

TESIS DOCTORAL

**Comportamiento de riesgo, impulsividad
y toma de decisiones ante eventos catastróficos.
Bases neurobiológicas y conectividad
efectiva como factores predictivos
y de prevención**

Laura Mas Cuesta

Granada, 2024



Tesis Doctoral

**Comportamiento de riesgo, impulsividad y toma de decisiones ante eventos
catastróficos. Bases neurobiológicas y conectividad efectiva como factores
predictivos y de prevención**

Programa de Doctorado en Psicología (B13.56.1)



Candidata al doctorado

Laura Mas Cuesta

Directores

Antonio Cándido Ortiz

Andrés Catena Martínez

Psicología Experimental y aplicada

Centro de Investigación Mente Cerebro y Comportamiento

UNIVERSIDAD DE GRANADA

2024

Editor: Universidad de Granada. Tesis Doctorales
Autor: Laura Mas Cuesta
ISBN: 978-84-1195-351-1
URI: <https://hdl.handle.net/10481/92759>

La presente tesis doctoral ha sido financiada por un contrato predoctoral del programa de Formación de Profesorado Universitario 2018 (FPU18/03263), del Ministerio de Ciencia Innovación y Universidades y por un proyecto de I+D+I 2016 (PSI2016-80558-R; IP: Andrés Catena Martínez), del Ministerio de Economía, Industria y Competitividad.

La doctoranda / The *doctoral candidate* **Laura Mas Cuesta** y los directores de la tesis / and the thesis supervisor/s: **Andrés Catena Martínez y Antonio Cándido Ortiz**

Garantizamos, al firmar esta tesis doctoral, que el trabajo ha sido realizado por la doctoranda bajo la dirección de los directores de la tesis y hasta donde nuestro conocimiento alcanza, en la realización del trabajo, se han respetado los derechos de otros autores a ser citados, cuando se han utilizado sus resultados o publicaciones.

Guarantee, by signing this doctoral thesis, that the work has been done by the doctoral candidate under the direction of the thesis supervisor/s and, as far as our knowledge reaches, in the performance of the work, the rights of other authors to be cited (when their results or publications have been used) have been respected.

Lugar y fecha / Place and date:

En Granada, a 13 de febrero del 2024

Director/es de la Tesis / *Thesis supervisor/s;*

Doctoranda / *Doctoral candidate:*

Andrés Catena Martínez

Antonio Cándido Ortiz

Laura Mas Cuesta

ÍNDICE

RESUMEN.....	11
SUMMARY	17
INTRODUCCIÓN	23
Modelos de toma de decisiones.....	23
Neurobiología y factores relacionados con el proceso de toma de decisiones	25
Formación de preferencias y factores de personalidad.....	25
Selección de la acción y decisiones disfuncionales.....	30
Valoración de resultados y eventos catastróficos.....	36
Prevención del comportamiento de riesgo	38
JUSTIFICACIÓN Y OBJETIVOS	45
ESTUDIO 1.....	49
ESTUDIO 2.....	103
ESTUDIO 3.....	143
DISCUSIÓN	183
CONCLUSIONES	195
CONCLUSIONS.....	197
REFERENCIAS	201
AGRADECIMIENTOS	239

RESUMEN/SUMMARY

RESUMEN

La toma de decisiones es un proceso complejo sustentado por múltiples redes cerebrales encargadas de valorar las alternativas de acción, controlar la conducta y evaluar los resultados para aprender de la experiencia. Los modelos neurobiológicos de toma de decisiones establecen que el sistema socioemocional o de recompensa cerebral desempeña un papel fundamental en la asignación de valor a las diferentes opciones de conducta. Durante este proceso, se valoran los posibles resultados en función de los beneficios y los costes esperados, de la incertidumbre asociada a la decisión y del tiempo transcurrido entre la acción y las consecuencias. Es por esto, y dado su carácter subjetivo, que ciertos factores de personalidad, como la impulsividad y la sensibilidad a las recompensas y castigos, también desempeñan un rol decisivo en la valoración de las opciones de elección.

Una vez que se han evaluado los cursos de acción posibles, el sistema de control cognitivo facilita la implementación de la conducta. Sin embargo, no todas las decisiones llevan a acciones adaptativas, como ocurren en el comportamiento de riesgo que, en cualquiera de sus dimensiones, implica elegir una alternativa que conlleva una alta probabilidad de que ocurran consecuencias negativas para la persona. Debido a la importancia de este tipo de conductas, diversos modelos de toma de decisiones han postulado la existencia de un mecanismo dual de procesamiento en su intento de explicar el comportamiento de riesgo. En esencia, se han postulado dos redes cerebrales, una de control cognitivo y otra de procesamiento de las recompensas. Además, debido a la complejidad de este proceso, factores como el contexto social, las emociones y los rasgos de personalidad influyen de manera fundamental en las decisiones arriesgadas.

Una vez que la acción se ha realizado, se evalúan sus consecuencias, para asignarle un valor y aprender de la experiencia. Las áreas cerebrales encargadas de procesar las recompensas y castigos intervienen durante la exposición al resultado y muestran actividad anticipatoria, previa a la obtención del mismo. De hecho, la anticipación de las situaciones futuras es un elemento clave para la conducta adaptativa, más aun ante resultados inesperados cuyas consecuencias no se puedan predecir.

Teniendo en cuenta lo anterior y dada la influencia que ejercen los estados emocionales y las características personales en las diferentes etapas de la toma de decisiones, no es de extrañar que las intervenciones diseñadas para regular estos factores, como los programas basados en mindfulness, sean efectivas para mejorar la conducta adaptativa. Más concretamente, la práctica de la atención plena se ha demostrado eficaz para reducir el comportamiento de riesgo y para mejorar las habilidades de regulación emocional, el bienestar y la salud psicológica general.

A pesar de la evidencia sobre los factores, tanto contextuales como personales, que determinan que la elección de la conducta sea más o menos funcional, falta investigación para esclarecer cómo se configuran los sistemas neurocognitivos y de personalidad implicados en las distintas etapas de la toma de decisiones, y cómo los cambios que se producen en estos sistemas permiten anticipar y procesar resultados inesperados y prevenir la conducta desadaptativa. El objetivo principal de la tesis es arrojar luz en los aspectos citados, utilizando contextos de riesgo reales y cotidianos. Un ejemplo diario de toma de decisiones donde pueden observarse comportamientos de riesgo, con resultados impredecibles y catastróficos, son los entornos de tráfico. Por ello, y debido a su gran validez ecológica y posibilidad de generalización, se utiliza la conducción para abordar los objetivos de los estudios de la tesis.

El estudio 1 explora las bases neuroanatómicas del comportamiento de conducción arriesgado en situaciones de la vida real, y su relación con la impulsividad cognitiva y la sensibilidad a las recompensas y castigos. Los resultados indican que existe una tendencia a presentar un menor volumen de materia gris total cuanto mayor es el nivel de riesgo. También se observa que las personas que conducen de manera arriesgada muestran un menor volumen en regiones que forman parte de las redes de control cognitivo y de recompensa cerebral, como la corteza frontal, parietal y temporal superior, los giros parahipocampal y fusiforme, la ínsula, el cerebelo y el estriado ventral. Por otro lado, observamos que, incluso ante la ausencia de diferencias en los rasgos de personalidad, la impulsividad y la sensibilidad a las recompensas y castigos se relacionan de manera distinta con las estructuras de las redes de control y recompensa, en función del nivel de riesgo en conducción, encontrando, en las personas más arriesgadas, correlaciones absolutas más bajas entre el volumen cerebral y los rasgos de personalidad. En conjunto, los resultados apoyan el modelo dual del comportamiento de riesgo e indican que existe una alteración en la configuración de los circuitos neurales implicados en la valoración de las recompensas, implementación de la acción y regulación del comportamiento en personas arriesgadas.

El estudio 2 investiga el procesamiento cerebral de los eventos catastróficos. Para ello se han utilizado los periodos previos y posteriores a la ocurrencia de accidentes en contextos de conducción simulada. En ambos periodos se ha analizado la actividad cerebral, estimada mediante el registro de electroencefalografía de alta densidad (EEG), y la conectividad efectiva de las siete redes principales del cerebro (VN: visual; SMN: somatomotora; LN: límbica, DAN: atencional dorsal; VAN: atencional ventral; FPN: frontoparietal y DMN: red por defecto). Los resultados indican que durante el periodo previo a la ocurrencia de un accidente se activan las cortezas parietal inferior y cingulada

anterior y la ínsula. Además, se produce un flujo de activación causal, o conectividad efectiva, entre los nodos de las redes atencionales, VAN y DAN, y dentro de los nodos de la red límbica. Por otro lado, cuando el accidente acaba de ocurrir, las cortezas orbitofrontal, parietal inferior y cingulada anterior, y los giros frontal superior y medio se activan, y se produce una mayor conectividad efectiva entre redes, desde la VAN hasta la SMN, y entre nodos, desde nodos de las redes visual, VAN y DMN, hasta nodos de las redes frontoparietal, atencionales y límbica. Estos patrones de actividad cerebral y conectividad efectiva sugieren que la activación de procesos relacionados con la saliencia y el procesamiento emocional permite la anticipación de la ocurrencia de eventos catastróficos, como los accidentes. Además, una vez que el accidente ha ocurrido, se inician los procesos de control necesarios para adaptar el comportamiento a las nuevas demandas del ambiente.

El estudio 3 explora los efectos de una intervención basada en mindfulness a nivel neuroanatómico y su relación con el mindfulness disposicional y la impulsividad. Nuestros resultados indican que el entrenamiento en mindfulness mejora el mindfulness disposicional, Además, el cambio en las habilidades de atención plena, después de la intervención, se relaciona con cambios en los niveles de impulsividad. Asimismo, observamos que el entrenamiento en mindfulness produce una reducción en el volumen del núcleo caudado que, su vez, se relaciona con una menor urgencia positiva. Es decir, el entrenamiento en mindfulness mejora la habilidad de observar las propias sensaciones y percepciones y la capacidad para dejar pasar los pensamientos y las emociones, sin aferrarse ni reaccionar ante su ocurrencia. Además, produce cambios a nivel de estructura cerebral que se relacionan con una disminución en los niveles de impulsividad, reduciendo la tendencia a actuar de manera precipitada ante situaciones que generan emociones positivas.

En conjunto, nuestros resultados muestran que los sistemas de control cognitivo, procesamiento emocional y recompensa cerebral actúan de manera interconectada en las diferentes etapas de la toma de decisiones, desde la formación de preferencias y selección de la acción, hasta la anticipación y valoración de resultados y la regulación de la conducta. Además, la impulsividad, la sensibilidad a las recompensas y castigos y la atención plena disposicional también se sustentan en estos sistemas neurocognitivos e influyen en el proceso de toma de decisiones y en la conducta adaptativa.

SUMMARY

Decision-making is a complex process supported by multiple brain networks responsible for valuing action alternatives, controlling behavior, and evaluating outcomes to learn from experience. Neurobiological models of decision-making posit that the socioemotional or reward brain system plays a crucial role in assigning value to different behavioral options. During this process, potential outcomes are evaluated based on the expected benefits and costs, uncertainty associated with the decision, and the time elapsed between the action and the consequences. Due to this, and given their subjective nature, personality factors such as impulsivity and sensitivity to rewards and punishments also play a decisive role in the valuation of choice options.

Once potential courses of action have been evaluated, the cognitive control system facilitates behavior implementation. However, not all decisions lead to adaptive actions, as occurs in risk behavior, which in any of its dimensions entails choosing an alternative that involves a high probability of negative consequences for the individual. Given the importance of such behaviors, various decision-making models have postulated the existence of a dual processing mechanism in their attempt to explain risk behavior. In essence, two brain networks have been hypothesized, one for cognitive control and the other for reward processing. Additionally, due to the complexity of this process, factors like social context, emotions, and personality traits fundamentally influence risky decisions.

Once the action has been performed, its consequences are evaluated to assign it a value and learn from the experience. Brain areas responsible for processing rewards and punishments come into play during outcome exposure, showing anticipatory activity before obtaining the outcome. In fact, anticipation of future situations is a key element

for adaptive behavior, especially in the face of unexpected outcomes with unpredictable consequences.

Considering the above and given the influence of emotional states and personal characteristics throughout decision-making stages, it is not surprising that interventions designed to regulate these factors, such as mindfulness-based programs, are effective in improving adaptive behavior. Specifically, mindfulness practice has been shown to be effective in reducing risk behavior and enhancing emotional regulation skills, well-being, and overall psychological health.

Despite the evidence regarding both contextual and personal factors that determine whether the choice of behavior is more or less functional, further research is needed to clarify how the neurocognitive and personality systems involved in the different stages of decision-making are configured. Additionally, understanding how changes in these systems allow anticipation and processing of unexpected outcomes, and prevent maladaptive behavior is crucial. The main aim of this thesis is to shed light on the aforementioned aspects using real and everyday risk contexts. A daily example of decision-making where risky behaviors can be observed with unpredictable and catastrophic outcomes may be provided by traffic environments. For this reason, and due to its high ecological validity and generalizability, driving is used to address the aims of the thesis studies.

Study 1 explores the neuroanatomical bases of risky driving behavior in real-life situations and their relationship with cognitive impulsivity and sensitivity to rewards and punishments. The results indicate a trend towards lower total gray matter volume as the level of risk increases. It is also observed that risky drivers show a lower volume in regions that are part of the cognitive control and reward brain networks, such as the

frontal, superior parietal and temporal cortices, parahippocampal and fusiform gyri, insula, cerebellum, and ventral striatum. On the other hand, we observe that even in the absence of differences in personality traits, impulsivity and sensitivity to rewards and punishments are differently related to the structures of the control and reward networks, depending on the level of risk in driving. In individuals with a higher propensity for risk-taking, we find lower absolute correlations between brain volume and personality traits. Overall, results support the dual model of risk behavior and indicate that there is an alteration in the configuration of neural circuits involved in reward valuation, action implementation, and behavior regulation in risky individuals.

Study 2 investigates the brain processing of catastrophic events. For this purpose, the periods before and after the occurrence of accidents in simulated driving contexts have been studied. Brain activity, estimated through high-density electroencephalography (EEG) recording, and the effective connectivity of the seven main brain networks (VN: visual network; SMN: somatomotor network; LN: limbic network, DAN: dorsal attention network; VAN: ventral attention network; FPN: frontoparietal network; DMN: default mode network) were analyzed during both periods. The results show that before the accident occurs, the inferior parietal and anterior cingulate cortices and the insula are activated. Additionally, causal activation flow or effective connectivity between nodes of the VAN and DAN, and within nodes of the limbic network occurs. On the other hand, immediately after the accident, the orbitofrontal, inferior parietal, and anterior cingulate cortices, and the superior and middle frontal gyri are activated. Greater effective connectivity between networks, from the VAN to the SMN, and within nodes, from nodes of the visual network, VAN, and DMN to nodes of the frontoparietal, attentional, and limbic networks, also occurs. These patterns of brain activity and effective connectivity suggest that the activation of salience and emotional processing enables the anticipation

of catastrophic events such as accidents. Moreover, once an accident has occurred, control processes are initiated to adapt behavior to the new environmental demands.

Study 3 explores the neuroanatomical effects of a mindfulness-based intervention and its relationship with dispositional mindfulness and impulsivity. Our results indicate that mindfulness training improves dispositional mindfulness. Additionally, the change in mindfulness skills after the intervention is related to changes in impulsivity levels. Furthermore, we observe that mindfulness training leads to a reduction in the caudate nucleus volume, which in turn is related to lower positive urgency. That is, mindfulness training improves the ability to observe one's own sensations and perceptions and the ability to let thoughts and emotions pass, without clinging or reacting to them. In addition, it produces changes in brain structure that are related to a decrease in impulsivity levels, reducing the tendency to act rashly in situations that generate positive emotions.

Overall, our results show that cognitive control, emotional processing, and reward brain systems act interconnectedly in the different stages of decision-making, from preference formation and action selection to anticipation and valuation of outcomes and behavior regulation. Moreover, impulsivity, sensitivity to rewards and punishments, and dispositional mindfulness are also underpinned by these neurocognitive systems and influence the decision-making process and adaptive behavior.

INTRODUCCIÓN

INTRODUCCIÓN

Modelos de toma de decisiones

La toma de decisiones es un proceso deliberativo complejo que implica valorar diferentes opciones para elegir la alternativa que se considera más adecuada (Gold y Shadlen, 2007; Rangel et al., 2008). Tanto las decisiones perceptivas como las basadas en el valor de las alternativas buscan el comportamiento más adaptativo, en función de las circunstancias de la situación, y comparten correlatos neurales (Izakson et al., 2023). Las decisiones perceptivas, como por ejemplo decidir si un semáforo está en rojo o en verde, son juicios sobre la información sensorial que describen los estados objetivos del ambiente (Gold y Heekeren, 2014), mientras que las decisiones basadas en valor, como por ejemplo decidir parar o pasar ante un semáforo en ámbar, implican juicios subjetivos, determinados por las propias preferencias, experiencias y creencias (Morelli et al., 2022).

Las decisiones basadas en valor, según Rangel et al. (2008), se sustentan en diferentes sistemas de valoración que se distinguen en función del tipo de aprendizaje asociado y los procesos cognitivos que activan. El sistema Pavloviano, mediante el aprendizaje asociativo, asigna un valor a algunos comportamientos que se han convertido en respuestas apropiadas a diversos estímulos del ambiente. Sin embargo, cuando las señales o estímulos predicen la ocurrencia de reforzadores o castigos, adquieren la propiedad de incentivos. Es decir, influyen el comportamiento para conseguir recompensas o evitar consecuencias negativas (Rescorla, 1994). Por eso es frecuente reducir la velocidad ante una señal que informa sobre la presencia de un control de velocidad. Este tipo de acciones, que pueden basarse en un sistema de hábitos o dirigido a objetivos, siguen un aprendizaje instrumental, donde se establece una relación causal entre conducta y consecuencia. Las acciones rutinarias, o hábitos, son conductas que se

inician y se llevan a cabo cuando el ambiente tiene unas características particulares. Además, son relativamente insensibles a la devaluación del reforzador y al cambio en la contingencia de acción-resultado (Balleine y Dezfouli, 2019). Esto ocurre, por ejemplo, cuando cada mañana se sigue la misma ruta para ir al trabajo, aunque ya no sea la alternativa más rápida. Por último, en las acciones basadas en objetivos, las decisiones se toman teniendo en cuenta el valor de los resultados que produce la conducta (Rangel et al., 2008). Es decir, se utiliza de manera flexible el conocimiento de la estructura de la situación y de sus posibles resultados para hacer predicciones y tomar decisiones. Por lo tanto, dado el caso, elegiremos una carretera de peaje para llegar al trabajo si lo que queremos es llegar antes.

Los modelos neurocognitivos de toma de decisiones conceptualizan las decisiones con una estructura genérica de *“input-process-output-feedback”*, donde se representan los estímulos que predicen resultados aversivos o reforzantes, se evalúan los mismos para formar las preferencias de acción, se ejecuta la conducta y se experimentan y evalúan los resultados para aprender sobre el valor de los estímulos (Ernst y Paulus, 2005). Gold y Shadlen (2007) establecen las decisiones como un proceso donde la variable de decisión representa la evidencia, las probabilidades y el valor; la regla de decisión indica cómo se interpreta la variable de decisión para elegir una alternativa y la monitorización de la ejecución analiza la eficacia de la acción respecto a sus objetivos particulares. Rangel et al. (2008) proponen cinco etapas secuenciales en la toma de decisiones: representar la situación, asignar un valor a las opciones, seleccionar la acción y ejecutarla, evaluar el resultado y actualizar los procesos anteriores para aprender de la experiencia. Por último, basándose en un modelo unificado de toma de decisiones (Coutlee y Huettel, 2012; Ernst y Paulus, 2005), Verdejo-García et al. (2018) describen los procesos cognitivos interactivos que tienen lugar durante las diferentes etapas: en la formación de preferencias

se analiza la información sobre las recompensas y los riesgos; en la implementación de la elección se ponen de manifiesto los recursos motivacionales, la inhibición y la autorregulación comportamental; y en el procesamiento del feedback se integran los errores de predicción y la historia previa para guiar el comportamiento futuro.

Los estudios que componen la presente tesis doctoral se enmarcan en el modelo de toma de decisiones propuesto por Ernst y Paulus (2005), incidiendo en los correlatos neurales y en los factores que afectan a las distintas etapas del proceso decisional, así como en las estrategias de prevención de las posibles decisiones disfuncionales.

Neurobiología y factores relacionados con el proceso de toma de decisiones

Formación de preferencias y factores de personalidad

La formación de las preferencias sobre las distintas alternativas en un proceso de decisión requiere, en primer lugar, representar la situación y las diferentes opciones de elección. Para ello, es necesario identificar los cursos de acción posibles (ej. pararse en un semáforo o saltárselo), así como los estados externos (ej. presión temporal) e internos (ej. búsqueda de sensaciones) que conforman el contexto de la situación (Rangel et al., 2008). En segundo lugar, es necesario asignar un valor a las diferentes alternativas de comportamiento. El valor puede definirse como los beneficios y costes subjetivos que se atribuyen a los potenciales resultados de las distintas opciones de conducta y que tienen un componente afectivo (Gold y Shadlen, 2007). Por ejemplo, pararse ante un semáforo puede conllevar llegar tarde a una cita y evitar una multa, donde el beneficio y/o coste asignado a cada resultado varía en función de las preferencias individuales. El sistema socioemocional o de recompensa cerebral, compuesto fundamentalmente por el estriado dorsal y ventral, el hipocampo, la corteza orbitofrontal y la corteza cingulada, junto con la amígdala y la ínsula desempeñan un papel fundamental en la valoración de posibles

resultados, ya que estas regiones están implicadas en la representación y prospección de las expectativas de refuerzo y castigo, basadas en la experiencia previa, en la sensibilidad, detección y procesamiento de las señales de incentivo, en la evaluación de la valencia y la saliencia emocional de los estímulos y en la búsqueda y aproximación a los reforzadores (Balleine et al., 2007; Bartra et al., 2013; Knutson y Cooper, 2005; J. Peters y Büchel, 2010; Rolls, 2023; Yao et al., 2023).

