M. J. (2006). Inversion and contrast-reversal effects on face processing assessed by MEG. *Brain Research*, *1115*(1), 108-120. doi:10.1016/j.brainres.2006.07.072
- Itier, R. J., & Taylor, M. J. (2004). N170 or N1? Spatiotemporal Differences between Object and Face Processing Using ERPs. *Cereb. Cortex*, *14*(2), 132-142. doi:10.1093/cercor/bhg111
- Jackson, M. C., & Raymond, J. E. (2008). Familiarity enhances visual working memory for faces. *Journal of Experimental Psychology. Human Perception and Performance*, *34*(3), 556-568. doi:10.1037/0096-1523.34.3.556
- Jacques, & Rossion. (2007). Early electrophysiological responses to multiple face orientations correlate with individual discrimination performance in humans. *NeuroImage*, *36*(3), 863-876. doi:10.1016/j.neuroimage.2007.04.016
- James, W. (1890). *The Principles of Psychology* (Holt.). New York.
- Jemel, B., Pisani, M., Calabria, M., Crommelinck, M., & Bruyer, R. (2003). Is the N170 for faces cognitively penetrable? Evidence from repetition priming of Mooney faces of familiar and unfamiliar persons. *Brain Research. Cognitive Brain Research*, *17*(2), 431-446.
- Johnson, M. R., Mitchell, K. J., Raye, C. L., D'Esposito, M., & Johnson, M. K. (2007). A brief thought can modulate activity in extrastriate visual areas: Top-down effects of refreshing just-seen visual stimuli. *NeuroImage*, *37*(1), 290-299. doi:10.1016/j.neuroimage.2007.05.017
- Johnston, R. A., & Edmonds, A. J. (2009). Familiar and unfamiliar face recognition: a review. *Memory (Hove, England)*, *17*(5), 577-596. doi:10.1080/09658210902976969
- Jokisch, D., Daum, I., & Troje, N. F. (2006). Self recognition versus recognition of others by biological motion: Viewpoint-dependent effects. *Perception*, *35*, 911-920.

- Kahneman, D. (1973). *Attention and Effort*. Prentice Hall.
- Kanwisher, N., Driver, J., & Machado, L. (1995). Spatial repetition blindness is modulated by selective attention to color or shape. *Cognitive Psychology*, 29(3), 303-337. doi:10.1006/cogp.1995.1017
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The Fusiform Face Area: A Module in Human Extrastriate Cortex Specialized for Face Perception. *J. Neurosci.*, 17(11), 4302-4311.
- Kasten, R., & Navon, D. (2008). Is location cueing inherently superior to color cueing? Not if color is presented early enough. *Acta Psychologica*, 127(1), 89-102. doi:10.1016/j.actpsy.2007.02.002
- Kaufmann, J. M., & Schweinberger. (2008). Distortions in the brain? ERP effects of caricaturing familiar and unfamiliar faces. *Brain Research*, 1228, 177-188. doi:10.1016/j.brainres.2008.06.092
- Kelley, W. M., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., & Heatherton, T. F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience*, 14(5), 785-794. doi:10.1162/08989290260138672
- Kim, & Cave. (1995). Spatial Attention in Visual Search for Features and Feature Conjunctions. *Psychological Science*, 6(6), 376-380.
- Kircher, T. T. J., Senior, C., Phillips, M. L., Benson, P. J., Bullmore, E. T., Brammer, M., Simmons, A., et al. (2000). Towards a functional neuroanatomy of self processing: effects of faces and words. *Cognitive Brain Research*, 10(1-2), 133-144. doi:10.1016/S0926-6410(00)00036-7
- Klein. (2004). On the control of visual orienting. En M. I. Posner (Ed.), *Cognitive Neuroscience of Attention* (págs. 29-44). New York: Guildford Press.
- Klein, Paradis, A. L., Poline, Kosslyn, S. M., & Le Bihan, D. (2000). Transient activity in the human calcarine cortex during visual-mental imagery: an event-related fMRI study. *Journal of Cognitive Neuroscience*, 12 Suppl 2, 15-23. doi:10.1162/089892900564037
- Klein, & Shore, D. I. (2000). Relations among modes of visual orienting. En S. Monsell & J. Driver (Eds.), *Attention and Performance XVIII: Control of cognitive processes*. Cambridge, MA: MIT Press.
- Knoblich, G., & Flach, R. (2003). Action identity: Evidence from self-recognition, prediction, and coordination. *Consciousness and Cognition*, 12(4), 620-632. doi:10.1016/S1053-

8100(03)00070-9

- Kosslyn, S. M. (1975). Information representation in visual images. *Cognitive Psychology*, 7(3), 341–370.
- Kosslyn, S. M., & Alper, S. N. (1977). On the pictorial properties of visual images: effects of image size on memory for words. *Canadian Journal of Psychology*, 31(1), 32-40.
- Kosslyn, S. M., Cave, Provost, D. A., & Von Gierke, S. M. (1988). Sequential processes in image generation. *Cognitive Psychology*, 20(3), 319-343.
- Kosslyn, S. M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J. P., Thompson, W. L., Ganis, G., et al. (1999). The role of area 17 in visual imagery: convergent evidence from PET and rTMS. *Science (New York, N.Y.)*, 284(5411), 167-170.
- Kosslyn, S. M., & Thompson, W. L. (2003). When is early visual cortex activated during visual mental imagery? *Psychological Bulletin*, 129(5), 723-746. doi:10.1037/0033-2909.129.5.723
- Kosslyn, S. M., Thompson, W. L., Kim, I. J., & Alpert, N. M. (1995). Topographical representations of mental images in primary visual cortex. *Nature*, 378(6556), 496-498. doi:10.1038/378496a0
- Kramer, A. F., & Jacobson, A. (1991). Perceptual organization and focused attention: the role of objects and proximity in visual processing. *Perception & Psychophysics*, 50(3), 267-284.
- Kramer, A. F., & Strayer, D. L. (1988). Assessing the development of automatic processing: an application of dual-task and event-related brain potential methodologies. *Biological Psychology*, 26(1-3), 231-267.
- Kramer, A. F., Strayer, D. L., & Buckley, J. (1991). Task versus component consistency in the development of automatic processing: a psychophysiological assessment. *Psychophysiology*, 28(4), 425-437.
- Krauzlis, R. J., & Adler, S. A. (2001). Effects of Directional Expectations on Motion Perception and Pursuit Eye Movements. *Visual Neuroscience*, 18(03), 365-376. doi:10.1017/S0952523801183033
- Lauwereyns, J. (1998). Exogenous/Endogenous Control of Space-based/ Object-based Attention: Four Types of Visual Selection? *European Journal of Cognitive Psychology*, 10(1), 41.

doi:10.1080/713752264

- Lavie, N., Ro, T., & Russell, C. (2003). The role of perceptual load in processing distractor faces. *Psychological Science: A Journal of the American Psychological Society / APS*, *14*(5), 510-515.
- Le Bihan, D., Turner, R., Zeffiro, T. A., Cuénod, C. A., Jezzard, P., & Bonnerot, V. (1993). Activation of human primary visual cortex during visual recall: a magnetic resonance imaging study. *Proceedings of the National Academy of Sciences of the United States of America*, *90*(24), 11802-11805.
- Le Grand, R., Mondloch, C. J., Maurer, & Brent, H. P. (2003). Expert face processing requires visual input to the right hemisphere during infancy. *Nature Neuroscience*, *6*(10), 1108-1112. doi:10.1038/nn1121
- Lehmann, D., & Skrandies, W. (1980). Reference-free identification of components of checkerboard-evoked multichannel potential fields. *Electroencephalography and Clinical Neurophysiology*, *48*(6), 609-621.
- Lepsien, J., & Nobre, A. (2007). Attentional Modulation of Object Representations in Working Memory. *Cereb. Cortex*, *17*(9), 2072-2083. doi:10.1093/cercor/bhl116
- Liu, J., Harris, A., & Kanwisher, N. (2002). Stages of processing in face perception: an MEG study. *Nature Neuroscience*, *5*(9), 910-916. doi:10.1038/nn909
- Loula, F., Prasad, S., Harber, K., & Shiffrar, M. (2005). Recognizing People from Their Movement. *Journal of Experimental Psychology Human Perception and Performance*, *31*(1), 210-220.
- Lu, Z. L., & Doshier, B. A. (2005). The Perceptual Template Model (PTM) approach. En L. Itti, G. Rees, & J. K. Tsotsos (Eds.), *Neurobiology of Attention*. Amsterdam: Elsevier Academic Press.
- Luck, S. J. (1995). Multiple mechanisms of visual-spatial attention: recent evidence from human electrophysiology. *Behavioural Brain Research*, *71*(1-2), 113-123. doi:10.1016/0166-4328(95)00041-0
- Luck, S. J., Hillyard, S. A., Mouloua, M., Woldorff, M. G., Clark, V. P., & Hawkins, H. L. (1994). Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology. Human Perception and*