Además, en la asignación final del valor a las diferentes alternativas intervienen otros sistemas neurocognitivos encargados de evaluar la probabilidad o la incertidumbre asociada a una decisión (el nivel de riesgo), así como la demora temporal entre la acción y el resultado (Rangel et al., 2008). En las acciones o decisiones de riesgo, donde se conocen las probabilidades de los resultados, los valores pueden calcularse teniendo en cuenta una aproximación normativa o descriptiva (van der Pligt, 2015). La aproximación normativa conceptualiza la *utilidad esperada*, donde el valor de las opciones se pondera en función de la probabilidad de ocurrencia de las posibles consecuencias (Von Neumann y Morgenstern, 1944). Por su parte, la aproximación descriptiva entiende los resultados en términos de ganancias y pérdidas y determina los valores en función de un punto de referencia y de un peso de decisión asignado a cada probabilidad de ocurrencia (Kahneman y Tversky, 1979). Sin embargo, en la mayoría de las situaciones de la vida cotidiana las probabilidades de los resultados son ambiguas, es decir, o bien no se conocen, o son muy similares entre las diferentes opciones (Krain et al., 2006; Levy et al., 2010; Paulus et al., 2002). En un metaanálisis donde estudiaron las bases cerebrales de la toma de decisiones en contextos de incertidumbre, Poudel et al. (2020) identificaron redes cerebrales diferenciales para las decisiones arriesgadas y las ambiguas. Por un lado, el núcleo caudado, la ínsula, la corteza cingulada anterior y la corteza parietal inferior estaban implicados en las decisiones donde las probabilidades de los resultados son

conocidas, y el giro frontal inferior y la ínsula en las decisiones donde las probabilidades son ambiguas.

Además de tener en cuenta las distintas probabilidades de los resultados, en todas las situaciones se sucede un intervalo temporal variable entre la acción y las consecuencias. Este intervalo también afecta a la formación de preferencias, ya que existe una tendencia general a asignar un mayor valor a los resultados inmediatos que a los demorados (Frederick et al., 2002). El descuento por demora se entiende como una función hiperbólica donde, cuando se tiene que elegir entre una recompensa más pequeña e inmediata y una mayor y demorada, el valor de la recompensa demorada se descuenta en función de la demora requerida para obtener dicho reforzador y de la propensión individual a descontar temporalmente las recompensas futuras (tasa de descuento) (Bickel et al., 2014; Kable y Glimcher, 2007). Como parte del proceso de asignación de valor, los correlatos neurales del descuento por demora se sustentan en el sistema de recompensa, monitorización del conflicto y prospección, estando implicadas regiones como el estriado, las cortezas orbitofrontal, prefrontal lateral y medial, parietal inferior y cingulada, el hipocampo y la amígdala (Loganathan y Tiego, 2023; McClure et al., 2004; J. Peters y Büchel, 2011; Q. Wang et al., 2021; Wesley y Bickel, 2014).

Como puede observarse, la formación de preferencias es el resultado de un cálculo subjetivo donde las diferencias individuales juegan un papel fundamental. Dado que en este proceso se valoran los resultados en función del tiempo y de los beneficios y los costes esperados, ciertos factores de personalidad, como la impulsividad y la sensibilidad a las recompensas y castigos tienen un rol decisivo en la evaluación de las diferentes opciones de elección. La impulsividad es un constructo multidimensional que refleja la tendencia a elegir alternativas rápidas, pero a menudo prematuras y sin la previsión adecuada (Dalley y Robbins, 2017). Desde el punto de vista de los factores de

personalidad, el modelo UPPS propone que el rasgo de impulsividad se caracteriza por la falta de premeditación y/o perseverancia en la toma de decisiones, la búsqueda de sensaciones a la hora de actuar y en la tendencia a tomar decisiones precipitadas en situaciones con alta carga emocional (Whiteside y Lynam, 2001). Desde una perspectiva más cercana a la ejecución de tareas, de manera simplificada, la impulsividad puede dividirse en dos constructos: impulsividad motora (*rapid-response impulsivity* o incapacidad de inhibir respuestas prepotentes) e impulsividad cognitiva (*choice impulsivity* o *impulsive decision-making*) (Bechara, 2002; Hamilton et al., 2015; Reynolds et al., 2006). La impulsividad cognitiva se relaciona con la (falta de) deliberación sobre las consecuencias de las acciones, lo que puede hacer que se elijan opciones no adaptativas (Perales et al., 2009). En este sentido, la tasa de descuento, o preferencia por recompensas inmediatas, se considera una medida de impulsividad cognitiva (Kirby y Maraković, 1996). Además, las medidas de impulsividad cognitiva se relacionan con la impulsividad como rasgo y con comportamientos impulsivos en el mundo real, como las conductas adictivas (MacKillop et al., 2011; Verdejo-García et al., 2021). A nivel neuroanatómico la impulsividad cognitiva se asocia con el volumen de las regiones cerebrales implicadas en el descuento por demora, aunque el sentido y el número de estas asociaciones varían en función del estudio. Por ejemplo, se han observado tanto correlaciones positivas como negativas entre el volumen de materia gris y la tasa de descuento en regiones prefrontales ventromediales, orbitales y laterales, el estriado y la corteza cingulada anterior y posterior, los giros fusiforme, lingual y parahipocámpal, la ínsula y la corteza occipital lateral (Bernhardt et al., 2014; Bjork et al., 2009; X. Li et al., 2019; Meade et al., 2020; Mohammadi et al., 2016; Owens et al., 2017; Pehlivanova et al., 2018; Tschernegg et al., 2015; Q. Wang et al., 2016). Recientemente, en un intento de desarrollar una métrica neurobiológica de la impulsividad cognitiva, Sadeh et al.

(2023) han identificado un marcador cortical de la preferencia por las recompensas inmediatas (C-DD), donde los valores elevados en C-DD se corresponden con un menor grosor cortical y una mayor impulsividad cognitiva. De hecho, los diferentes constructos de impulsividad forman parte de redes neurales interconectadas (Dalley y Robbins, 2017). En este sentido, las dimensiones de la impulsividad (urgencia positiva y negativa, falta de premeditación y perseverancia y búsqueda de sensaciones) también se relacionan con los sistemas de valoración, control cognitivo y procesamiento emocional (Baltruschat et al., 2020; Golchert et al., 2017; Hoptman et al., 2014; Kakoschke et al., 2019; Moreno-López, Catena, et al., 2012; Moreno-López, Soriano-Mas, et al., 2012; Muhlert y Lawrence, 2015; Owens et al., 2020; Ruiz de Lara et al., 2018; H. Wang et al., 2017).

Por otro lado, la sensibilidad a las recompensas y a los castigos refleja las diferencias individuales en los sistemas de activación e inhibición conductual (BAS/BIS), los cuales juegan un papel fundamental en la asignación de valor a las alternativas de comportamiento ya que controlan las conductas de aproximación y evitación a los estímulos apetitivos o aversivos (Gray, 1970). La sensibilidad al castigo se relaciona con la inhibición del comportamiento, la evitación pasiva de situaciones novedosas o que pueden conllevar consecuencias aversivas, la aversión al riesgo y la preocupación y los procesos cognitivos que tienen lugar ante la amenaza de castigo o fracaso (Torrubia et al., 2001). La sensibilidad a las recompensas, por su parte, se asocia con la búsqueda de sensaciones y la aproximación conductual en respuesta a recompensas específicas (ej., dinero, parejas sexuales, eventos sociales o poder) y se relaciona con la impulsividad como rasgo de personalidad (Aluja y Blanch, 2011; Carroll et al., 2022). Como parte del proceso de formación de preferencias, ambos factores se sustentan en estructuras cerebrales encargadas del manejo de la experiencia emocional y de la valoración de las recompensas (Adrián-Ventura et al., 2019b, 2023; Torrubia et al., 2001). Más

concretamente, investigaciones previas han encontrado tanto correlaciones positivas como negativas entre la sensibilidad a las recompensas y el volumen del estriado, el lóbulo temporal superior y la corteza prefrontal lateral y medial (Adrián-Ventura et al., 2019a; Barrós-Loscertales et al., 2006b; M. Li et al., 2019; Parcet et al., 2020; Urošević et al., 2015), y entre la sensibilidad al castigo y la amígdala, la formación hipocampal, la ínsula y la corteza orbitofrontal (Adrián-Ventura et al., 2019a; Barrós-Loscertales et al., 2006a; Fuentes et al., 2012; Holmes et al., 2012; Iidaka et al., 2006; Levita et al., 2014; Von Siebenthal et al., 2020).

Teniendo en cuenta lo anterior podemos concluir que distintos procesos cognitivos y factores de personalidad, sustentados en sistemas neurales interconectados, intervienen en la formación individual de preferencias, dentro del proceso de toma de decisiones. Por lo tanto, una persona con alta sensibilidad a los castigos y que tenga preferencias por recompensas demoradas y mayores, asignará más valor a la opción de pararse ante un semáforo que a la de saltárselo. Sin embargo, a pesar de la clara influencia de la impulsividad y la sensibilidad a las recompensas y castigos en la asignación de valor a las distintas alternativas de conducta, aún es necesario profundizar en el conocimiento de los sistemas neuroanatómicos que subyacen a este proceso y que se relacionan con ambos factores de personalidad. Este objetivo se aborda en el estudio 1 de la tesis.

Selección de la acción y decisiones disfuncionales

Una vez que se han evaluado los distintos cursos de acción posibles, se elige la alternativa a la que se le haya asignado un mayor valor. La selección y ejecución de la conducta implica iniciar, mantener, monitorizar y completar diversas secuencias de acción, planificar su implementación, inhibir o suprimir otras acciones competidoras y corregir los errores que tengan lugar (Coutlee y Huettel, 2012; Ernst y Paulus, 2005). A nivel neurobiológico este proceso se sustenta en el sistema de control cognitivo, formado

principalmente por las cortezas prefrontal lateral, cingulada anterior, parietal y temporal superior, y el cerebelo (Dosenbach et al., 2006; Luna et al., 2010; Niendam et al., 2012; Seeley et al., 2007; Si et al., 2019; Sokolov et al., 2017; Steinberg, 2008; Xie et al., 2017). Esta red cerebral, a través de la identificación de los estímulos relevantes, el control atencional e inhibitorio, la planificación, la memoria de trabajo, la flexibilidad cognitiva, la monitorización del conflicto y del error y la autorregulación del comportamiento, se encarga de controlar la implementación de las decisiones para una conducta funcional (Dosenbach et al., 2006; Lee et al., 2018; Luna et al., 2010; McClure et al., 2004; Menon y D'Esposito, 2022; Niendam et al., 2012; Seeley et al., 2007; Steinberg, 2008; Woolgar et al., 2015; Xie et al., 2017).

Sin embargo, existen decisiones que no son adaptativas. El comportamiento de riesgo, como por ejemplo el consumo de drogas o saltarse un semáforo, implica elegir una conducta que conlleva una probabilidad incierta, y más o menos alta, de que ocurran consecuencias altamente negativas para el bienestar, tanto físico como mental (Reyna y Farley, 2006; Yates, 1992). Este tipo de conductas no presentan una tendencia unitaria, si no que se conceptualizan en distintas dimensiones que difieren en las actitudes individuales, en su forma de manifestación y en el contexto en el que tienen lugar (Mischel y Shoda, 1995). En este sentido, podemos diferenciar entre el área financiera, ética, de salud/seguridad, recreativa y social, donde una misma persona puede tender a asumir riesgos en algunos contextos y en otros no (Weber et al., 2002). Véase el caso de alguien que haya invertido en fondos de rentabilidad variable y suele conducir por encima del límite de velocidad, y, sin embargo, no se plantee practicar paracaidismo ni defraudar en su declaración de impuestos.

Por otro lado, independientemente del contexto, la importancia de estudiar el comportamiento de riesgo radica en las consecuencias, tanto personales como sociales,

que derivan de este tipo de conductas y que, en muchas ocasiones, constituyen un problema de salud pública. Un claro ejemplo es la conducción arriesgada, responsable, en gran parte, de los accidentes de tráfico, los cuales implican 1.2 millones de muertes al año, situándose en la doceava posición entre las causas de mortalidad en el mundo (World Health Organization, 2023).

Debido a las graves consecuencias que pueden producir algunas decisiones y a las diferencias individuales y contextuales que intervienen en este tipo de conductas, los modelos de toma de decisiones han postulado la existencia de un mecanismo neurocognitivo de procesamiento dual para explicar el comportamiento de riesgo (Epstein, 1994; Evans, 2008; Frankish, 2010; Kahneman y Frederick, 2002; Loewenstein et al., 2001; Reyna, 2004; Sanfey y Chang, 2008; Slovic et al., 2007). Por un lado, un sistema de procesamiento controlado, consciente, explícito y analítico, que está basado en reglas racionales y requiere recursos atencionales, por lo que sigue un proceso serial y lento. Por otro lado, un sistema de procesamiento automático, implícito, intuitivo y emocional, que está basado en la propia experiencia de aprendizaje y en heurísticos cognitivos y afectivos, por lo que es más rápido y, a veces, irracional. A nivel neurobiológico, las regiones que conforman la red de control cognitivo -cortezas prefrontal, cingulada y parietal y temporal superior-, y de recompensa cerebral -estriado, corteza prefrontal medial y orbital, corteza cingulada anterior, amígdala e ínsula- son las que sustentan el procesamiento analítico y automático, respectivamente (Edelson y Reyna, 2023; Lambert et al., 2014; X. Li et al., 2020; Steinberg, 2010). Por lo tanto, la influencia que ejercen estos dos tipos de sistemas de procesamiento en la ejecución de la acción va a depender de la interacción entre ambos y de las características personales y situacionales que tengan lugar en el momento de la decisión (ej. carga emocional y presión temporal). Nuestro grupo de investigación ha evidenciado la existencia de los

procesos duales en el comportamiento de riesgo, tanto en tareas de percepción y decisión de riesgo como en los correlatos neurales asociados (Megías, Cándido, et al., 2018; Megías et al., 2011, 2013, 2015). Otras investigaciones también han observado alteraciones en las regiones cerebrales que conforman las redes de control cognitivo y de recompensa en el comportamiento de riesgo autoinformado y en contextos de laboratorio (Dantas et al., 2023; Goh et al., 2016; Han et al., 2024; Helfinstein et al., 2014; Levy, 2017; McIlvain et al., 2020; Nasiriavanaki et al., 2015; Nogueira et al., 2017; Xue et al., 2018). Sin embargo, todavía es necesario profundizar en las bases neuroanatómicas de estos sistemas en relación a la conducta arriesgada en contextos más ecológicos, como por ejemplo, la conducción. Este objetivo se aborda en el estudio 1.

En relación a los factores que influyen en que la selección final de la acción sea más o menos segura o funcional, es importante tener en cuenta los estados internos y externos que rodean a cada situación particular, por lo que el contexto social, las emociones y las características de personalidad juegan un rol fundamental. Una de las principales características de una conducta adaptativa es la capacidad de interactuar socialmente, ya que la mayoría de las decisiones se llevan a cabo en contextos sociales complejos que condicionan el comportamiento (Rilling y Sanfey, 2011; Tremblay et al., 2017). Es decir, una persona puede actuar de manera distinta si conduce sola, a si lo hace con su hija o con un amigo. En este sentido, nuestro grupo de investigación también ha evidenciado la influencia del contexto social, tanto en la percepción como en el comportamiento de riesgo (Baltruschat, Megías-Robles, et al., 2021; Megías, Cándido, et al., 2014), encontrando, además, que el tipo de situación social produce una interacción diferencial entre las redes cerebrales implicadas en la toma de decisiones (Baltruschat, Megías-Robles, et al., 2021).

Por otro lado, los modelos duales de toma de decisiones destacan el papel que juegan las emociones en la selección y la implementación de la acción, ya que las decisiones no siguen un proceso únicamente analítico y racional, sino que están influidas por el estado afectivo (Loewenstein et al., 2001; Slovic et al., 2004). El resultado de esta influencia puede ser beneficioso o perjudicial para la conducta adaptativa y el rendimiento en función de la valencia y de la carga afectiva que domine en cada situación (Angie et al., 2011; Engelmann y Hare, 2018; Lerner et al., 2015; Megías, Cándido, et al., 2014; Megías, Di Stasi, et al., 2014; Megías et al., 2011).

Por último, la impulsividad, la sensibilidad a las recompensas y castigos y la atención plena disposicional son factores de personalidad que se han postulado en la literatura como unos de los más influyentes en la elección de comportamientos arriesgados (Reniers et al., 2016; Shook et al., 2021; Zuckerman y Kuhlman, 2000). La atención plena o mindfulness es la tendencia natural de cada individuo a prestar atención de manera intencionada al momento presente, con apertura, aceptación y sin juicio (Brown y Ryan, 2003; Kabat-Zinn, 2005). Como rasgo de personalidad, el mindfulness comprende la habilidad para enfocarse en las actividades que se están llevando a cabo, observar o prestar atención a las percepciones y sensaciones propias, etiquetar estas experiencias con palabras, dejar que los pensamientos y emociones pasen sin aferrarse o reaccionar ante ellos y adoptar una postura no evaluativa ante lo que acontece (Baer et al., 2006). Por ende, este factor de personalidad se ha relacionado de manera positiva con conductas adaptativas y de manera negativa con comportamientos que suponen un riesgo para la salud, como el consumo de drogas o la conducción imprudente (Black et al., 2012; Eberth y Sedlmeier, 2012; Koppel et al., 2018, 2022; Lakey et al., 2007; Liu et al., 2021; Shook et al., 2021; Stephens et al., 2018; J. Yang et al., 2019). Además, el mindfulness disposicional también se ha relacionado con otros factores implicados en la toma de

decisiones y en el bienestar general, como las funciones ejecutivas y la impulsividad, aunque la magnitud y la dirección de las asociaciones depende de las dimensiones analizadas y varían en función del estudio (Aguerre et al., 2022; Gallo et al., 2021; Murphy y MacKillop, 2012; J. R. Peters et al., 2011; Royuela-Colomer et al., 2021; Tingaz et al., 2022; Tomlinson et al., 2018).

A la luz de lo anterior no es de extrañar que la impulsividad y la sensibilidad a las recompensas y castigos estén a la base de la toma de decisiones disfuncionales (C. Davis et al., 2007). Más concretamente, se encuentran mayores niveles de impulsividad y de sensibilidad a las recompensas en diversas manifestaciones del comportamiento de riesgo, como el juego patológico, el abuso de sustancias, los atracones, las conductas sexuales de riesgo y la conducción arriesgada (Baltruschat et al., 2020; Cosenza et al., 2017; Dir et al., 2014; MacKillop et al., 2011; Miglin et al., 2019; Navas et al., 2017, 2019; Scott-Parker y Weston, 2017; Smith et al., 2019; Story et al., 2014; Torres et al., 2013). La impulsividad también se relaciona con una menor evitación del riesgo (Megías-Robles et al., 2022) y, junto con la sensibilidad a las recompensas, actúa como un factor mediador en las relaciones entre la regulación emocional (otro componente fundamental en el proceso de toma de decisiones) y las conductas de riesgo relacionadas con la salud (Megías-Robles et al., 2023). Por otro lado, los niveles de impulsividad y de sensibilidad a las recompensas y castigos sirven para predecir la propensión al riesgo, y esta se relaciona con una menor percepción de riesgo y con un comportamiento de conducción más arriesgado (Baltruschat et al., 2020). Además, parece que los sistemas cerebrales que se relacionan con estos factores de personalidad comparten correlatos neurales con aquellos que subyacen al comportamiento de riesgo y muestran una interacción disfuncional durante las decisiones arriesgadas (Brevet-Aeby et al., 2016; Cui et al., 2022; Kohler et al., 2023; Van Leijenhorst et al., 2010). En este sentido, Baltruschat et al.

(2020) encuentran que la tendencia al riesgo modula la asociación entre la impulsividad y la sensibilidad a las recompensas y el acoplamiento funcional entre las redes cerebrales de recompensa y control cognitivo. Sin embargo, y a pesar de la evidencia previa, se necesita más investigación para establecer cómo se relacionan los distintos factores de personalidad, entre sí y con el comportamiento de riesgo, y cómo se configuran los correlatos neuroanatómicos que sustentan dichas relaciones. Estos objetivos se abordan en los estudios 1 y 3 de la tesis.

Valoración de resultados y eventos catastróficos

Una vez que la conducta se ha llevado a cabo, se deben evaluar las consecuencias de esa acción. De manera similar a lo que ocurre en la formación de preferencias, en este momento se analizan las características de los resultados obtenidos y se asigna un valor a la experiencia (Ernst y Paulus, 2005). Sin embargo, a diferencia de lo que ocurre en la primera fase, la función principal de este proceso es experimentar y aprender cuál es el valor real del resultado (no el esperado). En la experiencia del resultado real influye: qué podría haber ocurrido si se hubiera elegido otra opción (el arrepentimiento determina el comportamiento futuro), el ajuste del valor esperado en función del intervalo temporal que ha tenido lugar hasta la obtención de los resultados, o el grado de sorpresa (cómo de diferente es el valor esperado del real), ya que tienen mayor impacto emocional los resultados inesperados (Ainslie, 1992). De hecho, el desajuste entre cómo nos sentimos ante una situación y cómo nos esperábamos sentir determina las elecciones futuras en mayor medida que el desajuste en la cantidad de reforzador en sí mismo (Balleine, 2021; Heffner et al., 2021). Por eso, si sentimos decepción después de haber comido en un restaurante que nos habían recomendado, aunque hayamos comido lo suficiente, es bastante probable que no volvamos a ir. En definitiva, la diferencia de valor entre el

resultado real-esperado es crucial para el aprendizaje y para el objetivo último de adaptar el comportamiento (Rangel et al., 2008).

Las áreas cerebrales encargadas de procesar las recompensas y castigos muestran actividad durante la exposición al resultado, y dicha actividad se modula en función del valor real del mismo (Morelli et al., 2022). La corteza prefrontal medial está relacionada con el procesamiento de la retroalimentación o feedback (Knutson et al., 2003), la amígdala procesa la experiencia de las pérdidas (Gupta et al., 2011a), la corteza cingulada anterior codifica los errores de predicción (Grupe y Nitschke, 2013) y el estriado ventral, el giro paracentral y la corteza orbitofrontal están implicados en la detección de las diferencias entre el valor real y el esperado, y su respuesta ante los reforzadores es mayor cuanto más inesperados son (McClure et al., 2004). Además, estas áreas muestran actividad anticipatoria, previa a la obtención de recompensas o castigos (Kotani et al., 2015; Mento et al., 2015). La anticipación de las situaciones futuras normalmente se basa en las regularidades del entorno o en la presencia de señales ambientales, y es un elemento clave para la conducta adaptativa (Breska y Ivry, 2018; Coull, 2009). Sin embargo, existen resultados que no dependen de señales ni de regularidades, ni pueden compararse con un valor esperado, porque son acontecimientos impredecibles, lo que, por otro lado, no implica que el cerebro no los pueda anticipar. Cuando los eventos impredecibles ocurren en situaciones de la vida cotidiana, en muchas ocasiones generan consecuencias catastróficas. Un claro ejemplo son los accidentes de tráfico, que conllevan severos daños físicos y psicológicos, e incluso la muerte. Investigaciones previas muestran que la actividad predictiva anticipatoria cerebral permite distinguir entre situaciones estimulares con diferentes características que se presentan de manera aleatoria (Duggan y Tressoldi, 2018; Mossbridge et al., 2014). No obstante, la mayoría de los estudios que se han realizado en este campo se han llevado a cabo en contextos cuyas consecuencias son

irrelevantes. Por lo tanto, dada la importancia que tiene para la conducta adaptativa y el bienestar la anticipación y el procesamiento cerebral de los resultados impredecibles, es necesario profundizar en su estudio en contextos dinámicos ecológicos. Este objetivo se aborda en el estudio 2.