- Performance*, 20(4), 887-904.
- Luck, S. J., Woodman, & Vogel. (2000). Event-related potential studies of attention. *Trends in Cognitive Sciences*, 4(11), 432-440.
- Lueschow, A., Sander, T., Boehm, S. G., Nolte, G., Trahms, L., & Curio, G. (2004). Looking for faces: Attention modulates early occipitotemporal object processing. *Psychophysiology*, 41(3), 350-360. doi:10.1111/j.1469-8986.2004.00159.x
- MacDonald, A. W., Cohen, J. D., Stenger, V. A., & Carter, C. S. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science (New York, N.Y.)*, 288(5472), 1835-1838.
- Mahon, B., & Caramazza, A. (2009). Concepts and categories: a cognitive neuropsychological perspective. *Annual Review of Psychology*, 60, 27-51. doi:10.1146/annurev.psych.60.110707.163532
- Mangun, G. (1995). Neural mechanisms of visual selective attention. *Psychophysiology*, 32(1), 4-18. doi:10.1111/j.1469-8986.1995.tb03400.x
- Mangun, G., Hansen, & Hillyard, S. A. (1987). The spatial orienting of attention: Sensory facilitation or response bias? En R. Johnson, J. W. Rohrbaugh, & R. Parasuraman (Eds.), *Current trends in event-related potential research* (págs. 118-124). Amsterdam: Elsevier.
- Mangun, G., Hillyard, S. A., & Luck, S. J. (1993). Electrocortical substrates of visual selective attention. En *Attention and performance XIV (silver jubilee volume): synergies in experimental psychology, artificial intelligence, and cognitive neuroscience* (págs. 219-243). MIT Press. Recuperado a partir de <http://portal.acm.org/citation.cfm?id=165866>
- Marrocco, R., & Davidson, M. (1998). Neurochemistry of attention. En *The Attentive Brain* (Parasuraman, R., págs. 35-50). Cambridge: MIT Press.
- Martínez, A., DiRusso, F., Anllo-Vento, L., Sereno, M. I., Buxton, R. B., & Hillyard, S. A. (2001). Putting spatial attention on the map: timing and localization of stimulus selection processes in striate and extrastriate visual areas. *Vision Research*, 41(10-11), 1437-1457.
- Maurer, U., Brandeis, D., & McCandliss, B. D. (2005). Fast, visual specialization for reading in English

- revealed by the topography of the N170 ERP response. *Behavioral and brain functions : BBF*, 1, 13-13. doi:10.1186/1744-9081-1-13
- McCandliss, B. D., Cohen, & Dehaene, S. (2003). The visual word form area: expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences*, 7(7), 293-299.
- McCarthy, & Nobre, A. (1993). Modulation of semantic processing by spatial selective attention. *Electroencephalography and Clinical Neurophysiology*, 88(3), 210-219.
- McCarthy, Puce, Gore, & Allison. (1997). Face-specific processing in the human fusiform gyrus. *J. Cognitive Neuroscience*, 9(5), 605-610.
- Mellet, E., Tzourio, N., Denis, M., & Mazoyer, B. (1998). Cortical anatomy of mental imagery of concrete nouns based on their dictionary definition. *Neuroreport*, 9(5), 803-808.
- Mellet, E., Tzourio-Mazoyer, N., Bricogne, S., Mazoyer, B., Kosslyn, S. M., & Denis, M. (2000). Functional anatomy of high-resolution visual mental imagery. *Journal of Cognitive Neuroscience*, 12(1), 98-109.
- Metzler, J., & Shepard, R. N. (1974). Transformational studies of the internal representations of three-dimensional objects. En *Theories incognitive Psychology: The Loyola Symposium*. Hillsdale, NJ: LawrenceErlbaum Associates.
- Miniussi, C., Wilding, E. L., Coull, & Nobre, A. (1999). Orienting attention in time: Modulation of brain potentials. *Brain*, 122(8), 1507-1518. doi:10.1093/brain/122.8.1507
- Miyakoshi, M., Nomura, M., & Ohira, H. (2007). An ERP study on self-relevant object recognition. *Brain and Cognition*, 63(2), 182-189. doi:10.1016/j.bandc.2006.12.001
- Morgan, H. M., Klein, Boehm, S. G., Shapiro, K. L., & Linden, D. E. J. (2008). Working memory load for faces modulates P300, N170, and N250r. *Journal of Cognitive Neuroscience*, 20(6), 989-1002. doi:10.1162/jocn.2008.20072
- Morita, T., Kochiyama, T., Okada, T., Yonekura, Y., Matsumura, M., & Sadato, N. (2004). The neural substrates of conscious color perception demonstrated using fMRI. *NeuroImage*, 21(4), 1665-1673. doi:10.1016/j.neuroimage.2003.12.019
- Moro, V., Urgesi, C., Pernigo, S., Lanteri, P., Pazzaglia, M., & Aglioti, S. M. (2008). The neural basis of

- body form and body action agnosia. *Neuron*, 60(2), 235-246. doi:10.1016/j.neuron.2008.09.022
- Murray, M. M., Michel, C. M., Grave de Peralta, R., Ortigue, S., Brunet, D., Gonzalez Andino, S., & Schnider, A. (2004). Rapid discrimination of visual and multisensory memories revealed by electrical neuroimaging. *NeuroImage*, 21(1), 125-135.
- Murray, M. M., Wylie, G. R., Higgins, B. A., Javitt, D. C., Schroeder, C. E., & Foxe, J. J. (2002). The spatiotemporal dynamics of illusory contour processing: combined high-density electrical mapping, source analysis, and functional magnetic resonance imaging. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 22(12), 5055-5073.
- Müller, Andersen, S., Trujillo, N. J., Valdés-Sosa, P., Malinowski, P., & Hillyard, S. A. (2006). Feature-selective attention enhances color signals in early visual areas of the human brain. *Proceedings of the National Academy of Sciences*, 103(38), 14250-14254. doi:10.1073/pnas.0606668103
- Müller, & Rabbitt, P. M. (1989). Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *Journal of Experimental Psychology. Human Perception and Performance*, 15(2), 315-330.
- Myers, A., & Sowden, P. T. (2008). Your hand or mine? The extrastriate body area. *NeuroImage*, 42(4), 1669-1677. doi:10.1016/j.neuroimage.2008.05.045
- Navon, D. (1978). On a conceptual hierarchy of time, space, and other dimensions. *Cognition*, 6(3), 223-228. doi:10.1016/0010-0277(78)90014-8
- Näätänen, R., & Gaillard, A. (1983). The Orienting Reflex and the N2 Deflection of the Event-Related Potential (ERP). En *Tutorials in Event Related Potential Research: Endogenous Components* (Vol. 10, págs. 119-141). North-Holland. Recuperado a partir de <http://www.sciencedirect.com/science/article/B8G4W-4SC6YXF-8/2/bfd4e9cf7dc95f16230886db66863b52>
- Näätänen, R., & Picton, T. (1987). The N1 wave of the human electric and magnetic response to sound: a review and an analysis of the component structure. *Psychophysiology*, 24(4), 375-425.
- Nebes, R. (1978). Vocal Versus Manual Response As a Determinant of Age Difference in Simple Reaction Time. *The Journal of Gerontology*, 33(6), 884-889. doi:10.1093/geronj/33.6.884

- Neisser, U. (1967). *Cognitive Psychology* (1^o ed.). Prentice Hall.
- Neisser, U. (1988). Five kinds of self-knowledge. *Philosophical Psychology*, *1*(1), 35.
doi:10.1080/09515088808572924
- Neisser, U., & Becklen, R. (1975). Selective Looking: Attending to Visually Specified Events.
- Nobre, Allison, & McCarthy. (1994). Word recognition in the human inferior temporal lobe. *Nature*, *372*(6503), 260-263. doi:10.1038/372260a0
- Nobre, A. (2001). Orienting attention to instants in time. *Neuropsychologia*, *39*(12), 1317-1328.
doi:10.1016/S0028-3932(01)00120-8
- Nobre, A. (2004). Probing the flexibility of attentional orienting in the human brain. En *Cognitive Neuroscience of Attention* (M. Posner (Ed.)). Guildford Press.
- Nobre, A., Allison, & McCarthy. (1998). Modulation of human extrastriate visual processing by selective attention to colours and words. *Brain: A Journal of Neurology*, *121* (Pt 7), 1357-1368.
- Nobre, A., Rao, A., & Chelazzi, L. (2006). Selective attention to specific features within objects: behavioral and electrophysiological evidence. *Journal of Cognitive Neuroscience*, *18*(4), 539-561. doi:10.1162/jocn.2006.18.4.539
- Norman, Polyn, S. M., Detre, & Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, *10*(9), 424-430. doi:10.1016/j.tics.2006.07.005
- Norman, & Shallice. (1986). Attention to action: willed and automatic control of behaviour. En *Consciousness and self-regulation* (págs. 1-18). New York: Plenum press.
- Norman, D. A., & Bobrow, D. G. (1975). On Data-limited and Resource-limited Processes.
- Northoff, G., Heinzl, A., de Greck, M., Bermpohl, F., Dobrowolny, H., & Panksepp, J. (2006). Self-referential processing in our brain--a meta-analysis of imaging studies on the self. *NeuroImage*, *31*(1), 440-457. doi:10.1016/j.neuroimage.2005.12.002
- O'Craven, K. M., & Kanwisher, N. (2000). Mental Imagery of Faces and Places Activates Corresponding Stimulus-Specific Brain Regions. *J. Cognitive Neuroscience*, *12*(6), 1013-1023.
- O'Donnell, C., & Bruce. (2001). Familiarisation with faces selectively enhances sensitivity to changes made to the eyes. *Perception*, *30*(6), 755-764.