Prevención del comportamiento de riesgo

Un aspecto fundamental para el aprendizaje y la adaptación del comportamiento futuro, es la valoración de las consecuencias de las acciones que se realizan. Desde el punto de vista del aprendizaje instrumental, las consecuencias positivas o agradables aumentan la probabilidad de que una conducta se repita en el futuro, mientras que las negativas o desagradables disminuyen la probabilidad de que esta vuelva a realizarse (Ley del efecto; ver por ejemplo, Cándido (2000)). Respecto al comportamiento de riesgo, la aplicación de técnicas basadas en estos modelos de aprendizaje, como las sanciones o la retroalimentación contingente, se ha demostrado eficaz para reducir las decisiones arriesgadas (Maldonado et al., 2016; Megías et al., 2017). El ejemplo más cotidiano del uso de estas herramientas para la modificación de la conducta es el permiso de conducir por puntos, que ha sido el método más eficaz para reducir el comportamiento de conducción imprudente (Novoa et al., 2010). Además, estas estrategias mejoran la funcionalidad de las redes cerebrales implicadas en el control cognitivo (Megías, Torres, et al., 2018).

Por otro lado, teniendo en cuenta la influencia de los estados emocionales y de las características personales que intervienen en las diferentes etapas de la toma de decisiones, una estrategia efectiva para reducir el comportamiento de riesgo puede ser el uso de intervenciones que regulen estos factores. Dadas las particularidades del rasgo de mindfulness que influyen en la selección de la acción, como son la reorientación de la atención al momento presente, la observación de las propias sensaciones y la apertura y

la aceptación de la experiencia (Baer et al., 2006; Brown y Ryan, 2003; Kabat-Zinn, 2005), los programas que entrenan estas habilidades pueden repercutir en la conducta adaptativa (Liu et al., 2021; Quaglia et al., 2016; M. Y. Wang et al., 2021; Zuo et al., 2023). Las intervenciones basadas en mindfulness, como el programa de reducción del estrés (Kabat-Zinn et al., 1992), la terapia cognitiva basada en mindfulness (Segal et al., 2002), el programa de prevención de recaídas (Marlatt y Witkiewitz, 2002), la terapia dialéctica conductual (Linehan, 1993) o la terapia de aceptación y compromiso (Hayes et al., 2003), entrenan las habilidades de la atención plena mediante diversas prácticas de meditación (ej. atención a la respiración, escaneo corporal y meditación guiada) y yoga. También incluyen grupos de debate y enseñan herramientas de reestructuración cognitiva y gestión emocional, como por ejemplo hacer una pausa y detenerse para respirar, de manera que se facilita la observación de la situación, la atención a la experiencia externa e interna y la selección de una respuesta adecuada (Baer, 2003). De hecho, los programas basados en mindfulness mejoran las habilidades de regulación emocional y el bienestar y la salud psicológica general (Eberth y Sedlmeier, 2012; Garland et al., 2017; Gu et al., 2015; Roemer et al., 2015; Vanzhula y Levinson, 2020).

Sin embargo, respecto a otros factores que intervienen en la toma de decisiones, como la impulsividad, la mayoría de las investigaciones que utilizan los entrenamientos basados en mindfulness se han centrado en el tratamiento de trastornos mentales que conllevan conductas asociadas a estos rasgos, como el consumo de sustancias, los atracones, o el trastorno por déficit de atención e hiperactividad, por lo que los resultados son variados y pueden verse afectados por otras variables relacionadas con las características de la población clínica (Cairncross y Miller, 2020; Cavicchioli et al., 2018; J. P. Davis et al., 2019; Maddox, 2011; Vidrine et al., 2016). Por lo tanto, se necesita más

investigación para profundizar en los mecanismos específicos que se relacionan con los beneficios de la práctica del mindfulness.

No obstante, independientemente de los efectos que puedan generar en los procesos que subyacen a la toma de decisiones disfuncionales, las intervenciones basadas en mindfulness se han demostrado eficaces para reducir el comportamiento de riesgo autoinformado, así como las decisiones de riesgo en contextos de la vida cotidiana, como la conducción (Baltruschat, 2020; Baltruschat, Mas-Cuesta, et al., 2021; Koppel et al., 2019). Más concretamente, nuestro grupo de investigación ha observado que un grupo de conductores reincidentes mejoraba su ejecución al volante y tenían menos accidentes después de cinco semanas de entrenamiento en mindfulness (Baltruschat, Mas-Cuesta, et al., 2021). Por lo tanto, no es de extrañar que los mecanismos neurobiológicos de la práctica de la atención plena se relacionen con las redes de control cognitivo y de recompensa cerebral (Baltruschat, Cándido, et al., 2021; Bursky et al., 2022; Gotink et al., 2016; Pernet et al., 2021; Tang et al., 2015). En este sentido, se ha observado que el entrenamiento en mindfulness produce cambios estructurales en áreas como la corteza cingulada anterior y posterior, la amígdala, la ínsula, el núcleo caudado, el tálamo, las cortezas prefrontal y somatosensorial, el precuneus, el lóbulo parietal y la unión temporo-parietal, el giro lingual y el cerebelo (Fahmy et al., 2018; Hölzel et al., 2011; Melis et al., 2023; Pickut et al., 2013; Santarnecchi et al., 2014; Siew y Yu, 2023; Weder, 2022; C.-C. Yang et al., 2019; Yu et al., 2021; Yuan et al., 2020). Sin embargo, la naturaleza de los efectos en la modificación de la estructura cerebral varía en función del estudio y hay pocas investigaciones que los hayan relacionado con los mecanismos que se cree que sustentan las habilidades de mindfulness. Por lo tanto, es necesario profundizar en el estudio de los cambios, a nivel neuroanatómico, de la práctica de la atención plena y cómo estos cambios se relacionan con los procesos cognitivos y de personalidad que intervienen

en las habilidades de mindfulness y en el comportamiento de riesgo. Estos objetivos se abordan en el estudio 3 de la tesis.

JUSTIFICACIÓN Y OBJETIVOS

JUSTIFICACIÓN Y OBJETIVOS

La toma de decisiones es un proceso sustentado por múltiples redes cerebrales encargadas de valorar las alternativas de acción, controlar la conducta y evaluar los resultados para facilitar el aprendizaje. Aunque conocemos los factores contextuales y personales que determinan la funcionalidad de la elección de la conducta, todavía es necesaria investigación para esclarecer cómo se configuran los sistemas neurocognitivos y de personalidad implicados en las distintas etapas de la toma de decisiones y cómo los cambios que se producen en estos sistemas permiten anticipar y procesar resultados inesperados y prevenir el comportamiento desadaptativo. Es por esto que la presente tesis doctoral profundiza en las bases neuroanatómicas del comportamiento de riesgo y de sus factores de personalidad asociados. También aborda el estudio del procesamiento cerebral de las acciones cuyos resultados son impredecibles y conllevan consecuencias negativas para el bienestar, y examina cómo las intervenciones que se han demostrado eficaces para mejorar la conducta adaptativa producen cambios en los sistemas cerebrales que se relacionan con los procesos cognitivos y de personalidad que intervienen en la toma de decisiones y en el comportamiento de riesgo.

Un ejemplo cotidiano de toma de decisiones donde pueden observarse comportamientos arriesgados con resultados catastróficos, tanto a nivel personal como económico y social, son los entornos de tráfico. Por ello, y debido a su gran validez ecológica y posibilidad de generalización, se utiliza la conducción para abordar los objetivos de los estudios de la tesis.

El estudio 1 explora las bases neuroanatómicas del comportamiento de conducción arriesgado y su relación con los rasgos de personalidad que se asocian con este tipo de conducta. La tendencia al riesgo se ha determinado teniendo en cuenta

situaciones de conducción de la vida real y las variables de personalidad se han elegido en función de las que la literatura previa ha establecido como más influyentes en la toma de decisiones disfuncionales, en general, y en el comportamiento de riesgo en conducción, en particular. Por lo tanto, se han evaluado la impulsividad cognitiva y la sensibilidad a las recompensas y castigos.

El estudio 2 investiga el procesamiento cerebral de los eventos catastróficos. Para ello se han utilizado los milisegundos previos y posteriores a la ocurrencia de accidentes en contextos de conducción simulada. En ambos periodos se ha analizado la actividad cerebral, estimada mediante el registro de electroencefalografía, y la conectividad efectiva de las siete redes principales del cerebro (visual, somatomotora, límbica, atencional dorsal y ventral, frontoparietal y red por defecto) y se han estudiado las diferencias tanto a nivel intra-, como inter-sujetos.

El estudio 3 analiza los efectos neuroanatómicos de una intervención basada en mindfulness de cinco semanas. Dada la influencia de algunos factores de personalidad en la conducta adaptativa, también se ha investigado si la práctica de mindfulness puede afectar a la atención plena disposicional y a la impulsividad y si los cambios estructurales producidos por la intervención se relacionan con estos rasgos de personalidad.

Por lo tanto, los objetivos generales y específicos de los tres estudios son los siguientes:

Estudio 1: Explorar la relación entre la estructura cerebral, la conducción arriesgada y los rasgos de personalidad.

- Estudiar las bases neuroanatómicas del comportamiento de conducción arriesgado.
- Investigar la relación entre la impulsividad y la sensibilidad a las recompensas y castigos y el volumen de materia gris cerebral.
- Determinar cómo influye el nivel de riesgo en conducción en la relación entre la estructura cerebral y los rasgos de personalidad.

Estudio 2: Investigar cómo procesa el cerebro la ocurrencia de eventos catastróficos.

- Explorar los marcadores de la actividad cerebral anticipatoria de los accidentes.
- Examinar la actividad cerebral asociada al procesamiento de los accidentes.
- Estudiar cómo evoluciona la conectividad efectiva entre las redes cerebrales a lo largo de la ocurrencia de los accidentes.

Estudio 3: Examinar los cambios neuroanatómicos y en los rasgos de personalidad después de una intervención basada en mindfulness.

- Investigar los efectos de un entrenamiento en mindfulness en el mindfulness disposicional y la impulsividad.
- Estudiar la relación entre los cambios de los rasgos de personalidad.
- Explorar los efectos de una intervención basada en mindfulness en la estructura cerebral.
- Determinar cómo los efectos en la estructura cerebral se relacionan con los cambios en los rasgos de personalidad.

ESTUDIO 1

Relationships between personality traits and brain gray matter are different in risky and non-risky drivers.

Mas-Cuesta, L., Baltruschat, S., Cándido, A. y Catena, A. (2022). Relationships between Personality Traits and Brain Gray Matter Are Different in Risky and Non-risky Drivers. *Behavioural Neurology*, 2022, e1775777. <https://doi.org/10.1155/2022/1775777>

Abstract

Personality traits such as impulsivity or sensitivity to rewards and punishments have been associated with risky driving behavior, but it is still unclear how brain anatomy is related to these traits as a function of risky driving. In the present study, we explore the neuroanatomical basis of risky driving behavior and how the level of risk-taking influences the relationship between the traits of impulsivity and sensitivity to rewards and punishments and brain gray matter volume. One hundred forty-four participants with different risk-taking tendencies assessed by real-life driving situations underwent MRI. Personality traits were assessed with self-report measures. We observed that total gray matter volume varied as a function of risky driving tendencies, with higher risk individuals showing lower gray matter volumes. Similar results were found for volumes of brain areas involved in the reward and cognitive control networks, such as the frontotemporal, parietal, limbic, and cerebellar cortices. We have also shown that sensitivity to reward and punishment and impulsivity are differentially related to gray matter volumes as a function of risky driving tendencies. Highly risky individuals show lower absolute correlations with gray matter volumes than less risk-prone individuals. Taken together, our results show that risky drivers differ in the brain structure of the areas involved in reward processing, cognitive control, and behavioral modulation, which may lead to dysfunctional decision-making and riskier driving behavior.

Keywords: risky driving, gray matter, reward sensitivity, punishment sensitivity, delay discounting.

Introduction

A risky driving style, characterized by driving over the speed limit, not paying attention to traffic, driving under the influence of alcohol or drugs, or not wearing a seat belt or helmet, are behaviors associated with a history of traffic offenses (Taubman – Ben-Ari et al., 2016; Taubman - Ben-Ari & Yehiel, 2012) and is, in part, responsible for traffic accident fatalities that rank eighth among the causes of mortality worldwide (World Health Organization, 2015, 2018). Certain personality traits, such as impulsivity and sensitivity to rewards and punishments, have been linked to risky driving behavior styles (Padilla et al., 2018; Panayiotou, 2015). It seems that the brain systems related to these personality traits show a dysfunctional interaction when making risky decisions (Ferenczi et al., 2016). However, there is still a knowledge gap regarding the neuroanatomical bases of risky driving and the relationships between brain anatomy and personality traits such as sensitivity to reward and punishment or preference for immediate versus delayed rewards. Our main aim was to address this gap using a large sample of individuals with different risk tendencies assessed using self-reported real-life driving behaviors.

The brain networks supporting the processing of the subjective value of rewards and punishments and those involved in conflict monitoring in decision-making have been linked to risky behavior. These networks are located in brain regions such as the striatum, the orbitofrontal cortex (OFC), superior and posterior parietal cortex, the lateral prefrontal cortex (LPFC), the medial temporal lobe, the insula, or the anterior cingulate cortex (ACC) (Goh et al., 2016; Helfinstein et al., 2014; Lee et al., 2016; Levy, 2017; Peters & Büchel, 2009; Vorobyev et al., 2015; Xue et al., 2018). Only a few recent studies have investigated the relationship between risky driving behavior and the volume of brain gray matter of these structures. In a study with people with multiple sclerosis, Dehning et al. (2014) found that the size of the third ventricle, an indicator of thalamic atrophy, was

significantly correlated with traffic rule violations and predicted a significant portion of the variance in traffic offenses. Kwon et al. (2014) observed, in a computerized driving task, that more risky adolescents did not show differences in gray matter volume than less risk-prone individuals. However, they observed differences between these two groups in the integrity of the white matter in frontal regions. Sakai et al. (2012) found that older people with lower executive function had a lower volume in the supplementary motor area (SMA) and, more importantly, were prone to risky driving. Dedovic et al. (2016) found that men who had driven under the influence of alcohol (without engaging in other dangerous drinking patterns) showed a reduced cortical thickness of the posterior cingulate cortex (PCC) compared with drivers in the control group. Finally, Aydogan et al. (2021) observed that drivers who reported driving faster than the allowable speed limit had lower GMV in the ventromedial and dorsolateral prefrontal cortices, amygdala, and striatum. The evidence gathered to date shows the need to study further the neuroanatomical basis of risk-taking behavior in driving.

Sensitivity to reward (SR) and punishment (SP) reflect individual differences in the behavioral activation system (BAS) and the behavioral inhibition system (BIS), which control the approach and inhibitory responses to appetitive or aversive stimuli (Gray, 1970). Risky behavior has been linked to greater sensitivity to rewards and less sensitivity to punishment (Baltruschat et al., 2020). Scott-Parker & Weston (2017) found that drivers with high sensitivity to rewards and minor sensitivity to punishment behaved in a riskier way while driving and in health-related behaviors. However, other studies appear to indicate that sensitivity to punishment has little influence on risky driving and that sensitivity to rewards is a distal predictor of this behavior (Castellà & Pérez, 2004; Constantinou et al., 2011; Padilla et al., 2018). Therefore, the relationship between sensitivity to reward and punishment and risky driving behavior is still unclear.

Furthermore, the relationships between SR and SP and brain volume in risky driving contexts have not yet been studied, although some studies have explored the association between brain volume and personality traits such as SP and SR or impulsivity. Regarding SR, positive and negative correlations have been found with the volume of the striatum (Adrián-Ventura et al., 2019; Li et al., 2019; Parcet et al., 2020; Urošević et al., 2015) and negative correlations with the volumes of the lateral and medial prefrontal and superior temporal cortices (Adrián-Ventura et al., 2019; Barrós-Loscertales et al., 2006a; Parcet et al., 2020). On the other hand, SP has been positively correlated with volumes of the amygdala and hippocampal formation and negatively with the insula and OFC volumes (Adrián-Ventura et al., 2019; Barrós-Loscertales et al., 2006b; Fuentes et al., 2012; Holmes et al., 2012; Iidaka et al., 2006; Levita et al., 2014; Von Siebenthal et al., 2020). Thus, the correlations between brain structure and SR and SP could differ depending on the population under study. In this regard, Parvaz et al. (2011) found that the P300 (an event-related measure of reward sensitivity) was positively related to the volume of the frontostriatal circuit in healthy participants. However, in people addicted to cocaine, no relationship was observed between P300 and gray matter volume. Therefore, it is critical to determine whether the relationships between reward and punishment sensitivity and brain gray matter volumes vary depending on whether or not people exhibit risky driving behavior.

Another related and essential personality factor implicated in risk behavior is impulsivity. This personality trait is a multidimensional construct that includes the tendency to choose risky options, the inability to assess the risk associated with a decision, or the preference for immediate reinforcement (Cherek & Lane, 1999; Eysenck & McGurk, 1980). The preference for immediate reward in delayed discounting tasks (DDT) has been positively related to risk behavior, such as financial (Beauchaine et al.,

2017) or risky sexual behaviors (Chesson et al., 2006; Story et al., 2014). In stark contrast, other studies have not observed significant relationships between discounting rate and risk behavior (Mishra & Lalumière, 2011, 2017). Regarding risky driving behavior, some studies have found a positive relationship between the value placed on immediate rewards and self-reported risky driving (Murphy & Murphy, 2018; Zimbardo et al., 1997) or errors while driving in a simulator (Romanowich et al., 2020). It has also been observed that drivers who use a mobile phone while driving have a higher discounting rate than those who do not (Hayashi et al., 2015) although this finding was not replicated in subsequent studies (Hayashi et al., 2017). Furthermore, in a recent study, Qu et al. (2020) have observed no relationship between the preference for immediate reinforcement and risky driving behavior. However, these authors demonstrated that a higher discounting rate for large rewards significantly predicted safer driving behaviors. Therefore, the type of relationship between risky driving and a preference for immediate reinforcement seems questionable.

Regarding the brain correlates of cognitive impulsivity, the neural networks involved in valuation (striatum, OFC, medial prefrontal, lateral parietal, and posterior cingulate cortices), conflict monitoring and cognitive control (ACC and LPFC) and prospection (hippocampus and amygdala), have been assumed to underlie the process of delay discounting (Peters & Büchel, 2011; Wesley & Bickel, 2014). Some relationships between the preference for immediate reinforcement and gray matter volumes of various brain areas have been found at the neuroanatomical level. For instance, positive and negative correlations have been observed between the gray matter volume and the discounting rate in medial prefrontal regions, superior frontal gyrus, OFC, striatum, and ACC (Barry et al., 2020; Bernhardt et al., 2014; Cho et al., 2013; Freinhofer et al., 2020; Li et al., 2019; Meade et al., 2020; Pehlivanova et al., 2018; Schwartz et al., 2010;

Tschernegg et al., 2015; Wang et al., 2016). The preference for immediate reinforcement has also been negatively associated with volumes of the lingual gyrus, LPFC, entorhinal cortex, and medial temporal gyrus (Bjork et al., 2009; Owens et al., 2017). Likewise, positive relationships have been observed between volumes of the parahippocampal gyrus, PCC, insula, and lateral occipital cortex and the discounting rate (Guo et al., 2017; Mohammadi et al., 2016; Wang et al., 2016). Finally, regarding the total gray matter volume, Owens et al. (2017) have observed that a higher discounting rate is significantly associated with a lower total cortical, but not subcortical, gray matter. Despite previous evidence, the associations between gray matter volume and delay discounting seem inconclusive and vary depending on the population under study. In this regard, Wang et al. (2017) found that while impulsivity was negatively related to the volumes of frontal and limbic areas in healthy people, no such relationship was found in obese individuals.

To the best of our knowledge, no research has yet been done to examine the neuroanatomical correlates of delay discounting in drivers. Therefore, it is necessary to carry out an in-depth study of the associations between preference for immediate reinforcement and cerebral gray matter volume, which could be very helpful for determining whether these associations vary depending on the extent to which drivers are risk-prone. Thus, the main objective of this paper was to study the neuroanatomical bases of risky driving behavior and how the level of risk-taking influences the link between impulsivity and sensitivity to reward and punishment and the volume of brain gray matter. We hypothesized that riskier drivers would have a lower volume of brain gray matter than less risky drivers, particularly in areas related to reward and cognitive control processing and valuation. Furthermore, according to previous literature (Parvaz et al., 2011; Wang et al., 2017), we expect that the relationship between personality traits and brain gray matter volume depends on the level of risky driving.

Materials and methods

Participants

Participants in this study were part of a more extensive study aimed at revealing the brain basis of risk behavior in traffic situations. We used structural MRI from 144 participants (50 women, 32.06 years old, range= [18, 68]). None of the participants reported a history of head injury nor a history of neurological disorders. All participants signed an informed consent form, were informed of their rights, and were treated according to the Helsinki Declaration (World Medical Association, 2013). All participants were paid for their participation in the study. The Ethics Committee of Human Research of the University of Granada approved this research (204/CEIH/2016). Participants were then organized into three groups, according to their risky driving behavior in real life.

Risk classification

Each participant was asked to indicate whether and how many points they had lost in the Spanish fine system due to traffic rule violations, whether they have attended a rehabilitation course to recover these points, how many fines they had received for violating traffic rules, and if they usually exceed the speed limit by 20% or higher when driving. All these variables are binary and of different importance, which precludes their use as numerical variables or continuous variables. The Non-Risk Group (NR) was composed of 28 participants who had received up to two fines but had not lost points, had not attended a rehabilitation course, and did not exceed the speed limit by 20% when driving. The Medium-Risk (MR) group was composed of 53 participants who had retained all their points but had received more than two fines and usually exceed the speed limit by more than 20% when driving. Finally, the High-Risk (HR) group was composed of 63 participants who had lost more than one point from their driver's license due to severe violations of traffic rules.

Instruments

Sensitivity to punishment and sensitivity to reward questionnaire

The sensitivity to punishment and sensitivity to reward questionnaire (SPSRQ-20; Aluja & Blanch, 2011) consists of 20 dichotomic items (Yes/No) divided into two subscales: the sensitivity to reward (SR) and sensitivity to punishment (SP). The SR measures the BAS, and the SP measures the BIS (Torrubia et al., 2001).

Monetary Choice Questionnaire

The Monetary-Choice Questionnaire (MCQ; Kirby & Maraković, 1996) evaluates individual preferences between smaller, immediate rewards (SIRs) and more significant, delayed rewards (LDRs) that vary in their value and time to be delivered. Participants are presented with a fixed set of 27 choices between SIRs and LDRs. For example, on the first trial, participants were asked, "Would you prefer 54 euros today, or 55 euros in 117 days?" The trial order was arranged so that it did not correlate with the immediate or delayed reward amounts, their ratio, their difference, the delay to reward, or the discounting rate corresponding to indifference between the two rewards (Kirby & Petry, 2004). The preference for immediate rewards is calculated by counting the number of choices of SIRs.

Procedure

Participants came to the research center and, as a part of a broader project, signed the informed consent form, completed the questionnaires, and underwent the MRI scan. The order of the questionnaires and MRI scanning were arranged according to the availability of MRI and the participants' schedules.

MRI and data analysis

The MRI scans were conducted with a Siemens 3T Trio system equipped with a 32-channel head coil at the Mind, Brain, and Behavior Research Center of the University of

Granada. Participants were instructed not to move during the scan. Head restraint and foam padding around the head were used to limit head motion. A T1-weighted MPRAGE scan was obtained with a TR (repetition time) of 1900 ms, TE (echo time) of 2.52 ms, and a flip angle of 9°. For each volume, 176 slices of 1 mm thickness were obtained, which provide whole-brain coverage (voxel size = 1 × 1 × 1 mm; FOV = 256 mm; 256 × 256 data acquisition matrix).

The MRI scans were submitted to CAT12 toolbox (<http://www.neuro.uni-jena.de/cat/>) to obtain brain volumes, running under the umbrella of SPM12 (<https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>), using default parameters. In essence, CAT12 corrects for bias inhomogeneity, segmented into gray matter, white matter, and cerebrospinal fluid using the AMAP approach, and the images were spatially normalized using the Diffeomorphic Anatomical Registration through the Exponentiated Lie algebra (DARTEL) algorithm. Volumes were then normalized to the MNI neurological space and multiplied by the Jacobian determinant to preserve volume. Gray matter volumes were then smoothed using an 8 mm FWHM Gaussian kernel. This volumes were submitted to a voxel-wise analysis, as described below. After that, neuromorphometric anatomical areas were extracted to perform partial correlation analysis (see below for further details).

SPM 12 was used to perform the voxel-wise statistical analyses. The general linear model was used, in which a single factor (three levels) was manipulated between subjects. Comparisons between the three groups were made while controlling for age, gender, education level, and total intracranial volume (TIV) (results are also provided controlling only for age, gender and educational level, for sensitivity analysis and comparative purposes). FDR corrected the significance threshold to a cluster $q < 0.05$, we used an extended cluster size of 240 voxels based on simulations done with Rest-AlphaSim

(FWHM=8, mm=4, voxel threshold=0.001), 1000 iterations, to further control for the multiple comparison problem. The automated anatomic atlas (AAL) was used to label the significant clusters of interest.

Our second analysis was aimed at uncovering the relationships between SPSRQ and MCQ scores and brain, using a partial correlation approach. For this approach we used the anatomic parcellation provided by the computational anatomy toolbox (CAT12). This software provide volumetric information according to the neuromorphometric atlas. We obtained the volumes of 116 structures (only regions with gray matter were retained, so 26 of the 142 regions provided by the neuromorphometric atlas were excluded), which were then correlated using the partial correlation coefficients with the SPSRQ and the MCQ variables. This analysis also controlled for age, gender, education level and TIV (data are also provided controlling only for age, gender and education level, for comparative purpose). The differences between correlation coefficients were then obtained for the comparisons between non-risk versus medium- and high-risk, and medium versus high-risk groups. It is important to note that the size of the correlation coefficient is dependent on the sample size used to compute it. In line with a recent proposal regarding the significance threshold (Benjamin et al., 2018; Johnson, 2013), we adopted a p -value <0.005 to test for the statistical significance of these 348 differences.

Results

Table 1 displays the means and standard deviations for age, education level, TIV, total gray and white matter volumes, the number of women in each group, punishment and reward sensitivity, and the preference for an immediate reward. There were differences in age between group MR and HR ($p<0.05$) and in the number of women ($p<0.05$). No other differences were observed. No differences in sensitivity to punishment, sensitivity

to reward, or preference for immediate reward were observed between groups (min $p=0.11$).

No differences in TIV were observed between the three groups ($p>0.10$). However, differences in total gray matter volume were observed between the NR and HR groups ($p<0.01$), indicating larger volumes in the NR than the HR group (Table 1). This indicates the general tendency for risky individuals to have a lower total gray matter volume. No differences in white matter volumes were observed between the three groups (all $p>0.22$).

Table 1. Means and standard deviations for age, education level, number of women, total intracranial volume, total gray and white matter volumes, punishment and reward sensitivity, and preference for immediate rewards in each group.

Group	Age	Education	Gender	TIV	GMV	WMV	SP	SR	IR	N
NR	30.8 (14.9)	3.5 (0.5)	F=9	1614.1 (134.7)	741.5 (66.5)	540.4 (62.4)	2.9 (2.3)	4.4 (2.2)	15.0 (5.0)	28
MR	25.6 (10.7)	3.6 (0.5)	F=30	1541.7 (139.6)	722.4 (73.3)	511.0 (56.1)	3.9 (2.9)	4.4 (2.6)	14.2 (4.5)	53
HR	38.1 (12.4)	3.3 (0.8)	F=11	1565.6 (116.8)	692.1 (60.3)	532.2 (52.8)	3.4 (2.7)	3.8 (2.8)	14.9 (5.5)	63

Note NR: Non- risk; MR: Medium-risk; HR: High-risk; TIV: total intracranial volume; GMV: gray matter volume, WMV: white matter volume; SP: sensitivity to punishment, SR: sensitivity to reward; IR: immediate reward.

Table 2 displays the peak t-scores for the significant differences, corrected for multiple comparisons. Differences were observed in the left superior parietal cortex for the contrast NR>MR. Differences were also observed in the right parahippocampal gyrus, right cerebellum 6, and left caudate, volumes for the contrast MR>HR. Differences in volumes of the vermis, right middle frontal cortex, and left superior parietal cortex were observed for the contrast NR>HR. Note, however, that a larger set of differences were found significant when no TIV controlling was used.

Table 2. Between-group comparisons in brain gray matter volume, adjusted for age, sex and cultural level (left) and also by total intracranial volume (right).

Label	Controlled by Age, Sex, Education						and TIV	
	Size	t-peak	X	Y	Z	pFDR	Size	pFDR
NR>MR								
Parietal_Sup_L	1138	4,48	-33	-41	63	0,001	793	0,001
MR>HR								
ParaHippocampal_R	2355	4,72	47	5	-47	0,001	1250	0,001
Cerebellum_6_R	926	4,09	26	-48	-27	0,001	318	0,03
Caudate_L	660	4,01	-14	27	0	0,001	245	0,05
Putamen_R	430	3,9	35	2	0	0,01		
SupraMarginal_R	337	3,64	59	-30	35	0,023		
NR>HR								
Cerebellum_6_R	2014	4,17	35	-71	-30	0,001		
Cerebellum_9_L	412	3,72	15	-57	-56	0,005		
Cerebellum_Crus2_1	819	4,15	-45	-62	-26	0,001		
Vermis_1_2	1808	4,63	-15	-44	-23	0,001	527	0,004
Frontal_Inf_Orb_L	388	4,03	-53	42	-5	0,006		
Frontal_Inf_Tri_R	502	4,35	41	17	17	0,002		
Frontal_Med_Orb_L	364	3,49	15	5	-17	0,007		
Frontal_Mid_L	1741	4,53	-50	8	39	0,001		
Frontal_Mid_R	3940	4,97	27	29	41	0,001	335	0,014
Frontal_Sup_Medial_L	495	4,13	-5	56	32	0,002		
Fusiform_R	512	3,82	45	0	-51	0,002		
Heschl_R	368	4,17	63	-11	9	0,007		
Insula_R	1170	4,74	36	-5	-2	0,001		
Lingual_L	1087	4,71	-24	-90	-6	0,001		
Parietal_Sup_L	3092	4,69	-35	-39	53	0,001	435	0,006
Temporal_Sup_R	1087	4,64	59	-27	30	0,001		
Temporal_Sup_L	461	3,95	-41	14	-14	0,003		
Temporal_Pole_Mid_R	2375	4,13	45	21	-5	0,001		

Note: NR: Non-risk; MR: Medium-risk; HR: High-risk

We then used the neuromorphometric atlas to uncover the relationships between scores on the SPSRQ and the MCQ questionnaires and brain parcels (Table 3, Figure 1). We observed that for the NR-MR contrast, differences between correlations were significant for punishment sensitivity in the right medial precentral cortex, left superior medial frontal cortex and right posterior insula, while for the immediate reward differences were observed in bilateral nucleus accumbens (nAcc), right amygdala, right lingual, right PCC, and left inferior OFC. For the NR-HR contrast, differences were

observed for reward sensitivity in the left frontal operculum, left medial postcentral cortex, and left superior temporal cortex (STC), while for immediate reward, differences were observed in left nAcc and left inferior OFC. Finally, for the MR-HR contrast, differences were observed for punishment sensitivity in the bilateral medial precentral, reward sensitivity in the left occipital fusiform, and immediate reward in the left occipital pole and left PCC. Note that when no TIV control was applied, fewer brain areas remained significant.

Table 3. Between-groups contrast of the correlations between SPSRQ and MCQ scores and gray matter volume, after controlling for age, sex and cultural level (left) and also by total intracranial volume (right).

Variable	Controlling for age, sex and cultural level				And for TIV		
	Label	r1	r2	z	r1	r2	z
NR-MR							
IR	L Accumbens	-0,54*	0,18	-3,24	-0,57*	0,26*	-3,73
IR	R Accumbens				-0,48*	0,14	-2,73
IR	R Amygdala				-0,25	0,39*	-2,69
IR	R Lingual				-0,34*	0,40*	-3,18
IR	L Inferior Frontal Orbital	-0,63*	-0,04	-2,86	-0,68*	0,00	-3,40
IR	R Posterior Cingulate				-0,31*	0,36*	-2,88
SP	R Medial Precentral				0,32*	-0,34*	2,80
SP	L Superior Medial Frontal				-0,59*	0,02	-2,85
SP	R Posterior Insula	-0,5*	0,14	-2,83	-0,45*	0,26*	-3,09
NR-HR							
IR	L Accumbens				-0,57*	0,04	-2,89
IR	L Inferior Frontal Orbital	-0,63*	-0,11	-2,65	-0,68*	0,01	-3,51
SR	L Frontal Operculum				-0,42*	0,17	-2,61
SR	L Medial Poscentral	0,43*	-0,2*	2,8	0,43*	-0,22*	2,90
SR	L Superior Temporal				0,50*	-0,08	2,63
MR-HR							
IR	L Occipital Pole	0,23*	-0,3*	2,86	0,35*	-0,18	2,85
IR	L Posterior Cingulate	0,25*	-0,27*	2,76	0,42*	-0,10	2,88
SP	L Medial Precentral	-0,38*	0,27*	-3,53	-0,36*	0,30*	-3,60
SP	R Medial Precentral				-0,34*	0,15	-2,62
SR	L Occipital Fusiform	0,37*	-0,13	2,71	0,38*	-0,14	2,80

Note. NR: No-risk; MR: Medium-risk; HR: High-risk; r1 is the relationship between the first term of the comparison and the volume of gray matter, r2 is the relationship between the second term of the comparison and gray matter; SR= sensitivity to reward, SP: sensitivity to punishment, IR: immediate reward score. * These correlations were significant at an uncorrected $p < 0.05$. The differences between correlations were significant at $p < 0.005$.

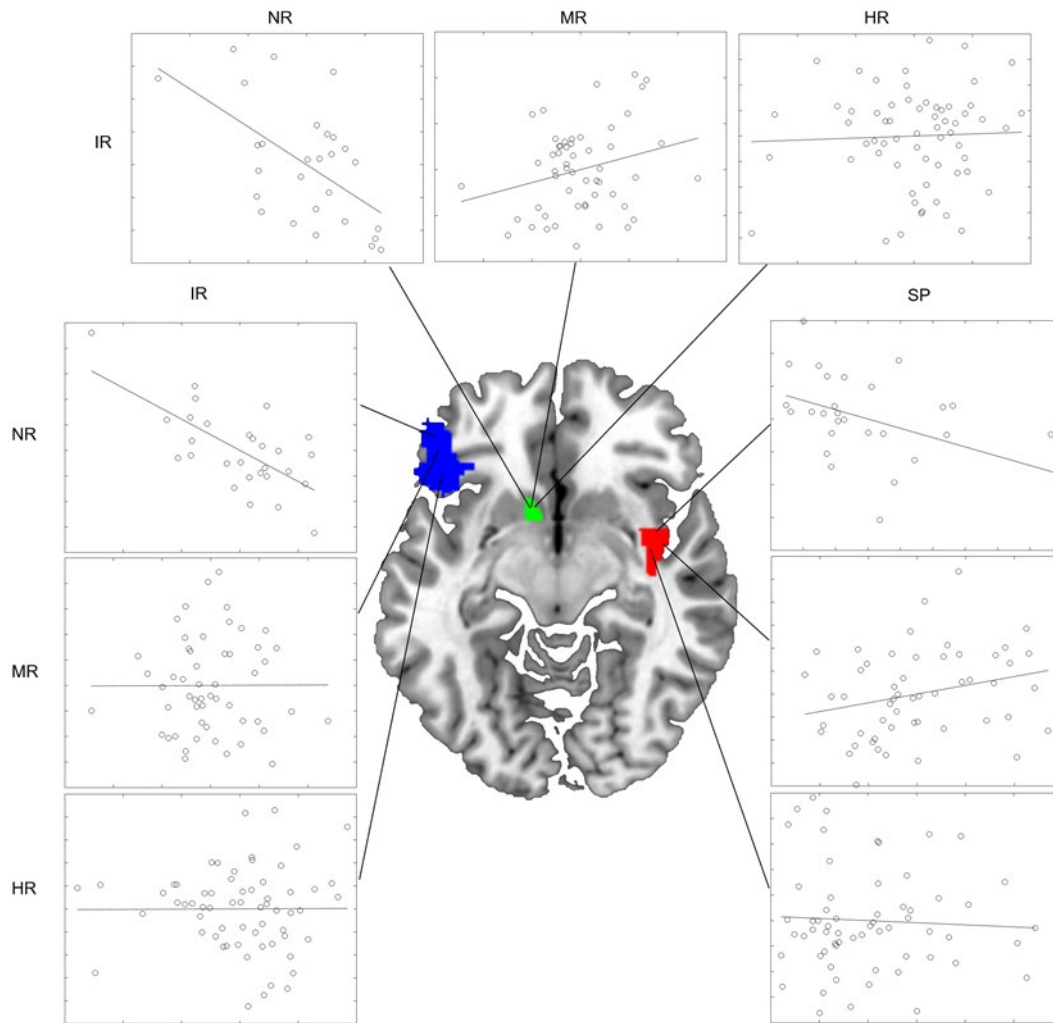


Fig.1 An illustration of the correlations between brain parcels (left accumbens, left inferior frontal orbital gyrus and right posterior insula) and preference for immediate rewards (IR) and sensitivity to punishment (SP), for each risk group.

Discussion

In the present research, we studied the anatomical bases of risky driving behavior and its relationships with reward and punishment sensitivity and the tendency to delay rewards. The main findings are that total gray matter volume varies as a function of risk proneness, with lower brain gray volumes related to higher risk tendencies. This finding applies to both total gray matter volumes and volumes of the frontotemporal, parietal, limbic, and cerebellar cortices (the total number of areas varies according to TIV control). The relationships between reward and punishment sensitivity and the ability to delay rewards

and gray matter volumes differ as a function of risk tendency. High risk individuals showed, in general, lower absolute correlations with gray matter volumes than the less risk-prone individuals. We have also shown that the level of risk is the main factor modulating the relationship between personality traits and brain gray matter volume. When the TIV control was applied, the relationship between preference for immediate reward and gray matter volume was observed to differ between the NR and MR groups in the nAcc, amygdala, lingual gyrus, inferior OFC and PCC, between the NR and HR groups in the left hemisphere structures (nAcc, inferior OFC) and between the MR and HR group in the occipital pole and posterior cingulate cortex. The relationships between sensitivity to punishment and brain gray matter volume also differed between the NR and MR groups in the right medial precentral cortex, left superior medial frontal cortex and right posterior insula, and between the MR and HR groups in the bilateral medial precentral cortex. Finally, the partial correlation between reward sensitivity and gray matter volume differed significantly between groups NR and HR in the left frontal operculum, left medial post-central and left STC, and between groups MR and HR in the left occipital fusiform cortex. When no TIV control was applied, fewer brain areas remained significant.

It is important to note that the use of two different control strategies, including or not the TIV as a covariate, has been done for comparative and sensitivity analysis purposes. The robustness of the data is confirmed by the fact that the control, or not, of the TIV does not modify the type of structure in which differences are found, but rather increases or decreases the significance of these differences. Regarding the study of the anatomical bases of risky driving, both analyses result in differences in GMV between the groups in the same structures. When controlling for TIV some differences are no longer significant, but no new structures appear, nor is the directionality of the differences

reversed. Previous studies confirm our results by finding that the different TIV adjustment methods provide different results and these do not eliminate the GMV differences between groups, but rather make them smaller and in a fewer structures (Hyatt et al., 2020; Sanchis-Segura et al., 2019, 2020). Something similar occurs when using the partial correlation coefficient to study the relationships between GMV and personality traits as a function of risk level. When controlling for TIV, significant relationships appear that were not previously significant and those that were already present when TIV was not taken into account are maintained. Previous studies have also found differences in the statistical power of the relationships between personality traits and GMV depending on the control variables used (Hu et al., 2011; Hyatt et al., 2020; Song et al., 2020). The point that when not controlling for TIV our results show a reduction in the number of structures that are related to personality traits may be due to the fact that these relationships appear but cannot be observed because they are masked by a TIV that is not being taken into account.

Risk-proneness in driving depends on differences in GMV

Our results demonstrate that risky drivers have a lower total gray matter volume than non-risky drivers. This negative relationship between brain total gray matter and risky behavior has also been observed in other measures of risky behavior, such as early use of addictive substances (Weiland et al., 2014). Regarding the brain areas, we have observed that the riskiest drivers have lower gray matter volume in the left superior frontal, medial frontal, triangular inferior frontal, medial and inferior orbital frontal, superior temporal, temporal, and superior parietal cortices, cerebellum, fusiform gyrus, insula, parahippocampus, caudate and putamen before controlling the TIV. The superior parietal and medial frontal cortices, cerebellum, parahippocampus and caudate remained significant after controlling the TIV.

Some of these regions, such as the OFC, the parahippocampus, the caudate, or the putamen, are part of the brain's socio-emotional or reward system (Albert et al., 2013; Bartra et al., 2013; Falk et al., 2012; Knutson & Cooper, 2005; Lambert et al., 2014; Lee et al., 2018; Peters & Büchel, 2011; Xie et al., 2017; Yang et al., 2019). This system is involved in the sensitivity, detection, and processing of incentive signals, the prospection and representation of reward expectations based on previous experience, and in the search, evaluation, and approach to reinforcers (Falk et al., 2012; Knutson & Cooper, 2005; Kohno et al., 2015; Lambert et al., 2014; Levy, 2017; Schweinhardt et al., 2009; Yang et al., 2019). Thus, our results suggest an alteration in the detection, processing, and valuation of rewards in the riskiest drivers, which may involve maladaptive decision-making in traffic situations.

On the other hand, other regions in which we observe lower gray matter volume in risky drivers, such as the superior, medial, and inferior frontal cortex, the superior and medial temporal cortex, the fusiform gyrus, the cerebellum, and the superior parietal cortex, are part of the cognitive control network (Dosenbach et al., 2006; Lee et al., 2018; Luna et al., 2010; McClure et al., 2004; Niendam et al., 2012; Seeley et al., 2007; Sokolov et al., 2017; Steinberg, 2008; Xie et al., 2017). This network is responsible for controlling the general implementation of tasks, particularly during the decision-making phase in probabilistic or intertemporal choice tasks (Dosenbach et al., 2006; McClure et al., 2004). More specifically, this network is involved in the identification of stimuli relevant for the task, inhibitory and attentional control, working memory, conflict and error monitoring, and self-regulation of behavior (Dosenbach et al., 2006; Lee et al., 2018; Luna et al., 2010; McClure et al., 2004; Niendam et al., 2012; Seeley et al., 2007; Steinberg, 2008; Ware et al., 2020; Xie et al., 2017). These executive functions related to cognitive control have been associated with better execution of driving and less risky behavior while

driving (Guinosso et al., 2016; Jongen et al., 2011; León-Domínguez et al., 2017; Mäntylä et al., 2009; O'Brien & Gormley, 2013; Ross et al., 2015; Sakai et al., 2017; Walshe et al., 2017). Thus, consistent with the previous literature, our results indicate an alteration in cognitive control processes in risky drivers, resulting in risky driving decisions.

The reduced volume of brain structures in risky drivers could alter the reward and cognitive control brain networks. These networks act as a dual neurobiological system that works interactively to modulate the decision-making process (Li et al., 2020). On the one hand, the socio-emotional system processes the reinforcers and biases decision-making based on assessing and predicting possible rewards and punishments. On the other hand, the cognitive control system is involved in the selection of actions, conflict monitoring, impulse inhibition, and regulation of the influence of the reward system on the decision-making process (Barry et al., 2020; Chein et al., 2011; Lambert et al., 2014; McIlvain et al., 2020; Nasirivanaki et al., 2015; Noël et al., 2013; Parvaz et al., 2011; Peters & Büchel, 2011; Yang et al., 2019). Gray matter volume alterations in these areas have been described in executive functioning alterations (Ramanoël et al., 2018) and manifestations of risk behavior in both self-reported and laboratory tasks (Li et al., 2020; Lin et al., 2016; Miglin et al., 2019; Nasirivanaki et al., 2015; Yokoyama et al., 2014).