- Paillard, J. (1999). Body schema and body image: a double dissociation in deafferented patients. En *Motor control, today and tomorrow* (págs. 197-214). Sofia: Academic Publishing House.
- Paradis, Cornilleau-Peres, V., Droulez, J., Van de Moortele, P., Lobel, E., Berthoz, A., Le Bihan, D., et al. (2000). Visual Perception of Motion and 3-D Structure from Motion: an fMRI Study. *Cereb. Cortex*, *10*(8), 772-783. doi:10.1093/cercor/10.8.772
- Pascual-Marqui, R. D., Michel, & Lehmann, D. (1995). Segmentation of brain electrical activity into microstates: model estimation and validation. *IEEE Transactions on Bio-Medical Engineering*, *42*(7), 658-665. doi:10.1109/10.391164
- Perrin, Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, *72*(2), 184-187.
- Perrin, F., García-Larrea, L., Mauguière, F., & Bastuji, H. (1999). A differential brain response to the subject's own name persists during sleep. *Clinical Neurophysiology*, *110*(12), 2153-2164. doi:10.1016/S1388-2457(99)00177-7
- Piaget, J. (1929). *The child's conception of the world*. Routledge.
- Polk, T. A., & Farah, M. J. (2002). Functional MRI evidence for an abstract, not perceptual, word-form area. *Journal of Experimental Psychology. General*, *131*(1), 65-72.
- Posner. (1978). *Chronometric Explorations of Mind*. Oxford University Press, USA.
- Posner, & Cohen. (1984a). Components of visual orienting. En *Attention and performance X: control of language processes* (Bouma H, Bouwhuis D., págs. 531-556). London: Lawrence Erlbaum.
- Posner, & Cohen. (1984b). Components of visual orienting. En H. Bouma & D. Bouwhuis (Eds.), *Attention and Performance X* (págs. 531-556). London: Lawrence Erlbaum.
- Posner, & Dehaene. (1994). Attentional networks. *Trends in Neurosciences*, *17*(2), 75-79. doi:10.1016/0166-2236(94)90078-7
- Posner, & Petersen, S. E. (1990). The Attention System of the Human Brain. *Annual Review of Neuroscience*, *13*(1), 25-42. doi:10.1146/annurev.ne.13.030190.000325
- Posner, & Presti, D. E. (1987). Selective attention and cognitive control. *Trends in Neurosciences*, *10*(1), 13-17. doi:10.1016/0166-2236(87)90116-0

- Posner, M. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, 32(1), 3-25.
- Posner, M., Snyder, & Davidson. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, 109(2), 160–174.
- Postle, B. R., Druzgal, T. J., & D'Esposito, M. (2003). Seeking the neural substrates of visual working memory storage. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, 39(4-5), 927-946.
- Price, C. J., & Devlin, J. (2003). The myth of the visual word form area. *NeuroImage*, 19(3), 473-481.
- Puce, A., Allison, T., Gore, J. C., & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *J Neurophysiol*, 74(3), 1192-1199.
- Puri, A. M., & Wojciulik, E. (2008). Expectation both helps and hinders object perception. *Vision Research*, 48(4), 589-597. doi:10.1016/j.visres.2007.11.017
- Puri, A. M., Wojciulik, E., & Ranganath, C. (2009). Category expectation modulates baseline and stimulus-evoked activity in human inferotemporal cortex. *Brain Research*, 1301, 89-99. doi:10.1016/j.brainres.2009.08.085
- Pylyshyn, Z. W. (1973). What the Mind's Eye Tells the Mind's Brain: A Critique of Mental Imagery. *Psychological Bulletin*, 80, 1-25.
- Ranganath, & D'Esposito, M. (2005). Directing the mind's eye: prefrontal, inferior and medial temporal mechanisms for visual working memory. *Current Opinion in Neurobiology*, 15(2), 175-182. doi:10.1016/j.conb.2005.03.017
- Ranganath, DeGutis, J., & D'Esposito, M. (2004). Category-specific modulation of inferior temporal activity during working memory encoding and maintenance. *Brain Research. Cognitive Brain Research*, 20(1), 37-45. doi:10.1016/j.cogbrainres.2003.11.017
- Rayner, K., & Pollatsek, A. (1989). *The Psychology of Reading*. Englewood Clis. NJ: Prentice Hall.
- Reder, L. M., Nhouyvanisvong, A., Schunn, C. D., Ayers, M. S., Angstadt, P., & Hiraki, K. (2000). A mechanistic account of the mirror effect for word frequency: a computational model of remember-know judgments in a continuous recognition paradigm. *Journal of Experimental*

- Psychology. Learning, Memory, and Cognition*, 26(2), 294-320.
- Rhodes, Brake, S., & Atkinson, A. P. (1993). What's lost in inverted faces? *Cognition*, 47(1), 25-57.
- Richardson, A. (1969). *Mental Imagery*. London: Routledge & Kegan Paul.
- Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nat Neurosci*, 2(11), 1019-1025. doi:10.1038/14819
- Roland, P. E., & Gulyás, B. (1995). Visual memory, visual imagery, and visual recognition of large field patterns by the human brain: functional anatomy by positron emission tomography. *Cerebral Cortex (New York, N.Y.: 1991)*, 5(1), 79-93.
- Rossion. (2002). Is sex categorization from faces really parallel to face recognition? *Visual Cognition*, 9(8), 1003. doi:10.1080/13506280143000485
- Rossion, Gauthier, Tarr, Despland, Bruyer, Linotte, & Crommelinck. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. *Neuroreport*, 11(1), 69-74.
- Rossion, B., Delvenne, J. F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., & Guérit, J. M. (1999). Spatio-temporal localization of the face inversion effect: an event-related potentials study. *Biological Psychology*, 50(3), 173-189.
- Ruchkin, D. S., Grafman, J., Cameron, & Berndt, R. S. (2003). Working memory retention systems: a state of activated long-term memory. *The Behavioral and Brain Sciences*, 26(6), 709-728; discussion 728-777.
- Rugg, M. D., & Coles, M. (1995). *Electrophysiology of mind: event-related brain potentials and cognition*. Oxford University Press.
- Rushworth, M. F. S., Johansen-Berg, H., Göbel, S. M., & Devlin, J. (2003). The left parietal and premotor cortices: motor attention and selection. *NeuroImage*, 20 Suppl 1, S89-100.
- Ruz, & Nobre. (2008). Attention modulates initial stages of visual word processing. *Journal of Cognitive Neuroscience*, 20(9), 1727-1736. doi:10.1162/jocn.2008.20119
- Ruz, M., & Nobre, A. (2008a). Dissociable top-down anticipatory neural states for different linguistic

- dimensions. *Neuropsychologia*, 46(4), 1151-1160. doi:10.1016/j.neuropsychologia.2007.10.021
- Ruz, M., & Nobre, A. (2008b). Attention modulates initial stages of visual word processing. *Journal of Cognitive Neuroscience*, 20(9), 1727-1736. doi:10.1162/jocn.2008.20119
- Sagiv, N., & Bentin, S. (2001). Structural encoding of human and schematic faces: holistic and part-based processes. *Journal of Cognitive Neuroscience*, 13(7), 937-951. doi:10.1162/089892901753165854
- Sàenz, M., Buracas, G. T., & Boynton, G. M. (2003). Global feature-based attention for motion and color. *Vision Research*, 43(6), 629-637. doi:10.1016/S0042-6989(02)00595-3
- Scholl, B. (2001). Objects and attention: the state of the art. *Cognition*, 80(1-2), 46, 1.
- Schwoebel, J., & Coslett, H. B. (2005). Evidence for multiple, distinct representations of the human body. *Journal of Cognitive Neuroscience*, 17(4), 543-553. doi:10.1162/0898929053467587
- Serences, J. T., Ester, E. F., Vogel, E. K., & Awh, E. (2009). Stimulus-Specific Delay Activity in Human Primary Visual Cortex. *Psychological Science*, 20(2), 207-214. doi:10.1111/j.1467-9280.2009.02276.x
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science (New York, N.Y.)*, 171(972), 701-703.
- Shulman, G. L., Ollinger, J. M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Petersen, S. E., & Corbetta, M. (1999). Areas involved in encoding and applying directional expectations to moving objects. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 19(21), 9480-9496.
- Sirigu, A., Grafman, J., Bressler, K., & Sunderland, T. (1991). Multiple representations contribute to body knowledge processing. Evidence from a case of autotopagnosia. *Brain: A Journal of Neurology*, 114 (Pt 1B), 629-642.
- Sreenivasan, K. K., Goldstein, J. M., Lustig, A. G., Rivas, L. R., & Jha, A. P. (2009). Attention to faces modulates early face processing during low but not high face discriminability. *Attention, Perception & Psychophysics*, 71(4), 837-846. doi:10.3758/APP.71.4.837
- Sreenivasan, K. K., & Jha, A. P. (2007). Selective attention supports working memory maintenance by