With regard to driving, Beeli et al. (2008) observed that transcranial magnetic stimulation of the LPFC, one of the most critical areas in the cognitive control system, caused drivers to behave in a less risky way (as measured by speed, distance from another car, and speed violations) while driving in a simulator. In another study, Chein et al. (2011) found that adolescents presented more extensive activation of the brain regions involved in reward and took more risks in a driving game in the presence of peers. Moreover, compared with adults, they showed less activation of the regions related to

cognitive control. However, adolescents with greater activation of the control network behaved more safely while driving (Cascio et al., 2015). On the other hand, Aydogan et al. (2021) have found that people who reported higher risk behavior related to alcohol, smoking, sex, or driving had a lower gray matter volume in areas such as the striatum, putamen, ventromedial, and dorsolateral prefrontal cortex, insula, and cerebellum. In another recent study, Yamamoto et al. (2020) have evaluated, using realistic driving situations, risky driving at intersections with stop signs in a group of older adults without cognitive impairment. The best predictors for classifying risky and non-risky drivers were age and the gray matter volume of areas related to executive functions, cognitive control, and incentive processing in the frontal and parietal cortices. These studies support our results regarding the negative relationship between risky driving and gray matter volume of the areas involved in the reward and cognitive control circuits.

The reduced volume of brain structures in risky drivers could also be related to different functionality since any alteration of gray matter volumes appears to influence functional neural activity (Honey et al., 2007). Aydogan et al. (2021) compared their results on brain structure and risk behavior with a meta-analysis of functional magnetic resonance imaging and risk behavior studies (<https://neurosynth.org/>). These authors observed that many brain structures that were anatomically associated with risk behavior were also functionally related to such behavior. On the other hand, a wide variety of studies have observed differential brain activation when performing various laboratory tasks depending on the individuals' level of risk proneness (Barkley-Levenson et al., 2018; Barkley-Levenson & Galván, 2014; Engelmann & Tamir, 2009; Helfinstein et al., 2014; Kohno et al., 2015). These results show that people who engage in risky behaviors, such as reckless driving, could use a different distribution of cognitive resources to non-risky people.

Thus, our results suggest that, in risky drivers, there is an alteration at the level of brain structure in the neural circuits involved in reward processing and cognitive control. Furthermore, these alterations could reflect a distinctive brain activation pattern, which could imply that these drivers show maladaptive information processing and dysfunctional decision making (Baltruschat et al., 2020; Barkley-Levenson et al., 2018).

Personality factors and risk driving

Regarding the sensitivity to rewards and punishments, our results are in line with those obtained by Brown et al. (2016). These authors examined the personality characteristics of three different forms of risky driving: driving while impaired (alcohol-related traffic offenses), speed (non-alcohol-related traffic offenses), and mixed (alcohol-related and speed-related traffic offenses). They found no differences in SPSRQ scores between any of the groups and the control group (no traffic offenses), except for the mixed group, which showed greater sensitivity to rewards than the control group. In another study with repeat offenders, Padilla et al. (2018) have found that sensitivity to rewards, but not sensitivity to punishment, acted as a distal predictor of recidivism. In reference to other risk behavior measures, Navas et al. (2016) found that, although obese people made riskier choices, there were no differences between them and the control group in terms of SPSRQ scores.

Regarding impulsivity, our results are consistent with those obtained by Qu et al. (2020), who found no significant relationships between the preference for immediate reinforcements and risky driving behavior. Hlavatá et al. (2020) investigated the relationship between impulsivity and impulse control disorder in a group of patients with Parkinson's disease. They found that, although the experimental group differed from the control group in self-reported impulsivity and risk behavior, the groups did not differ in DDT scores. In another study with Parkinson's disease patients, no relationships were

observed between performance on various tasks that measure risk behavior (BART; IGT) and DDT (Marín-Lahoz et al., 2020).

However, many studies have found relationships between personality traits and risk behavior (Baltruschat et al., 2020; Beauchaine et al., 2017; Romanowich et al., 2020; Scott-Parker & Weston, 2017). It seems that the association between risk behavior and certain personality factors, such as sensitivity to rewards and punishments or cognitive impulsivity, may depend on the dimension of risk evaluated and the population under study.

In this vein, it is essential to note that most studies that have found relationships between risky driving and SPSRQ or delay discounting scores evaluate driving risk through self-report measures (Murphy & Murphy, 2018; Scott-Parker & Weston, 2017; Zimbardo et al., 1997). We have used a more ecological measure to determine individual risk proneness (points lost from the driver's license, attendance to recovery courses, fines for traffic violations, and driving over the speed limit), which can influence how risky driving relates to the different personality measures.

Risk as a modulator of the relationships between personality factors and brain gray matter

Our results show that the relationship between sensitivity to reward and punishment and impulsivity and brain gray matter are different for different levels of risky driving. In the absence of risk, these personality factors are positively or negatively related to the volume of brain areas involved in cognitive control and incentive processing. However, for medium and high-risk drivers, the association between gray matter volume and impulsivity and reward or punishment sensitivity disappears or is reversed.

Differences in the association between gray matter volume and personality variables were found in the absence of significant group differences in the SPSRQ and MCQ scores. Therefore, it seems that these significant differences between the correlation

coefficients of the groups genuinely indicate how brain gray matter volume of the areas involved in decision-making-related vary as a function of the risk proneness of the drivers. This could mean that risky drivers process information differently to non-risky drivers. This notion is in line with the results reported by Delgado-Rico et al. (2013), who found no differences in a risky decision-making task between obese people and healthy controls. However, during the execution of the task, they observed significant differences between the groups in terms of brain activation in the insula and midbrain.

We observed, after controlling also the TIV, a negative relationship between preference for an immediate reward and cerebral gray matter volumes of the nAcc, amygdala, OFC, PCC, and lingual gyrus, but a positive relationship between this preference and occipital cortex volume in less risky drivers. However, this relationship either disappears or is reversed in the riskiest driver groups. Previous studies have shown that these brain areas are included within the neural networks associated with the delay discounting process (Peters & Büchel, 2011; Wesley & Bickel, 2014). The nAcc is part of the ventral striatum, which is involved in the sensory processing and valuation of rewards and the anticipation and learning of reinforcement (Bartra et al., 2013; Lambert et al., 2014; Schultz et al., 1997; Schweinhardt et al., 2009). Rats with lesions in this area were found to make fewer good choices and showed a decrease in gain rates on delay discounting tasks (Steele et al., 2018). The OFC integrates the information from the limbic areas to determine the value of rewards and to control the decision-making process (Lee et al., 2018; Peters & Büchel, 2010; Yang et al., 2019). Several studies have linked the gray matter volume of the OFC with cognitive impulsivity or sensitivity to immediate reinforcements (Cho et al., 2013; Guo et al., 2017; Li et al., 2019; Matsuo et al., 2009; Mohammadi et al., 2016). The PCC, which is connected to the OFC and is part of the DMN, is also involved in the subjective value of rewards and is responsible for

responding to environmental variations that require behavioral change (Cavada et al., 2000; Greicius et al., 2003; Leech & Sharp, 2014; Peters & Büchel, 2011). The structure and activation of the PCC have been related to the decision-making process in delay discounting tasks (Li et al., 2013; Schwartz et al., 2010; Weber & Huettel, 2008; Wesley & Bickel, 2014). Furthermore, Dedovic et al. (2016) have found a reduced cortical thickness in this area in men who had driven under the influence of alcohol. Regarding the occipital cortex, structure and functional connectivity data have related this area to delay discounting rates (Mohammadi et al., 2016; Wang et al., 2016).

Our results agree with those observed on the neural networks involved in delay-discounting and suggest that the trait-structure association could be altered in risky drivers. Numerous studies have concluded that, in pathological gamblers and patients with other psychiatric disorders, there is an alteration in the processing and decision-making related to the delay discounting process, as reflected in activation patterns and differential brain structure, when compared with healthy controls (for a review, see Noda et al. (2020). More specifically, Hobkirk et al. (2019) found that, in cocaine users, the delay discounting rate was not related to resting-state functional connectivity between the reinforcement and attentional salience networks, a correlation that was significant in the control group. On the other hand, Wang et al. (2017) observed that impulsivity was negatively related to the gray matter volume of areas responsible for cognitive control and incentive processing in healthy people. However, similar to our results, this relationship disappeared in obese people, and this occurred in the absence of significant differences between groups on the impulsivity measure. In a similar vein, Freinhofer et al. (2020) examined the relationship between DDT performance and brain gray matter volume in a group of patients addicted to gambling, and a control group. These authors observed a negative correlation between gray matter volume of the medial OFC and the

choice of immediate reinforcement in the control group, a relationship that disappeared in the group of patients addicted to gambling. Furthermore, they found no associations between performance on a risky decision-making task and discounting delay scores in the whole sample. Therefore, our results support the idea that there is an alteration in the relationship between delay discounting and brain gray matter in various manifestations of risky behavior, such as risky driving.

Regarding the relationship between reward sensitivity and brain gray matter, we observed, after controlling also the TIV, that the former is positively related to the volume of the STC, occipital fusiform gyrus, and medial postcentral gyrus, but negatively related to the left frontal operculum, in less risky drivers. However, this relationship was almost non-existent in the riskiest driver groups in all comparisons. Similarly, in less risky drivers, sensitivity to punishment was negatively related to the gray matter volumes of the insula, the superior medial frontal cortex, and the medial precentral gyrus. Again, these relationships were lost or reversed in medium or high-risk level drivers.

The STC is involved in controlling the decision-making process by integrating the results of previous actions, particularly when these entail rewards (Paulus et al., 2005). The functional connectivity of this area, such as the nAcc, has been specifically related to sensitivity to music reinforcement (Martínez-Molina et al., 2016). Other authors find that reward sensitivity is negatively related to the gray matter volume of the STC and, therefore, with poorer cognitive control (Adrián-Ventura et al., 2019). The pre and postcentral gyrus and the fusiform gyrus have been related to the behavioral activation and inhibition systems and have been implicated in the responses to reinforcing and aversive stimuli (De Pascalis et al., 2010; Dutra et al., 2015; Fuentes et al., 2012; Li et al., 2006; Montoya et al., 2012; Pawliczek et al., 2013; Stice et al., 2011). More specifically, Sakai et al. (2012) show that, in older people, the volume of the SMA is a good predictor

of individual differences in executive functions, and these act as a risk factor for traffic accidents. The insula and the superior frontal cortex are part of the cognitive control network necessary for driving (Navarro et al., 2018). These areas are responsible for the identification of the relevant stimuli, the integration of interoceptive stimuli, the prediction of the error to obtain reinforcement or avoid damage, the inhibition of responses, and behavioral regulation (Nasiriavanaki et al., 2015; Niendam et al., 2012; Noël et al., 2013; Seeley et al., 2007; Weller et al., 2009). Von Siebenthal et al. (2020) found that activation of the insula during the decision phase of a roulette task was negatively related to punishment sensitivity, regardless of the value of the outcome. These authors explain the negative correlation between insula volume and sensitivity to punishment by relating sensitivity to punishment with pessimism and with the certainty of obtaining negative results. Sensitivity to punishment has also been negatively related to the activation of the superior frontal cortex in people with borderline personality disorder and healthy controls (Mortensen et al., 2010).

Our results agree with previous evidence on the neural networks involved in reward and punishment sensitivity and suggest that the trait-structure association could be altered in risky drivers. Previous studies on other manifestations of risk behavior support this idea. Parvaz et al. (2011) found that the P300 potential, used as a measure of sensitivity to reinforcement, was positively related to volumes of prefrontal regions involved in the brain's reward system in healthy controls. However, no such relationship was found in people addicted to cocaine. In another study, Moreno-López et al. (2012) observed a negative correlation between the volume of the somatosensory cortex and sensitivity to reinforcement in healthy controls. However, this relationship disappeared for obese participants. Furthermore, they also found no differences between the groups in terms of the SPSRQ scores.

Taken together, our results show that the differences observed in the relationships between sensitivity to reward and punishment and delay of reward and brain gray matter volumes, as a function of risk level, could reflect a structural alteration and a change in the neural mechanism underlying these personality traits (Wang et al., 2017). In other words, in risky drivers, it seems that the function of brain regions involved in reward and punishment sensitivity and impulsivity is masked by the specific mechanisms involved in risky behavior, which has been demonstrated in functional connectivity studies (Baltruschat et al., 2020). Our results support this idea, since the gray matter volumes of many of these brain regions, such as the striatum, OFC, STC, fusiform gyrus, lingual gyrus, and insula, are lower in riskier drivers.

Conclusions

Our results show that drivers with a high-risk proneness in traffic situations have a lower total gray matter volume. We have also found that risky drivers have lower gray matter volume in the brain structures responsible for cognitive control and incentive processing. On the other hand, we found that it is the level of risk that determines how these areas are related to personality factors such as impulsivity and sensitivity to reward and punishment. This suggests that, in risky drivers, there is an alteration in the brain structure of the areas involved in reward processing, cognitive control, and behavioral modulation, which could indicate dysfunctional decision-making and riskier driving behavior.

References

Adrián-Ventura, J., Costumero, V., Parcet, M. A., & Ávila, C. (2019). Linking personality and brain anatomy: A structural MRI approach to Reinforcement Sensitivity Theory. *Social Cognitive and Affective Neuroscience*, *14*(3), 329-338. <https://doi.org/10.1093/scan/nsz011>

- Albert, D., Chein, J., & Steinberg, L. (2013). The Teenage Brain: Peer Influences on Adolescent Decision Making. *Current Directions in Psychological Science*, *22*(2), 114-120. <https://doi.org/10.1177/0963721412471347>
- Aluja, A., & Blanch, A. (2011). Neuropsychological Behavioral Inhibition System (BIS) and Behavioral Approach System (BAS) Assessment: A Shortened Sensitivity to Punishment and Sensitivity to Reward Questionnaire Version (SPSRQ–20). *Journal of Personality Assessment*, *93*(6), 628-636. <https://doi.org/10.1080/00223891.2011.608760>
- Aydogan, G., Daviet, R., Karlsson Linnér, R., Hare, T. A., Kable, J. W., Kranzler, H. R., Wetherill, R. R., Ruff, C. C., Koellinger, P. D., & Nave, G. (2021). Genetic underpinnings of risky behaviour relate to altered neuroanatomy. *Nature Human Behaviour*, 1-8. <https://doi.org/10.1038/s41562-020-01027-y>
- Baltruschat, S., Cándido, A., Megías, A., Maldonado, A., & Catena, A. (2020). Risk proneness modulates the impact of impulsivity on brain functional connectivity. *Human Brain Mapping*, *41*(4), 943-951. <https://doi.org/10.1002/hbm.24851>
- Barkley-Levenson, E., & Galván, A. (2014). Neural representation of expected value in the adolescent brain. *Proceedings of the National Academy of Sciences*, *111*(4), 1646-1651. <https://doi.org/10.1073/pnas.1319762111>
- Barkley-Levenson, E., Xue, F., Droutman, V., Miller, L. C., Smith, B. J., Jeong, D., Lu, Z.-L., Bechara, A., & Read, S. J. (2018). Prefrontal Cortical Activity During the Stroop Task: New Insights into the Why and the Who of Real-World Risky Sexual Behavior. *Annals of Behavioral Medicine*, *52*(5), 367-379. <https://doi.org/10.1093/abm/kax019>

- Barrós-Loscertales, A., Meseguer, V., Sanjuán, A., Belloch, V., Parcet, M. A., Torrubia, R., & Ávila, C. (2006b). Behavioral Inhibition System activity is associated with increased amygdala and hippocampal gray matter volume: A voxel-based morphometry study. *NeuroImage*, *33*(3), 1011-1015. <https://doi.org/10.1016/j.neuroimage.2006.07.025>
- Barrós-Loscertales, A., Meseguer, V., Sanjuán, A., Belloch, V., Parcet, M. A., Torrubia, R., & Avila, C. (2006a). Striatum gray matter reduction in males with an overactive behavioral activation system. *The European Journal of Neuroscience*, *24*(7), 2071-2074. <https://doi.org/10.1111/j.1460-9568.2006.05084.x>
- Barry, A. B., Koepfel, J. A., & Ho, B.-C. (2020). Impulsive decision making, brain cortical thickness and familial schizophrenia risk. *Schizophrenia Research*. <https://doi.org/10.1016/j.schres.2020.03.072>
- Bartra, O., McGuire, J. T., & Kable, J. W. (2013). The valuation system: A coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. *NeuroImage*, *76*, 412-427. <https://doi.org/10.1016/j.neuroimage.2013.02.063>
- Beauchaine, T. P., Ben-David, I., & Sela, A. (2017). Attention-deficit/hyperactivity disorder, delay discounting, and risky financial behaviors: A preliminary analysis of self-report data. *PloS One*, *12*(5), e0176933. <https://doi.org/10.1371/journal.pone.0176933>
- Beeli, G., Koeneke, S., Gasser, K., & Jancke, L. (2008). Brain stimulation modulates driving behavior. *Behavioral and Brain Functions: BBF*, *4*, 34. <https://doi.org/10.1186/1744-9081-4-34>

- Benjamin, D. J., Berger, J. O., Johannesson, M., Nosek, B. A., Wagenmakers, E.-J., Berk, R., Bollen, K. A., Brembs, B., Brown, L., Camerer, C., Cesarini, D., Chambers, C. D., Clyde, M., Cook, T. D., De Boeck, P., Dienes, Z., Dreber, A., Easwaran, K., Efferson, C., ... Johnson, V. E. (2018). Redefine statistical significance. *Nature Human Behaviour*, *2*(1), 6-10. <https://doi.org/10.1038/s41562-017-0189-z>
- Bernhardt, B. C., Smallwood, J., Tusche, A., Ruby, F. J. M., Engen, H. G., Steinbeis, N., & Singer, T. (2014). Medial prefrontal and anterior cingulate cortical thickness predicts shared individual differences in self-generated thought and temporal discounting. *NeuroImage*, *90*, 290-297. <https://doi.org/10.1016/j.neuroimage.2013.12.040>
- Bjork, J. M., Momenan, R., & Hommer, D. W. (2009). Delay discounting correlates with proportional lateral frontal cortex volumes. *Biological Psychiatry*, *65*(8), 710-713. <https://doi.org/10.1016/j.biopsych.2008.11.023>
- Brown, T. G., Ouimet, M. C., Eldeb, M., Tremblay, J., Vingilis, E., Nadeau, L., Pruessner, J., & Bechara, A. (2016). Personality, Executive Control, and Neurobiological Characteristics Associated with Different Forms of Risky Driving. *PLOS ONE*, *11*(2), e0150227. <https://doi.org/10.1371/journal.pone.0150227>
- Cascio, C. N., Carp, J., O'Donnell, M. B., Tinney, F. J., Bingham, C. R., Shope, J. T., Ouimet, M. C., Pradhan, A. K., Simons-Morton, B. G., & Falk, E. B. (2015). Buffering social influence: Neural correlates of response inhibition predict driving safety in the presence of a peer. *Journal of Cognitive Neuroscience*, *27*(1), 83-95. https://doi.org/10.1162/jocn_a_00693

- Castellà, J., & Pérez, J. (2004). Sensitivity to punishment and sensitivity to reward and traffic violations. *Accident Analysis and Prevention*, *36*(6), 947-952. <https://doi.org/10.1016/j.aap.2003.10.003>
- Cavada, C., Compañy, T., Tejedor, J., Cruz-Rizzolo, R. J., & Reinoso-Suárez, F. (2000). The anatomical connections of the macaque monkey orbitofrontal cortex. A review. *Cerebral Cortex (New York, N.Y.: 1991)*, *10*(3), 220-242. <https://doi.org/10.1093/cercor/10.3.220>
- Chein, J., Albert, D., O'Brien, L., Uckert, K., & Steinberg, L. (2011). Peers increase adolescent risk taking by enhancing activity in the brain's reward circuitry. *Developmental science*, *14*(2), F1-F10. <https://doi.org/10.1111/j.1467-7687.2010.01035.x>
- Cherek, D. R., & Lane, S. D. (1999). Laboratory and psychometric measurements of impulsivity among violent and nonviolent female parolees. *Biological Psychiatry*, *46*(2), 273-280. [https://doi.org/10.1016/S0006-3223\(98\)00309-6](https://doi.org/10.1016/S0006-3223(98)00309-6)
- Chesson, H. W., Leichliter, J. S., Zimet, G. D., Rosenthal, S. L., Bernstein, D. I., & Fife, K. H. (2006). Discount rates and risky sexual behaviors among teenagers and young adults. *Journal of Risk and Uncertainty*, *32*(3), 217-230. <https://doi.org/10.1007/s11166-006-9520-1>
- Cho, S. S., Pellecchia, G., Aminian, K., Ray, N., Segura, B., Obeso, I., & Strafella, A. P. (2013). Morphometric correlation of impulsivity in medial prefrontal cortex. *Brain Topography*, *26*(3), 479-487. <https://doi.org/10.1007/s10548-012-0270-x>
- Constantinou, E., Panayiotou, G., Konstantinou, N., Loutsiou-Ladd, A., & Kapardis, A. (2011). Risky and aggressive driving in young adults: Personality matters. *Accident Analysis and Prevention*, *43*(4), 1323-1331. <https://doi.org/10.1016/j.aap.2011.02.002>