- modulating perceptual processing of distractors. *Journal of Cognitive Neuroscience*, *19*(1), 32-41. doi:10.1162/jocn.2007.19.1.32
- Stokes, M., Thompson, W. L., Cusack, R., & Duncan, J. (2009). Top-down activation of shape-specific population codes in visual cortex during mental imagery. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *29*(5), 1565-1572. doi:10.1523/JNEUROSCI.4657-08.2009
- Stokes, M., Thompson, W. L., Nobre, A., & Duncan, J. (2009). Shape-specific preparatory activity mediates attention to targets in human visual cortex. *Proceedings of the National Academy of Sciences*, *106*(46), 19569-19574. doi:10.1073/pnas.0905306106
- Sugiura, Kawashima, R., Nakamura, K., Okada, K., Kato, T., Nakamura, A., Hatano, K., et al. (2000). Passive and active recognition of one's own face. *NeuroImage*, *11*(1), 36-48. doi:10.1006/nimg.1999.0519
- Sugiura, Sassa, Y., Jeong, H., Miura, N., Akitsuki, Y., Horie, K., Sato, S., et al. (2006). Multiple brain networks for visual self-recognition with different sensitivity for motion and body part. *NeuroImage*, *32*(4), 1905-1917. doi:10.1016/j.neuroimage.2006.05.026
- Sugiura, Watanabe, Maeda, Y., Matsue, Y., Fukuda, H., & Kawashima, R. (2005). Cortical mechanisms of visual self-recognition. *NeuroImage*, *24*(1), 143-149. doi:10.1016/j.neuroimage.2004.07.063
- Summerfield, C., Egnér, T., Greene, M., Koechlin, E., Mangels, J., & Hirsch, J. (2006). Predictive codes for forthcoming perception in the frontal cortex. *Science (New York, N.Y.)*, *314*(5803), 1311-1314. doi:10.1126/science.1132028
- Summerfield, C., Egnér, T., Mangels, J., & Hirsch, J. (2006). Mistaking a house for a face: neural correlates of misperception in healthy humans. *Cerebral Cortex (New York, N.Y.: 1991)*, *16*(4), 500-508. doi:10.1093/cercor/bhi129
- Tanaka, & Farah, M. J. (1993). Parts and wholes in face recognition. *The Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology*, *46*(2), 225-245.
- Tarkiainen, A., Helenius, P., Hansen, P. C., Cornelissen, P. L., & Salmelin, R. (1999). Dynamics of letter string perception in the human occipitotemporal cortex. *Brain: A Journal of Neurology*, *122* (Pt

- 11), 2119-2132.
- Taylor, M. J. (2002). Non-spatial attentional effects on P1. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, 113(12), 1903-1908.
- Taylor, M. J., Arsalidou, M., Bayless, S. J., Morris, D., Evans, J. W., & Barbeau, E. J. (2009). Neural correlates of personally familiar faces: parents, partner and own faces. *Human Brain Mapping*, 30(7), 2008-2020. doi:10.1002/hbm.20646
- Thierry, G., Martin, Downing, P., & Pegna, A. J. (2007). Controlling for interstimulus perceptual variance abolishes N170 face selectivity. *Nature Neuroscience*, 10(4), 505-511. doi:10.1038/nn1864
- Thompson, W. L., Kosslyn, S. M., Suckel, K. E., & Alpert, N. M. (2001). Mental imagery of high- and low-resolution gratings activates area 17. *NeuroImage*, 14(2), 454-464. doi:10.1006/nimg.2001.0803
- Tong, & Nakayama, K. (1999). Robust representations for faces: evidence from visual search. *Journal of Experimental Psychology. Human Perception and Performance*, 25(4), 1016-1035.
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12(1), 97-136.
- Troje, N. F., & Kersten, D. (1999). Viewpoint-dependent recognition of familiar faces. *Perception*, 28(4), 483-487.
- Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology. Human Perception and Performance*, 31(1), 80-91. doi:10.1037/0096-1523.31.1.80
- Tsakiris, M., Schütz-Bosbach, S., & Gallagher, S. (2007). On agency and body-ownership: Phenomenological and neurocognitive reflections. *Consciousness and Cognition*, 16(3), 645-660. doi:10.1016/j.concog.2007.05.012
- Tsal, Y., & Lavie, N. (1988). Attending to color and shape: the special role of location in selective visual processing. *Perception & Psychophysics*, 44(1), 15-21.
- Tsal, Y., & Lavie, N. (1993). Location dominance in attending to color and shape. *Journal of*

- Experimental Psychology. Human Perception and Performance*, 19(1), 131-139.
- Tucker, D. M., Liotti, M., Potts, G. F., Russell, G. S., & Posner, M. I. (1994). Spatiotemporal analysis of brain electrical fields. *Human Brain Mapping*, 1(2), 134-152. doi:10.1002/hbm.460010206
- Tudela, P. (1992). Atención. En *Atención y Percepción*. Madrid: Alhambra Ed.
- Valdes-Sosa, M., Bobes, M. A., Rodriguez, V., & Pinilla, T. (1998). Switching attention without shifting the spotlight object-based attentional modulation of brain potentials. *Journal of Cognitive Neuroscience*, 10(1), 137-151.
- Vierck, E., & Miller, J. (2008). Electrophysiological correlates of direct selection by color. *Psychophysiology*, 45(4), 621-631. doi:10.1111/j.1469-8986.2008.00650.x
- Vizioli, L., Foreman, K., Rousselet, G. A., & Caldara, R. (2010). Inverting faces elicits sensitivity to race on the N170 component: A cross-cultural study. *Journal of Vision*, 10(1). doi:10.1167/10.1.15
- Vossel, S., Weidner, R., Thiel, C. M., & Fink, G. R. (2009). What is "odd" in Posner's location-cueing paradigm? Neural responses to unexpected location and feature changes compared. *Journal of Cognitive Neuroscience*, 21(1), 30-41. doi:10.1162/jocn.2009.21003
- Warrington, E. K., & Shallice, T. (1980). Word-form dyslexia. *Brain: A Journal of Neurology*, 103(1), 99-112.
- Watanabe, S., Kakigi, R., Koyama, S., & Kirino, E. (1999). Human face perception traced by magneto- and electro-encephalography. *Cognitive Brain Research*, 8(2), 125-142. doi:10.1016/S0926-6410(99)00013-0
- Watter, Geffen, & Geffen. (2001). The n-back as a dual-task: P300 morphology under divided attention. *Psychophysiology*, 38(6), 998-1003.
- Wells, F. (1924). Vocal and Manual Mechanisms in Choice Reactions. *Journal of Experimental Psychology*, 7(1), 59-66. doi:10.1037/h0070515
- Wickens, C., Kramer, A., Vanasse, L., & Donchin, E. (1983). Performance of concurrent tasks: a psychophysiological analysis of the reciprocity of information-processing resources. *Science (New York, N.Y.)*, 221(4615), 1080-1082.
- Wilson, K. D., Maxwell Drain, H., & Tanaka, J. R. (1995). The inverted face inversion effect in

- prosopagnosia: Evidence for mandatory, face-specific perceptual mechanisms. *Vision Research*, 35(14), 2089-2093. doi:10.1016/0042-6989(94)00273-O
- Yantis, S. (1998). Control of visual attention. En H. Pashler (Ed.), *Attention* (págs. 223-256). London: Psychology Press.
- Yantis, S. (2000). Goal directed and stimulus driven determinants of attentional control. En S. Monsell & J. Driver (Eds.), *Control of cognitive processes: Attention and performance XVIII* (págs. 73-103). Cambridge: MA: MIT Press.
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, 81(1), 141-145.
- Yonelinas, A. P. (1994). Receiver-operating characteristics in recognition memory: evidence for a dual-process model. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, 20(6), 1341-1354.
- Zhao, K., Yuan, J., Zhong, Y., Peng, Y., Chen, Zhou, L., Fan, et al. (2009). Event-related potential correlates of the collective self-relevant effect. *Neuroscience Letters*, 464(1), 57-61. doi:10.1016/j.neulet.2009.07.017

Every manuscript needs a beginning.

And the seed of the present one started growing up long ago...

...once upon a time, when I became interested in the emotional and cognitive processes underlying human behaviour. There is not a single pathway to approach this goal. The study of mind takes us from philosophy and psychodynamic theories to brain functioning. These different views are not mutually exclusive. In fact, only through a multidisciplinary perspective we will be able to achieve a broad understanding of the complex human nature.

Voluntary control, attention and mental representations are crucial terms that will lead us throughout the present project, which, although written from a neuroscientific perspective, does not consign to oblivion the subjective experience of the studied processes.