- De Pascalis, V., Varriale, V., & D'Antuono, L. (2010). Event-related components of the punishment and reward sensitivity. *Clinical Neurophysiology*, *121*(1), 60-76. <https://doi.org/10.1016/j.clinph.2009.10.004>
- Dedovic, K., Pruessner, J., Tremblay, J., Nadeau, L., Ouimet, M. C., Lepage, M., & Brown, T. G. (2016). Examining cortical thickness in male and female DWI offenders. *Neuroscience Letters*, *619*, 189-195. <https://doi.org/10.1016/j.neulet.2016.03.034>
- Dehning, M., Kim, J., Nguyen, C. M., Shivapour, E., & Denburg, N. L. (2014). Neuropsychological performance, brain imaging, and driving violations in multiple sclerosis. *Archives of Physical Medicine and Rehabilitation*, *95*(10), 1818-1823. Scopus. <https://doi.org/10.1016/j.apmr.2014.05.022>
- Delgado-Rico, E., Soriano-Mas, C., Verdejo-Román, J., Río-Valle, J. S., & Verdejo-García, A. (2013). Decreased insular and increased midbrain activations during decision-making under risk in adolescents with excess weight. *Obesity*, *21*(8), 1662-1668. <https://doi.org/10.1002/oby.20375>
- Dosenbach, N. U. F., Visscher, K. M., Palmer, E. D., Miezin, F. M., Wenger, K. K., Kang, H. C., Burgund, E. D., Grimes, A. L., Schlaggar, B. L., & Petersen, S. E. (2006). A Core System for the Implementation of Task Sets. *Neuron*, *50*(5), 799-812. <https://doi.org/10.1016/j.neuron.2006.04.031>
- Dutra, S. J., Cunningham, W. A., Kober, H., & Gruber, J. (2015). Elevated Striatal Reactivity Across Monetary and Social Rewards in Bipolar I Disorder. *Journal of abnormal psychology*, *124*(4), 890-904. <https://doi.org/10.1037/abn0000092>
- Engelmann, J. B., & Tamir, D. (2009). Individual differences in risk preference predict neural responses during financial decision-making. *Brain Research*, *1290*, 28-51. <https://doi.org/10.1016/j.brainres.2009.06.078>

- Eysenck, S. B., & McGurk, B. J. (1980). Impulsiveness and venturesomeness in a detention center population. *Psychological Reports*, *47*(3 Pt 2), 1299-1306.
<https://doi.org/10.2466/pr0.1980.47.3f.1299>
- Falk, E. B., Way, B. M., & Jasinska, A. J. (2012). An imaging genetics approach to understanding social influence. *Frontiers in Human Neuroscience*, *6*.
<https://doi.org/10.3389/fnhum.2012.00168>
- Ferenczi, E. A., Zalocusky, K. A., Liston, C., Grosenick, L., Warden, M. R., Amatya, D., Katovich, K., Mehta, H., Patenaude, B., Ramakrishnan, C., Kalanithi, P., Etkin, A., Knutson, B., Glover, G. H., & Deisseroth, K. (2016). Prefrontal cortical regulation of brainwide circuit dynamics and reward-related behavior. *Science*, *351*(6268). <https://doi.org/10.1126/science.aac9698>
- Freinhofer, D., Schwartenbeck, P., Thon, N., Eigenberger, T., Aichhorn, W., Lenger, M., Wurst, F. M., & Kronbichler, M. (2020). Deficient Decision Making in Pathological Gamblers Correlates With Gray Matter Volume in Medial Orbitofrontal Cortex. *Frontiers in Psychiatry*, *11*.
<https://doi.org/10.3389/fpsyt.2020.00109>
- Fuentes, P., Barrós-Loscertales, A., Bustamante, J. C., Rosell, P., Costumero, V., & Ávila, C. (2012). Individual differences in the Behavioral Inhibition System are associated with orbitofrontal cortex and precuneus gray matter volume. *Cognitive, Affective and Behavioral Neuroscience*, *12*(3), 491-498.
<https://doi.org/10.3758/s13415-012-0099-5>

- Goh, J. O. S., Su, Y.-S., Tang, Y.-J., McCarrey, A. C., Tereshchenko, A., Elkins, W., & Resnick, S. M. (2016). Frontal, Striatal, and Medial Temporal Sensitivity to Value Distinguishes Risk-Taking from Risk-Aversive Older Adults during Decision Making. *Journal of Neuroscience*, *36*(49), 12498-12509. <https://doi.org/10.1523/JNEUROSCI.1386-16.2016>
- Gray, J. A. (1970). The psychophysiological basis of introversion-extraversion. *Behaviour Research and Therapy*, *8*(3), 249-266. [https://doi.org/10.1016/0005-7967\(70\)90069-0](https://doi.org/10.1016/0005-7967(70)90069-0)
- Greicius, M. D., Krasnow, B., Reiss, A. L., & Menon, V. (2003). Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(1), 253-258. <https://doi.org/10.1073/pnas.0135058100>
- Guinosso, S. A., Johnson, S. B., Schultheis, M. T., Graefe, A. C., & Bishai, D. M. (2016). Neurocognitive Correlates of Young Drivers' Performance in a Driving Simulator. *Journal of Adolescent Health*, *58*(4), 467-473. <https://doi.org/10.1016/j.jadohealth.2015.12.018>
- Guo, Y., Chen, Z., & Feng, T. (2017). The effect of future time perspective on delay discounting is mediated by the gray matter volume of vmPFC. *Neuropsychologia*, *102*, 229-236. <https://doi.org/10.1016/j.neuropsychologia.2017.06.021>
- Hayashi, Y., Rivera, E. A., Modico, J. G., Foreman, A. M., & Wirth, O. (2017). Texting while driving, executive function, and impulsivity in college students. *Accident Analysis & Prevention*, *102*, 72-80. <https://doi.org/10.1016/j.aap.2017.02.016>
- Hayashi, Y., Russo, C. T., & Wirth, O. (2015). Texting while driving as impulsive choice: A behavioral economic analysis. *Accident Analysis & Prevention*, *83*, 182-189. <https://doi.org/10.1016/j.aap.2015.07.025>

- Helfinstein, S. M., Schonberg, T., Congdon, E., Karlsgodt, K. H., Mumford, J. A., Sabb, F. W., Cannon, T. D., London, E. D., Bilder, R. M., & Poldrack, R. A. (2014). Predicting risky choices from brain activity patterns. *Proceedings of the National Academy of Sciences*, *111*(7), 2470-2475. <https://doi.org/10.1073/pnas.1321728111>
- Hlavatá, P., Linhartová, P., Šumec, R., Filip, P., Světlák, M., Baláž, M., Kašpárek, T., & Bareš, M. (2020). Behavioral and Neuroanatomical Account of Impulsivity in Parkinson's Disease. *Frontiers in Neurology*, *10*. <https://doi.org/10.3389/fneur.2019.01338>
- Hobkirk, A. L., Bell, R. P., Utevsky, A. V., Huettel, S., & Meade, C. S. (2019). Reward and executive control network resting-state functional connectivity is associated with impulsivity during reward-based decision making for cocaine users. *Drug and Alcohol Dependence*, *194*, 32-39. <https://doi.org/10.1016/j.drugalcdep.2018.09.013>
- Holmes, A. J., Lee, P. H., Hollinshead, M. O., Bakst, L., Roffman, J. L., Smoller, J. W., & Buckner, R. L. (2012). Individual Differences in Amygdala-Medial Prefrontal Anatomy Link Negative Affect, Impaired Social Functioning, and Polygenic Depression Risk. *The Journal of Neuroscience*, *32*(50), 18087-18100. <https://doi.org/10.1523/JNEUROSCI.2531-12.2012>
- Honey, C. J., Kötter, R., Breakspear, M., & Sporns, O. (2007). Network structure of cerebral cortex shapes functional connectivity on multiple time scales. *Proceedings of the National Academy of Sciences*, *104*(24), 10240-10245. <https://doi.org/10.1073/pnas.0701519104>

- Hu, X., Erb, M., Ackermann, H., Martin, J. A., Grodd, W., & Reiterer, S. M. (2011).
Voxel-based morphometry studies of personality: Issue of statistical model
specification—effect of nuisance covariates. *NeuroImage*, *54*(3), 1994-2005.
<https://doi.org/10.1016/j.neuroimage.2010.10.024>
- Hyatt, C. S., Owens, M. M., Crowe, M. L., Carter, N. T., Lynam, D. R., & Miller, J. D.
(2020). The quandary of covarying: A brief review and empirical examination of
covariate use in structural neuroimaging studies on psychological variables.
NeuroImage, *205*, 116225. <https://doi.org/10.1016/j.neuroimage.2019.116225>
- Iidaka, T., Matsumoto, A., Ozaki, N., Suzuki, T., Iwata, N., Yamamoto, Y., Okada, T., &
Sadato, N. (2006). Volume of left amygdala subregion predicted temperamental
trait of harm avoidance in female young subjects. A voxel-based morphometry
study. *Brain Research*, *1125*(1), 85-93.
<https://doi.org/10.1016/j.brainres.2006.09.015>
- Johnson, V. E. (2013). Revised standards for statistical evidence. *Proceedings of the
National Academy of Sciences*, *110*(48), 19313-19317.
<https://doi.org/10.1073/pnas.1313476110>
- Jongen, E. M. M., Brijs, K., Komlos, M., Brijs, T., & Wets, G. (2011). Inhibitory control
and reward predict risky driving in young novice drivers—A simulator study.
Procedia - Social and Behavioral Sciences, *20*, 604-612.
<https://doi.org/10.1016/j.sbspro.2011.08.067>
- Kirby, K. N., & Maraković, N. N. (1996). Delay-discounting probabilistic rewards: Rates
decrease as amounts increase. *Psychonomic Bulletin & Review*, *3*(1), 100-104.
<https://doi.org/10.3758/BF03210748>

- Kirby, K. N., & Petry, N. M. (2004). Heroin and cocaine abusers have higher discount rates for delayed rewards than alcoholics or non-drug-using controls. *Addiction*, *99*(4), 461-471. <https://doi.org/10.1111/j.1360-0443.2003.00669.x>
- Knutson, B., & Cooper, J. C. (2005). Functional magnetic resonance imaging of reward prediction. *Current Opinion in Neurology*, *18*(4), 411-417. <https://doi.org/10.1097/01.wco.0000173463.24758.f6>
- Kohno, M., Ghahremani, D. G., Morales, A. M., Robertson, C. L., Ishibashi, K., Morgan, A. T., Mandelkern, M. A., & London, E. D. (2015). Risk-taking behavior: Dopamine D2/D3 receptors, feedback, and frontolimbic activity. *Cerebral Cortex*, *25*(1), 236-245. <https://doi.org/10.1093/cercor/bht218>
- Kwon, M. S., Vorobyev, V., Moe, D., Parkkola, R., & Hämäläinen, H. (2014). Brain structural correlates of risk-taking behavior and effects of peer influence in adolescents. *PLoS ONE*, *9*(11). <https://doi.org/10.1371/journal.pone.0112780>
- Lambert, A. E., Simons-Morton, B. G., Cain, S. A., Weisz, S., & Cox, D. J. (2014). Considerations of a Dual-Systems Model of Cognitive Development and Risky Driving. *Journal of Research on Adolescence*, *24*(3), 541-550. <https://doi.org/10.1111/jora.12126>
- Lee, D., Lee, J., Yoon, K. J., Kee, N., & Jung, Y.-C. (2016). Impaired anterior insular activation during risky decision making in young adults with internet gaming disorder. *NeuroReport*, *27*(8), 605-609. <https://doi.org/10.1097/WNR.0000000000000584>
- Lee, D., Park, J., Namkoong, K., Kim, I. Y., & Jung, Y.-C. (2018). Gray matter differences in the anterior cingulate and orbitofrontal cortex of young adults with Internet gaming disorder: Surface-based morphometry. *Journal of Behavioral Addictions*, *7*(1), 21-30. <https://doi.org/10.1556/2006.7.2018.20>

- Leech, R., & Sharp, D. J. (2014). The role of the posterior cingulate cortex in cognition and disease. *Brain*, *137*(1), 12-32. <https://doi.org/10.1093/brain/awt162>
- León-Domínguez, U., Solís-Marcos, I., Barrio-Álvarez, E., Barroso y Martín, J. M., & León-Carrión, J. (2017). Safe driving and executive functions in healthy middle-aged drivers. *Applied Neuropsychology:Adult*, *24*(5), 395-403. <https://doi.org/10.1080/23279095.2015.1137296>
- Levita, L., Bois, C., Healey, A., Smyllie, E., Papakonstantinou, E., Hartley, T., & Lever, C. (2014). The Behavioural Inhibition System, anxiety and hippocampal volume in a non-clinical population. *Biology of Mood and Anxiety Disorders*, *4*(1). <https://doi.org/10.1186/2045-5380-4-4>
- Levy, I. (2017). Neuroanatomical Substrates for Risk Behavior. *Neuroscientist*, *23*(3), 275-286. <https://doi.org/10.1177/1073858416672414>
- Li, C. R., Huang, C., Constable, R. T., & Sinha, R. (2006). Imaging response inhibition in a stop-signal task: Neural correlates independent of signal monitoring and post-response processing. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *26*(1), 186-192. <https://doi.org/10.1523/JNEUROSCI.3741-05.2006>
- Li, M., Wei, D., Yang, W., Zhang, J., & Qiu, J. (2019). Neuroanatomical correlates of extraversion: A test-retest study implicating gray matter volume in the caudate nucleus. *NeuroReport*, *30*(14), 953-959. <https://doi.org/10.1097/WNR.0000000000001306>
- Li, N., Ma, N., Liu, Y., He, X.-S., Sun, D.-L., Fu, X.-M., Zhang, X., Han, S., & Zhang, D.-R. (2013). Resting-State Functional Connectivity Predicts Impulsivity in Economic Decision-Making. *The Journal of Neuroscience*, *33*(11), 4886-4895. <https://doi.org/10.1523/JNEUROSCI.1342-12.2013>

- Li, X., Hu, P., & Liu, J. (2019). The neuroanatomical correlates of individual differences in delay discounting: A voxel-based morphometry study. *Journal of Pacific Rim Psychology, 13*. <https://doi.org/10.1017/prp.2019.22>
- Li, X., Xu, S., Fang, Z., & Smith, A. (2020). Individual intelligence and brain neural correlates associated with outcome expectancies for risk behaviors in adults. *Neuroscience Letters, 725*. <https://doi.org/10.1016/j.neulet.2019.134720>
- Lin, C.-S., Lin, H.-H., & Wu, S.-Y. (2016). Functional and Structural Signatures of the Anterior Insula are associated with Risk-taking Tendency of Analgesic Decision-making. *Scientific Reports, 6*(1), 37816. <https://doi.org/10.1038/srep37816>
- Luna, B., Padmanabhan, A., & O’Hearn, K. (2010). What has fMRI told us about the Development of Cognitive Control through Adolescence? *Brain and Cognition, 72*(1), 101-113. <https://doi.org/10.1016/j.bandc.2009.08.005>
- Mäntylä, T., Karlsson, M. J., & Marklund, M. (2009). Executive Control Functions in Simulated Driving. *Applied Neuropsychology, 16*(1), 11-18. <https://doi.org/10.1080/09084280802644086>
- Marín-Lahoz, J., Martínez-Horta, S., Sampedro, F., Pagonabarraga, J., Horta-Barba, A., Bejr-kasem, H., Botí, M. Á., Fernández-Bobadilla, R., Pascual-Sedano, B., Pérez-Pérez, J., Aracil-Bolaños, I., Gironell, A., Gómez-Ansón, B., & Kulisevsky, J. (2020). Measuring impulsivity in Parkinson’s disease: A correlational and structural neuroimaging study using different tests. *European Journal of Neurology, 27*(8), 1478-1486. <https://doi.org/10.1111/ene.14235>
- Martínez-Molina, N., Mas-Herrero, E., Rodríguez-Fornells, A., Zatorre, R. J., & Marco-Pallarés, J. (2016). Neural correlates of specific musical anhedonia. *Proceedings of the National Academy of Sciences, 113*(46), E7337-E7345. <https://doi.org/10.1073/pnas.1611211113>

- Matsuo, K., Nicoletti, M., Nemoto, K., Hatch, J. P., Peluso, M. A. M., Nery, F. G., & Soares, J. C. (2009). A voxel-based morphometry study of frontal gray matter correlates of impulsivity. *Human Brain Mapping, 30*(4), 1188-1195. <https://doi.org/10.1002/hbm.20588>
- McClure, S. M., Laibson, D. I., Loewenstein, G., & Cohen, J. D. (2004). Separate Neural Systems Value Immediate and Delayed Monetary Rewards. *Science, 306*(5695), 503-507. <https://doi.org/10.1126/science.1100907>
- McIlvain, G., Clements, R. G., Magoon, E. M., Spielberg, J. M., Telzer, E. H., & Johnson, C. L. (2020). Viscoelasticity of reward and control systems in adolescent risk taking. *NeuroImage, 215*. <https://doi.org/10.1016/j.neuroimage.2020.116850>
- Meade, C. S., Bell, R. P., Towe, S. L., & Hall, S. A. (2020). Cocaine-related alterations in fronto-parietal gray matter volume correlate with trait and behavioral impulsivity. *Drug and Alcohol Dependence, 206*. <https://doi.org/10.1016/j.drugalcdep.2019.107757>
- Miglin, R., Bounoua, N., Goodling, S., Sheehan, A., Spielberg, J. M., & Sadeh, N. (2019). Cortical thickness links impulsive personality traits and risky behavior. *Brain Sciences, 9*(12). <https://doi.org/10.3390/brainsci9120373>
- Mishra, S., & Lalumière, M. L. (2011). Individual differences in risk-propensity: Associations between personality and behavioral measures of risk. *Personality and Individual Differences, 50*(6), 869-873. <https://doi.org/10.1016/j.paid.2010.11.037>
- Mishra, S., & Lalumière, M. L. (2017). Associations Between Delay Discounting and Risk-Related Behaviors, Traits, Attitudes, and Outcomes. *Journal of Behavioral Decision Making, 30*(3), 769-781. <https://doi.org/10.1002/bdm.2000>

- Mohammadi, B., Hammer, A., Miedl, S. F., Wiswede, D., Marco-Pallarés, J., Herrmann, M., & Münte, T. F. (2016). Intertemporal choice behavior is constrained by brain structure in healthy participants and pathological gamblers. *Brain Structure and Function*, *221*(6), 3157-3170. <https://doi.org/10.1007/s00429-015-1093-9>
- Montoya, J. L., Landi, N., Kober, H., Worhunsky, P. D., Rutherford, H. J. V., Mencl, W. E., Mayes, L. C., & Potenza, M. N. (2012). Regional brain responses in nulliparous women to emotional infant stimuli. *PLoS ONE*, *7*(5). <https://doi.org/10.1371/journal.pone.0036270>
- Moreno-López, L., Soriano-Mas, C., Delgado-Rico, E., Rio-Valle, J. S., & Verdejo-García, A. (2012). Brain Structural Correlates of Reward Sensitivity and Impulsivity in Adolescents with Normal and Excess Weight. *PLoS ONE*, *7*(11). <https://doi.org/10.1371/journal.pone.0049185>
- Mortensen, J. A., Rasmussen, L. A., & Håberg, A. (2010). Trait impulsivity in female patients with borderline personality disorder and matched controls. *Acta Neuropsychiatrica*, *22*(3), 139-149. <https://doi.org/10.1111/j.1601-5215.2010.00468.x>
- Murphy, L., & Murphy, G. (2018). Time to drive: Present vs. future orientation and self-reported driving behaviour. *Transportation Research Part F: Traffic Psychology and Behaviour*, *56*, 1-13. <https://doi.org/10.1016/j.trf.2018.03.026>
- Nasirivanaki, Z., ArianNik, M., Abbassian, A., Mahmoudi, E., Roufigari, N., Shahzadi, S., Nasirivanaki, M., & Bahrami, B. (2015). Prediction of individual differences in risky behavior in young adults via variations in local brain structure. *Frontiers in Neuroscience*, *9*. <https://doi.org/10.3389/fnins.2015.00359>

- Navarro, J., Reynaud, E., & Osiurak, F. (2018). Neuroergonomics of car driving: A critical meta-analysis of neuroimaging data on the human brain behind the wheel. *Neuroscience and Biobehavioral Reviews*, *95*, 464-479. <https://doi.org/10.1016/j.neubiorev.2018.10.016>
- Navas, J. F., Vilar-López, R., Perales, J. C., Steward, T., Fernández-Aranda, F., & Verdejo-García, A. (2016). Altered decision-making under risk in obesity. *PLoS ONE*, *11*(6). <https://doi.org/10.1371/journal.pone.0155600>
- Niendam, T. A., Laird, A. R., Ray, K. L., Dean, Y. M., Glahn, D. C., & Carter, C. S. (2012). Meta-analytic evidence for a superordinate cognitive control network subserving diverse executive functions. *Cognitive, Affective and Behavioral Neuroscience*, *12*(2), 241-268. <https://doi.org/10.3758/s13415-011-0083-5>
- Noda, Y., Barr, M. S., ElSalhy, M., Masuda, F., Tarumi, R., Ogyu, K., Wada, M., Tsugawa, S., Miyazaki, T., Nakajima, S., & Mimura, M. (2020). Neural correlates of delay discount alterations in addiction and psychiatric disorders: A systematic review of magnetic resonance imaging studies. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *99*. <https://doi.org/10.1016/j.pnpbp.2019.109822>
- Noël, X., Brevers, D., & Bechara, A. (2013). A neurocognitive approach to understanding the neurobiology of addiction. *Current opinion in neurobiology*, *23*(4), 632-638. <https://doi.org/10.1016/j.conb.2013.01.018>
- O'Brien, F., & Gormley, M. (2013). The contribution of inhibitory deficits to dangerous driving among young people. *Accident Analysis & Prevention*, *51*, 238-242. <https://doi.org/10.1016/j.aap.2012.11.024>

- Owens, M. M., Gray, J. C., Amlung, M. T., Oshri, A., Sweet, L. H., & MacKillop, J. (2017). Neuroanatomical foundations of delayed reward discounting decision making. *NeuroImage*, *161*, 261-270. <https://doi.org/10.1016/j.neuroimage.2017.08.045>
- Padilla, J.-L., Doncel, P., Gugliotta, A., & Castro, C. (2018). Which drivers are at risk? Factors that determine the profile of the reoffender driver. *Accident Analysis and Prevention*, *119*, 237-247. <https://doi.org/10.1016/j.aap.2018.07.021>
- Panayiotou, G. (2015). The bold and the fearless among us: Elevated psychopathic traits and levels of anxiety and fear are associated with specific aberrant driving behaviors. *Accident Analysis & Prevention*, *79*, 117-125. <https://doi.org/10.1016/j.aap.2015.03.007>
- Parcet, M. A., Adrián-Ventura, J., Costumero, V., & Ávila, C. (2020). Individual Differences in Hippocampal Volume as a Function of BMI and Reward Sensitivity. *Frontiers in Behavioral Neuroscience*, *14*. <https://doi.org/10.3389/fnbeh.2020.00053>
- Parvaz, M. A., Konova, A. B., Tomasi, D., Volkow, N. D., & Goldstein, R. Z. (2011). Structural Integrity of the Prefrontal Cortex Modulates Electrocortical Sensitivity to Reward. *Journal of Cognitive Neuroscience*, *24*(7), 1560-1570. https://doi.org/10.1162/jocn_a_00166
- Paulus, M. P., Feinstein, J. S., Leland, D., & Simmons, A. N. (2005). Superior temporal gyrus and insula provide response and outcome-dependent information during assessment and action selection in a decision-making situation. *NeuroImage*, *25*(2), 607-615. <https://doi.org/10.1016/j.neuroimage.2004.12.055>

- Pawliczek, C. M., Derntl, B., Kellermann, T., Kohn, N., Gur, R. C., & Habel, U. (2013). Inhibitory control and trait aggression: Neural and behavioral insights using the emotional stop signal task. *NeuroImage*, *79*, 264-274. <https://doi.org/10.1016/j.neuroimage.2013.04.104>
- Pehlivanova, M., Wolf, D. H., Sotiras, A., Kaczkurkin, A. N., Moore, T. M., Ciric, R., Cook, P. A., Garza, A. G. de L., Rosen, A. F. G., Ruparel, K., Sharma, A., Shinohara, R. T., Roalf, D. R., Gur, R. C., Davatzikos, C., Gur, R. E., Kable, J. W., & Satterthwaite, T. D. (2018). Diminished Cortical Thickness Is Associated with Impulsive Choice in Adolescence. *Journal of Neuroscience*, *38*(10), 2471-2481. <https://doi.org/10.1523/JNEUROSCI.2200-17.2018>
- Peters, J., & Büchel, C. (2009). Overlapping and Distinct Neural Systems Code for Subjective Value during Intertemporal and Risky Decision Making. *Journal of Neuroscience*, *29*(50), 15727-15734. <https://doi.org/10.1523/JNEUROSCI.3489-09.2009>
- Peters, J., & Büchel, C. (2010). Neural representations of subjective reward value. *Behavioural Brain Research*, *213*(2), 135-141. <https://doi.org/10.1016/j.bbr.2010.04.031>
- Peters, J., & Büchel, C. (2011). The neural mechanisms of inter-temporal decision-making: Understanding variability. *Trends in Cognitive Sciences*, *15*(5), 227-239. <https://doi.org/10.1016/j.tics.2011.03.002>
- Qu, W., Zhang, W., & Ge, Y. (2020). The moderating effect of delay discounting between sensation seeking and risky driving behavior. *Safety Science*, *123*. <https://doi.org/10.1016/j.ssci.2019.104558>

- Ramanoël, S., Hoyau, E., Kauffmann, L., Renard, F., Pichat, C., Boudiaf, N., Krainik, A., Jaillard, A., & Baciú, M. (2018). Gray Matter Volume and Cognitive Performance During Normal Aging. A Voxel-Based Morphometry Study. *Frontiers in Aging Neuroscience, 10*. <https://doi.org/10.3389/fnagi.2018.00235>
- Romanowich, P., Chen, Q., & Xu, S. (2020). Relationships between Driver Errors and Delay Discounting in a Simulated Driving Task. *Perspectives on Behavior Science*. <https://doi.org/10.1007/s40614-020-00246-y>
- Ross, V., Jongen, E., Brijs, T., Ruiters, R., Brijs, K., & Wets, G. (2015). The relation between cognitive control and risky driving in young novice drivers. *Applied Neuropsychology: Adult, 22*(1), 61-72. <https://doi.org/10.1080/23279095.2013.838958>
- Sakai, H., Ando, T., Sadato, N., & Uchiyama, Y. (2017). Greater cerebellar gray matter volume in car drivers: An exploratory voxel-based morphometry study. *Scientific Reports, 7*. <https://doi.org/10.1038/srep46526>
- Sakai, H., Takahara, M., Honjo, N. F., Doi, S., Sadato, N., & Uchiyama, Y. (2012). Regional Frontal Gray Matter Volume Associated with Executive Function Capacity as a Risk Factor for Vehicle Crashes in Normal Aging Adults. *PLoS ONE, 7*(9). <https://doi.org/10.1371/journal.pone.0045920>
- Sanchis-Segura, C., Ibañez-Gual, M. V., Adrián-Ventura, J., Aguirre, N., Gómez-Cruz, Á. J., Avila, C., & Forn, C. (2019). Sex differences in gray matter volume: How many and how large are they really? *Biology of Sex Differences, 10*(1), 32. <https://doi.org/10.1186/s13293-019-0245-7>

- Sanchis-Segura, C., Ibañez-Gual, M. V., Aguirre, N., Cruz-Gómez, Á. J., & Forn, C. (2020). Effects of different intracranial volume correction methods on univariate sex differences in grey matter volume and multivariate sex prediction. *Scientific Reports*, *10*(1), 12953. <https://doi.org/10.1038/s41598-020-69361-9>
- Schultz, W., Dayan, P., & Montague, P. R. (1997). A Neural Substrate of Prediction and Reward. *Science*, *275*(5306), 1593-1599. <https://doi.org/10.1126/science.275.5306.1593>
- Schwartz, D. L., Mitchell, A. D., Lahna, D. L., Luber, H. S., Huckans, M. S., Mitchell, S. H., & Hoffman, W. F. (2010). Global and local morphometric differences in recently abstinent methamphetamine-dependent individuals. *NeuroImage*, *50*(4), 1392-1401. <https://doi.org/10.1016/j.neuroimage.2010.01.056>
- Schweinhart, P., Seminowicz, D. A., Jaeger, E., Duncan, G. H., & Bushnell, M. C. (2009). The Anatomy of the Mesolimbic Reward System: A Link between Personality and the Placebo Analgesic Response. *Journal of Neuroscience*, *29*(15), 4882-4887. <https://doi.org/10.1523/JNEUROSCI.5634-08.2009>
- Scott-Parker, B., & Weston, L. (2017). Sensitivity to reward and risky driving, risky decision making, and risky health behaviour: A literature review. *Transportation Research Part F: Traffic Psychology and Behaviour*, *49*, 93-109. <https://doi.org/10.1016/j.trf.2017.05.008>
- Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., Reiss, A. L., & Greicius, M. D. (2007). Dissociable Intrinsic Connectivity Networks for Salience Processing and Executive Control. *Journal of Neuroscience*, *27*(9), 2349-2356. <https://doi.org/10.1523/JNEUROSCI.5587-06.2007>

- Sokolov, A. A., Miall, R. C., & Ivry, R. B. (2017). The Cerebellum: Adaptive Prediction for Movement and Cognition. *Trends in cognitive sciences*, *21*(5), 313-332. <https://doi.org/10.1016/j.tics.2017.02.005>
- Song, H., Chon, M.-W., Ryu, V., Yu, R., Lee, D.-K., Lee, H., Lee, W., Lee, J. H., & Park, D. Y. (2020). Cortical Volumetric Correlates of Childhood Trauma, Anxiety, and Impulsivity in Bipolar Disorder. *Psychiatry Investigation*, *17*(7), 627-635. <https://doi.org/10.30773/pi.2019.0305>
- Steele, C. C., Peterson, J. R., Marshall, A. T., Stuebing, S. L., & Kirkpatrick, K. (2018). Nucleus accumbens core lesions induce sub-optimal choice and reduce sensitivity to magnitude and delay in impulsive choice tasks. *Behavioural Brain Research*, *339*, 28-38. <https://doi.org/10.1016/j.bbr.2017.11.013>
- Steinberg, L. (2008). A social neuroscience perspective on adolescent risk-taking. *Developmental Review*, *28*(1), 78-106. <https://doi.org/10.1016/j.dr.2007.08.002>
- Stice, E., Yokum, S., Burger, K. S., Epstein, L. H., & Small, D. M. (2011). Youth at Risk for Obesity Show Greater Activation of Striatal and Somatosensory Regions to Food. *Journal of Neuroscience*, *31*(12), 4360-4366. <https://doi.org/10.1523/JNEUROSCI.6604-10.2011>
- Story, G., Vlaev, I., Seymour, B., Darzi, A., & Dolan, R. (2014). Does temporal discounting explain unhealthy behavior? A systematic review and reinforcement learning perspective. *Frontiers in Behavioral Neuroscience*, *8*. <https://doi.org/10.3389/fnbeh.2014.00076>

- Taubman – Ben-Ari, O., Kaplan, S., Lotan, T., & Prato, C. G. (2016). The combined contribution of personality, family traits, and reckless driving intentions to young men's risky driving: What role does anger play? *Transportation Research Part F: Traffic Psychology and Behaviour*, *42*, 299-306. <https://doi.org/10.1016/j.trf.2015.10.025>
- Taubman - Ben-Ari, O., & Yehiel, D. (2012). Driving styles and their associations with personality and motivation. *Accident Analysis & Prevention*, *45*, 416-422. <https://doi.org/10.1016/j.aap.2011.08.007>
- Torrubia, R., Ávila, C., Moltó, J., & Caseras, X. (2001). The Sensitivity to Punishment and Sensitivity to Reward Questionnaire (SPSRQ) as a measure of Gray's anxiety and impulsivity dimensions. *Personality and Individual Differences*, *31*(6), 837-862. [https://doi.org/10.1016/S0191-8869\(00\)00183-5](https://doi.org/10.1016/S0191-8869(00)00183-5)
- Tschernegg, M., Pletzer, B., Schwartenbeck, P., Ludersdorfer, P., Hoffmann, U., & Kronbichler, M. (2015). Impulsivity relates to striatal gray matter volumes in humans: Evidence from a delay discounting paradigm. *Frontiers in Human Neuroscience*, *9*. <https://doi.org/10.3389/fnhum.2015.00384>
- Urošević, S., Collins, P., Muetzel, R., Schissel, A., Lim, K. O., & Luciana, M. (2015). Effects of reward sensitivity and regional brain volumes on substance use initiation in adolescence. *Social Cognitive and Affective Neuroscience*, *10*(1), 106-113. <https://doi.org/10.1093/scan/nsu022>
- Von Siebenthal, Z., Boucher, O., Lazzouni, L., Taylor, V., Martinu, K., Roy, M., Rainville, P., Lepore, F., & Nguyen, D. K. (2020). Expected value and sensitivity to punishment modulate insular cortex activity during risky decision making. *Scientific Reports*, *10*(1), 11920. <https://doi.org/10.1038/s41598-020-68644-5>

- Vorobyev, V., Kwon, M. S., Moe, D., Parkkola, R., & Hämäläinen, H. (2015). Risk-taking behavior in a computerized driving task: Brain activation correlates of decision-making, outcome, and peer influence in male adolescents. *PLoS ONE*, *10*(6). <https://doi.org/10.1371/journal.pone.0129516>
- Walshe, E. A., McIntosh, C. W., Romer, D., & Winston, F. K. (2017). Executive function capacities, negative driving behavior and crashes in young drivers. *International Journal of Environmental Research and Public Health*, *14*(11). <https://doi.org/10.3390/ijerph14111314>
- Wang, H., Wen, B., Cheng, J., & Li, H. (2017). Brain Structural Differences between Normal and Obese Adults and their Links with Lack of Perseverance, Negative Urgency, and Sensation Seeking. *Scientific Reports*, *7*(1), 40595. <https://doi.org/10.1038/srep40595>
- Wang, Q., Chen, C., Cai, Y., Li, S., Zhao, X., Zheng, L., Zhang, H., Liu, J., Chen, C., & Xue, G. (2016). Dissociated neural substrates underlying impulsive choice and impulsive action. *NeuroImage*, *134*, 540-549. <https://doi.org/10.1016/j.neuroimage.2016.04.010>
- Ware, M., Feng, J., & Nam, C. S. (2020). Neuroergonomics Behind the Wheel: Neural Correlates of Driving. En C. S. Nam (Ed.), *Neuroergonomics: Principles and Practice* (pp. 353-388). Springer International Publishing. https://doi.org/10.1007/978-3-030-34784-0_18
- Weber, B. J., & Huettel, S. A. (2008). The neural substrates of probabilistic and intertemporal decision making. *Brain Research*, *1234*, 104-115. <https://doi.org/10.1016/j.brainres.2008.07.105>

- Weiland, B. J., Korycinski, S. T., Soules, M., Zubieta, J.-K., Zucker, R. A., & Heitzeg, M. M. (2014). Substance abuse risk in emerging adults associated with smaller frontal gray matter volumes and higher externalizing behaviors. *Drug and Alcohol Dependence*, *137*(1), 68-75. Scopus.
<https://doi.org/10.1016/j.drugalcdep.2014.01.005>
- Weller, J. A., Levin, I. P., Shiv, B., & Bechara, A. (2009). The effects of insula damage on decision-making for risky gains and losses. *Social Neuroscience*, *4*(4), 347-358. <https://doi.org/10.1080/17470910902934400>
- Wesley, M. J., & Bickel, W. K. (2014). Remember the future II: Meta-analyses and functional overlap of working memory and delay discounting. *Biological Psychiatry*, *75*(6), 435-448. <https://doi.org/10.1016/j.biopsych.2013.08.008>
- World Health Organization. (2015). *Global status report on road safety 2015*. World Health Organization.
http://www.who.int/violence_injury_prevention/road_safety_status/2015/en/
- World Health Organization. (2018). *Global status report on road safety 2018*.
<https://www.who.int/publications-detail/global-status-report-on-road-safety-2018>
- World Medical Association. (2013). World Medical Association Declaration of Helsinki: Ethical Principles for Medical Research Involving Human Subjects. *JAMA*, *310*(20), 2191-2194. <https://doi.org/10.1001/jama.2013.281053>
- Xie, C., Ma, L., Jiang, N., Huang, R., Li, L., Gong, L., He, C., Xiao, C., Liu, W., Xu, S., & Zhang, Z. (2017). Imbalanced functional link between reward circuits and the cognitive control system in patients with obsessive-compulsive disorder. *Brain Imaging and Behavior*, *11*(4), 1099-1109. <https://doi.org/10.1007/s11682-016-9585-7>

- Xue, F., Drouman, V., Barkley-Levenson, E. E., Smith, B. J., Xue, G., Miller, L. C., Bechara, A., Lu, Z.-L., & Read, S. J. (2018). The role of the dorsal anterior insula in sexual risk: Evidence from an erotic Go/NoGo task and real-world risk-taking. *Human Brain Mapping, 39*(4), 1555-1562. <https://doi.org/10.1002/hbm.23931>
- Yamamoto, Y., Yamagata, B., Hirano, J., Ueda, R., Yoshitake, H., Negishi, K., Yamagishi, M., Kimura, M., Kamiya, K., Shino, M., & Mimura, M. (2020). Regional Gray Matter Volume Identifies High Risk of Unsafe Driving in Healthy Older People. *Frontiers in Aging Neuroscience, 12*. <https://doi.org/10.3389/fnagi.2020.592979>
- Yang, J., Wang, W., Cao, Z., Deng, Z., Weng, W., Feng, S., Liu, H., & Lu, M. (2019). Brain structural abnormalities in reward and emotion system in internet addiction disorder. *Smart Innovation, Systems and Technologies, 129*, 394-401. https://doi.org/10.1007/978-3-030-04582-1_46
- Yokoyama, R., Nozawa, T., Takeuchi, H., Taki, Y., Sekiguchi, A., Nouchi, R., Kotozaki, Y., Nakagawa, S., Miyauchi, C. M., Iizuka, K., Shinada, T., Yamamoto, Y., Hanawa, S., Araki, T., Hashizume, H., Kunitoki, K., Hanihara, M., Sassa, Y., & Kawashima, R. (2014). Association between gray matter volume in the caudate nucleus and financial extravagance: Findings from voxel-based morphometry. *Neuroscience Letters, 563*, 28-32. <https://doi.org/10.1016/j.neulet.2014.01.026>
- Zimbardo, P. G., Keough, K. A., & Boyd, J. N. (1997). Present time perspective as a predictor of risky driving. *Personality and Individual Differences, 23*(6), 1007-1023. [https://doi.org/10.1016/S0191-8869\(97\)00113-X](https://doi.org/10.1016/S0191-8869(97)00113-X)

ESTUDIO 2

Brain signatures of catastrophic events: Emotion, Saliency and Cognitive Control.

Mas-Cuesta, L., Baltruschat, S., Cándido, A. y Catena, A. (En revisión). Brain signatures of catastrophic events: Emotion, Saliency and Cognitive Control. Psychophysiology. ID: PsyP-2023-0700

Abstract

Anticipatory brain activity makes it possible to predict the occurrence of expected situations. However, events such as traffic accidents are statistically unpredictable and can generate catastrophic consequences. This study investigates the brain activity and effective connectivity associated with anticipating and processing such unexpected, unavoidable accidents. We asked 161 participants to ride a motorcycle simulator while recording their electroencephalographic activity. Of these, 90 participants experienced at least one accident while driving. We conducted both within-subjects and between-subjects comparisons. During the pre-accident period, the right inferior parietal lobe (IPL), left anterior cingulate cortex (ACC), and right insula showed higher activity in the accident condition. In the post-accident period, the bilateral orbitofrontal cortex, right IPL, bilateral ACC, and middle and superior frontal gyrus also showed increased activity in the accident condition. We observed greater effective connectivity within the nodes of the Limbic Network (LN) and between the nodes of the attentional networks in the pre-accident period. In the post-accident period, we also observed greater effective connectivity between networks, from the Ventral Attention network (VAN) to the Somatomotor Network and from nodes in the Visual Network, VAN, and Default Mode Network to nodes in the Frontoparietal Network, LN, and attentional networks. This suggests that activating salience-related processes and emotional processing allows the anticipation of accidents. Once an accident has occurred, integration and valuation of the new information takes place, and control processes are initiated to adapt behavior to the new demands of the environment.

Keywords: *accident, simulator, unpredictable, EEG, effective connectivity, brain network.*

Introduction

The human brain is primarily designed to predict the future and thus optimize behavior. This anticipatory brain activity is triggered by environmental cues or regularities that signal an upcoming event (Breska & Ivry, 2018; Coull, 2009). However, there are certain situations that are statistically unpredictable due to their very low frequency or lack of regularity and can have severe consequences if not avoided. One striking example of such situations is traffic accidents, which result in significant physical and psychological harm and account for more than 1.3 million deaths per year worldwide (World Health Organization, 2021). However, the study of the neural mechanisms underlying the anticipation and processing of unexpected events in dynamic ecological contexts, such as accidents, has received little attention in the scientific literature, despite its substantial practical significance for designing prevention strategies. Therefore, there remains a gap in our understanding of what occurs in the brain when we are confronted with situations that we could not foresee.

Electroencephalography studies indicate that contingent negative variation (CNV) and stimulus-preceding (SPN), two types of event-related potentials (ERPs), serve as reliable indicators of the anticipation of expected events, even in situations of uncertainty (Catena et al., 2012; Guo et al., 2019; Mento, 2017). Furthermore, source analysis suggests that these ERPs are distributed across brain regions such as the supplementary motor area (SMA), insula, anterior cingulate cortex (ACC), and medial and lateral frontal cortices (Kotani et al., 2015; Mento et al., 2015). Some studies have raised the question of whether anticipatory brain activity can still be observed when events are statistically unpredictable. For example, Radin et al. (2011) observed significant differences in cortical activity between meditators and non-meditators before the random presentation of a light flash or tone, equating this with SPN. In fact, the concept of Predictive

Anticipatory Activity (Mossbridge et al., 2014) allows us to distinguish between stimuli with different characteristics that are randomly presented (Duggan & Tressoldi, 2018). However, it is important to note that most of these studies were conducted with stimuli presented in non-real-life settings with irrelevant consequences. Our study focuses on accidents, events that have catastrophic consequences when they occur in real life. Additionally, these accidents are highly uncommon and unexpected, but this does not necessarily preclude the possibility that they can be anticipated.

Driving is a complex task that relies on visual perception and multi-domain executive functioning (Calhoun et al., 2002; Ware et al., 2020). Studies on effective connectivity, which examine how one brain node influences another (Friston, 2011), have revealed the involvement of various processes in driving, such as visual attention, episodic memory retrieval, goal direction, motor planning, and inhibitory control pathways (Almahasneh et al., 2018; Choi et al., 2020; Liu et al., 2017). Normal driving activates brain regions including the lateral occipital, superior and inferior parietal and inferior temporal cortices, as well as the frontal gyrus, motor areas, and cerebellum (Kan et al., 2013; Ware et al., 2020; Yan et al., 2019). However, when driving presents distractions or becomes more challenging, areas associated with cognitive control networks, relevant stimulus processing, and error monitoring, such as the superior frontal cortex, ACC, and insula, are also activated (Oba et al., 2022; Yuen et al., 2021). In the context of crashes, some studies have noted changes in the power of different EEG frequency bands in the moments before and after a simulated crash (Li et al., 2022; Zhang & Yan, 2023). Additionally, Sun et al. (2013) observed a rapid shift in ERPs occurring 500 ms after a collision in a simulated driving task compared to normal driving. Furthermore, Duma et al. (2017) observed increased negativity in frontocentral electrodes in both the "accident" (where an unpredictable simulated accident occurred) and

"baseline" (where there was the certainty that an accident would not occur, inducing a strong expectancy about the end of the trial) conditions, in the interval between 1000 and 0 ms pre-accident. In other words, the authors found anticipation markers in the accident condition, which arose before the occurrence of a statistically unpredictable and unavoidable stimulus. However, these studies have primarily focused on sensor-level analysis, leaving a gap in our understanding about which brain networks are involved in these effects, the point at which specific brain areas are recruited, and their connectivity during the peri-accident period.

This study aimed to explore the markers of anticipatory brain activity when individuals are confronted with unavoidable, catastrophic events (accidents in simulated driving contexts). Additionally, we aimed to investigate how the brain processes the occurrence of accidents and how connectivity between different brain networks evolves during the peri-accident periods. Based on previous evidence, we hypothesized that brain regions associated with expectation and uncertainty would be activated in the pre-accident period, leading to increased connectivity within the limbic and attentional networks responsible for emotional processing and salience. Conversely, all brain networks (Yeo et al., 2011) will be involved during the post-accident period, initiating the control and regulatory processes inherent to driving (Ware et al., 2020).

Method

Participants

A total of 161 (54 women) healthy participants took part in this study, which was carried out as part of a larger study on the neural basis of risk behavior in driving. The mean age of the participants was 32.6 years, ranging from 18-68 years, with a medium-high educational level. After being debriefed on the aims of the study and their rights, all

participants signed an informed consent form. All participants were paid for their participation in the study and were treated according to the Helsinki Declaration (World Medical Association, 2013). The study was approved by the Ethics Committee on Human Research of the University of Granada (n° 204/CEIH/2016). The sample size was calculated using G*Power 3.1.9.7 (Faul et al., 2009), with a moderate effect size ($f=0.25$), an alpha error of 0.05, and a power of 0.90 ($n=130$). A further 24% of participants were added to the sample to account for potential drop-outs.

Procedure

The participants visited the research center and took part in the HRT motorcycle simulator, described elsewhere (Di Stasi et al., 2009; Megías et al., 2017). In brief, this simulator is a realistic but static setup equipped with a seat, handlebar, pedals, accelerator, brakes, turn indicators, and horn. The simulation session consisted of two main parts: a practice and a driving task. Following the practice session, participants drove through a night circuit featuring eight risky scenarios (e.g., doors opening suddenly, pedestrians crossing) while their electrical brain activity was being recorded. The road scenario was projected on a screen measuring 110x180cm, positioned 185 cm in front of the driver. The screen had a refresh rate of 30 Hz and a resolution of 1024x768 pixels. The duration of the driving task, which depended on factors such as speed and the occurrence of accidents, averaged approximately 5 minutes. Our analysis focused exclusively on the data obtained during the risky scenarios and accident events recorded by the HRT motorcycle simulator.

EEG Recordings

Electrical activity of the brain (EEG) was recorded during the motorcycle riding task using a 64-channel active system (Brain Products, Inc.) mounted on an elastic cap and arranged according to the extended 10–20 system. The data were sampled at a rate of

1,000 Hz, amplified with a 0.016–1,000 Hz band-pass filter, and referenced online to FCz. Electrode impedances were maintained below 25 k Ω , as recommended by the manufacturer.

Data processing

Seven participants did not fully complete the task and were excluded from the analysis. Of the 154 remaining participants, only 90 experienced at least one accident during the course (Accident condition). Therefore, these 90 participants were used to compare their brain activity before and after having an accident with their non-accident periods (referred to as the Baseline condition). The remaining 64 participants (No-accident condition) were used for between-group comparisons with the Accident and the Baseline conditions.

The preprocessing of the continuous EEG signals was conducted using EEGLab software (Delorme & Makeig, 2004; <https://scn.ucsd.edu/eeGLab>) using the following protocol: 1) The continuous EEG recording was initially downsampled to 250 Hz; 2) the data were then re-referenced offline to the average reference; 3) Any problematic channels were identified and removed based on their spectral characteristics using EEGLab's default parameters; 4) Band-pass filtering was applied to the data (0.5-37 Hz); and 5) the data were segmented into epoch [-6000 to 1500 ms], which were time-locked to the trigger corresponding to either the occurrence of an accident (for participants with accidents), or the risky scenario trigger associated with safe segments (for these participants and those who did not experience an accident). In cases where an accident occurred, the triggers for both the preceding and subsequent scenarios were deleted. This was done to ensure a minimum of 20 seconds between the accident and the next trigger, or between the risky scene and the next scene trigger. Subsequently, the SOBI ICA decomposition was conducted to remove any artifacts using the ICLabel plugin implemented in EEGLab (<https://github.com/scn/ICLabel>). Removed channels were

interpolated using the spherical spline method. The online FCz reference was restored, and the data were then analyzed using standardized low-resolution brain electromagnetic tomography software (sLORETA; Pascual-Marqui, 2002; <http://www.uzh.ch/keyinst/loreta.htm>). This software was employed to calculate the current source density (CSD) of brain sources underlying the recorded EEG signals. The exact Loreta (eLORETA) approach was used, with sLORETA computing the CSD using 6239 voxels and using the Montreal Neurological Institute (MNI) template as the solution space.

Next, following Baltruschat et al. (2020), we used the Brainnetome atlas (BNA; Fan et al., 2016; <http://atlas.brainnetome.org>) to determine the effective connectivity between and within the seven brain networks identified by Yeo et al. (2011). For this purpose, we used the multivariate Granger causality software developed by Seth (2010; <https://users.sussex.ac.uk/~lionelb/MVGC/html/mvgchelp.html>). The time series for each network and its nodes were spatially averaged using the first eigenvariate of the singular value decomposition of the cluster of voxels.

Statistical analysis

Two separate analyses were conducted, one focusing on the estimated brain activities and the other on the estimated effective connectivity. In both cases, we employed a nonparametric permutation t-test using t-max statistics. This involved generating 5000 random samples to account for multiple comparisons, while an adjusted significance level was set at 0.05. Two main comparisons were conducted. First, a within-subjects analysis involved comparing the accident condition against the baseline (Accident-Baseline). Second, a between-subjects analysis was conducted to compare the accident condition against the No-accident condition (Accident-No accident). Separate comparisons were also carried out for the pre- and post-accident periods. For the connectivity analysis, in

each case, comparisons were made between the networks and between the nodes within the networks. Additionally, as a control test, the No-accidents condition was compared with the Baseline condition (Figure 1).

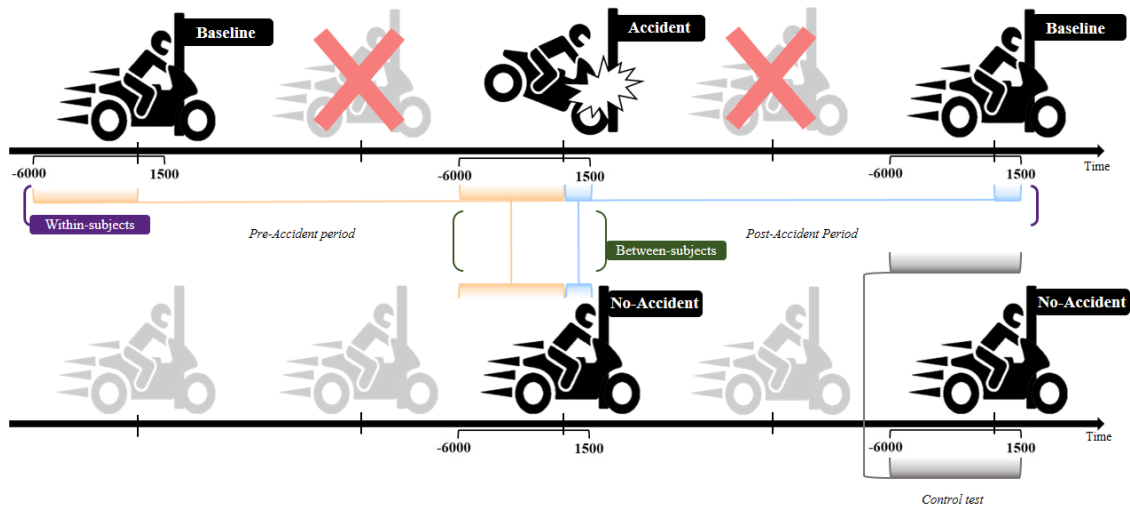


Figure 1. Timeline and segmentation of the driving task in the Accident (upper part) and No-accident (lower part) conditions along with comparisons made in the pre-accident (left) and post-accident (right) periods, and control test.

Results

On average, participants experienced 1.16 accidents (SD=0.91, range=1-4). Specifically, 56 participants had only one accident, 18 had two accidents, 11 had three, five had four, and the remaining 64 participants experienced no accidents. The mean age of the participants was 32.60 years (SD=13.76), with 54 women, and a mean educational level of 3.44 (SD=0.64).

Brain activity

During the pre-accident period, significant differences were observed for the within-subjects comparison Accident-Baseline (Figure 2). At 896 ms before the accident, there

was a difference favoring the accident condition in the right area 40 in the inferior parietal lobe (IPL). At 144 ms before the accident, the difference was located in the left area 32 (ACC), and 60 ms before the accident, the difference was found in the right insula.

For the between-groups comparison Accident-No accident, we observed significant differences favoring the accident condition at area 40 (880 ms), at right area 5 (232 ms), and at left area 32 and right area 40 (approximately 112 ms before the accident).

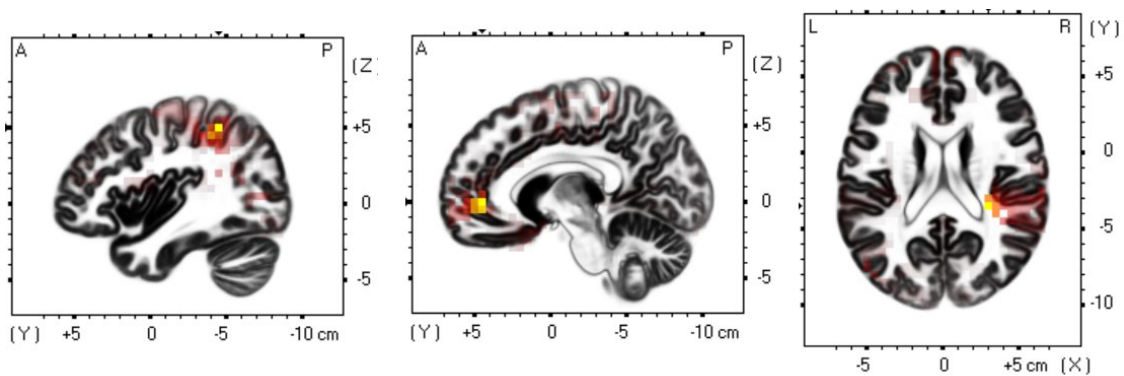


Figure 2. Differences between the Accident and Baseline conditions during the pre-accident period.

At post-accident (Figure 3, upper panel), we observed a substantial number of significant differences between the Accident and Baseline conditions, which can be summarized into three distinct time intervals: early (104-192 ms), middle (788-880 ms), and late (1260-1404 ms). These differences were associated with specific brain regions. The difference during the early period was identified in bilateral area 11, in the medial orbitofrontal gyrus, and the right area 40. During the middle period, the difference was located in bilateral (but mostly left hemisphere) area 24 in the cingulate gyrus, in the right area 6 of the middle frontal gyrus, and in bilateral areas 9 and 11 in the medial frontal gyrus. During the late period, the difference was located in bilateral areas 10/11 in the medial frontal gyrus, and bilateral area 32 (predominantly the right hemisphere). Similar differences emerged when comparing the Accident with the No-accidents condition (Figure 3, lower

panel). The difference during the early period was observed at around 104 ms post-trigger and located in bilateral area 11, while differences during the middle period appeared at 772 ms and were located in the right area 11 and bilateral area 32. Differences during the late period emerged at 1264 ms and were located in the right area 32, bilateral area 11/10 in the medial frontal gyrus, and bilateral area 24 in the anterior cingulate. Interestingly, no significant differences were observed in this period when we compared the Baseline and No-accident conditions.

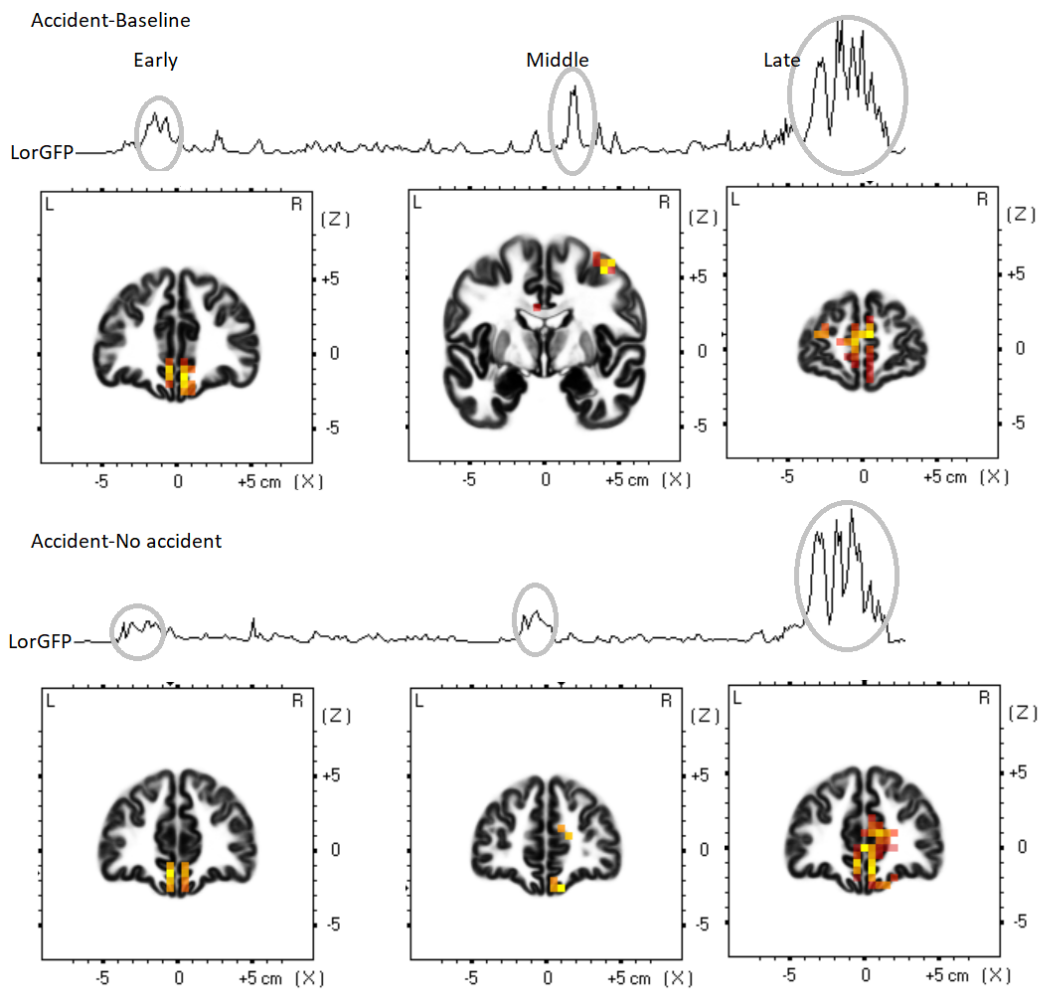


Figure 3. Profiles of statistical significance and significant brain areas in the post-trigger differences between the Accident and Baseline conditions (upper panel), and between the Accident and No-accident conditions (lower panel). The LorGFP curve is marked at the three most significant points, and differential activations favoring the Accident conditions are displayed in the brain maps.

Effective connectivity

Pre-accident period

In the pre-accident period no significant differences were found between networks for the within- or between-subjects comparisons. However, we found significant differences within networks when comparing the Accident and Baseline conditions (Table 1; Figure 4).

Table 1. Within-network differences in the pre-accident period for the within-subjects comparison (Accident-Baseline).

Node net 1	Net 1		Node net 2	net 2	p
RH medial area 38	LN	>	LH area 13	LN	0.05
RH rostral area 20	LN	>	LH area 13	LN	0.02
RH rostral area 35/36	LN	>	LH area 13	LN	0.04
RH TI (T agr insular cortex)	LN	>	LH area 13	LN	0.00
RH TI (T agr insular cortex)	LN	>	LH area 4	VAN	0.05
LH area1/2/3 (lower limb region)	VAN	<	LH ventrolateral area 37	DAN	0.05

Note. RH/LH: right/left hemisphere. LN: Limbic network, VAN: Ventral attention network, FPN: Fronto-parietal network, DAN: Dorsal attention network. >: causal link from Node 1 to Node 2, <: causal link from Node 2 to Node 1.

Post-accident

The Accident vs Baseline comparison revealed two significant differences in the efficiency of between-network connections. The first difference was directed from the ventral attention network (VAN) to the somatomotor network (SMN) ($p=0.05$). Although marginally significant, the second was directed from the default mode network (DMN) to the ventral attention network ($p=0.07$). Additionally, within the same comparison, we observed a substantial number of significant connections at the within- network level (Table 2; Figure 4). Comparison between the Accident and No-accident conditions yielded fewer significant differences (Table 3).

Table 2. Significant within-network connections during the post-accident period in the within-subjects comparison (Accidents – Baseline).

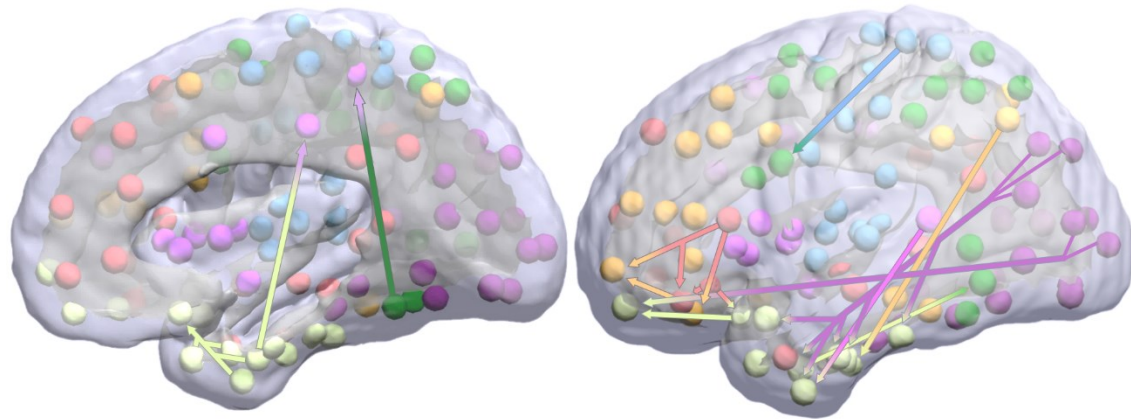
Node net 1	Net 1		Node net 2	Net 2	p
LH area 4ul, (upper limb region)	SMN	>	RH dorsal area 44	DAN	0.02
LH caudal cuneus gyrus	VN	>	RH opercular area 44	VAN	0.05
RH lateral area 10	FPN	<	RH lateral area 11	FPN	0.02
LH caudal cuneus gyrus	VN	>	RH lateral area 11	FPN	0.01
LH occipital polar cortex	VN	>	RH lateral area 11	FPN	0.03
RH area 13	LN	>	LH medial area 11	LN	0.02
LH lateral superior occipital gyrus	VN	>	RH medial area 38	LN	0.03
LH caudal area 39	VN	>	RH intermediate ventral area 20	LN	0.04
LH rostradorsal area 39	FPN	>	RH rostral area 20	LN	0.02
LH dorsomedial parietooccipital sulcus	VN	>	RH rostral area 20	LN	0.04
LH lateral superior occipital gyrus	VN	>	RH rostral area 20	LN	0.01
LH caudal area 39	VN	>	RH intermediate lateral area 20	LN	0.02
LH lateral superior occipital gyrus	VN	>	RH caudoventral of area 20	LN	0.01
RH dorsolateral area 37	DAN	<	RH area TI (T agr insular cortex)	LN	0.03
RH caudoposterior sup temporal sulcus	VAN	>	RH TI (T agr insular cortex)	LN	0.01
LH dorsomedial parietooccipital S	VN	>	RH area TI (T agr insular cortex)	LN	0.03
RH lateral área 10	FPN	<	RH rostroventral area 24	-	0.03
RH orbital area 12/47	DMN	<	RH rostroventral area 24	-	0.02
RH lateral area 11	FPN	<	RH rostroventral area 24	-	0.01
RH orbital area 12/47	DMN	<	RH subgenual area 32	DMN	0.05
RH area 13	LN	<	RH subgenual area 32	DMN	0.03

Note. RH/LH: right/left hemisphere. VN: Visual network, SMN: Somatomotor network, LN: Limbic network, DAN: Dorsal attention network, VAN: Ventral attention network, FPN: Fronto-parietal network, DMN: Default mode network. >: causal link from Node 1 to Node2, <: causal link from Node 2 to Node 1.

Table 3. Significant within-network connections during the post-accident period in the between-subjects comparison (Accidents – No-accidents).

Node net 1	Net 1		Node net 2	Net 2	p
RH area TI (T agr insular cortex)	LN	>	RH medial area 11	LN	0.05
RH area TI (T agr insular cortex)	LN	>	RH area 13	LN	0.01
RH dorsal agranular insula	VAN	>	RH area 13	LN	0.05
LH medial superior occipital gy	VN	>	RH medial area 38	LN	0.01
LH lateral superior occipital gyrus	VN	>	RH intermediate ventral area 20	LN	0.02
LH medial superior occipital gyrus	VN	>	RH area TI (T agr insular cortex)	LN	0.02
LH occipital polar cortex	VN	>	RH dorsal agranular insula	VAN	0.04
RH lateral area 11	FPN	<	RH rostroventral area 24	-	0.04
RH lateral area 11	FPN	<	LH subgenual area 32	DMN	0.04

Note. RH/LH: right/left hemisphere. VN: Visual network, LN: Limbic network, VAN: Ventral Attention network, FPN: Frontoparietal network, DMN: Default mode network. >: causal link from Node 1 to Node 2, <: causal link from Node 2 to Node 1.



a. b.
Figure 4. Within-network effective connectivity in the pre-accident (a) and post-accident periods (b) for the within-subjects comparison. *Note:* Node color represents the network they are forming part of: purple (visual) blue (somatomotor), green (dorsal attention), violet (ventral attention), cream (limbic) orange (frontoparietal), and red (default mode). Arrow direction represents the causal activation flow from one node to another. Adapted from Baltruschat et al. (2020).

Discussion

This study aimed to determine the brain activity and effective connectivity associated with the anticipation and processing of catastrophic events that are both unexpected and impossible to avoid. For this purpose, we measured brain activation patterns before and after a traffic accident in a simulated driving context. In the pre-accident period, we observed increased activity in the right IPL, the left ACC, and the right insula in the accident condition. In the post-accident period, we detected heightened activity in the bilateral orbitofrontal cortex/ventromedial prefrontal cortex (OFC/vmPFC), right IPL, bilateral ACC, and middle and superior frontal gyrus in the accident condition. Regarding effective connectivity, our analysis revealed a causal activation flow within the various nodes of the LN and between the nodes of the attentional networks during the pre-accident period. In the post-accident period, we also observed greater effective connectivity between networks, from the VAN to the SMN and from nodes in the VN, VAN, and DMN to nodes in the FPN, LN, and attentional networks.

Brain activity

Pre-accident period

Our findings revealed notable activation in the right IPL, left ACC, and right insula when comparing Accident and Baseline conditions. We observed similar activation patterns when comparing the Accident and No-accident groups. These findings align with previous research indicating the involvement of these brain regions during driving and the anticipation of unexpected and potentially dangerous situations. Specifically, IPL activation has been linked to anticipating outcomes following decision-making processes as well as reinforcing or aversive stimuli (Gaudio & Quattrocchi, 2012; Liu et al., 2011; Seidel et al., 2015). In this regard, the IPL is associated with monitoring attentional shifts in space, and with visuospatial perception and memory functions (Chen et al., 2012; Chung et al., 2014). The ACC has been associated with uncertainty processing, conflict detection, and error monitoring from the time an action is performed to the results of this action (Ernst & Paulus, 2005; Grupe & Nitschke, 2013). In addition, Calhoun et al. (2002) also identified the activation of an attentional modulation network during driving, which includes the ACC and the IPL. On the other hand, the insular cortex responds to painful stimuli and the anticipation of harm (Centanni et al., 2021; Drabant et al., 2011; Seidel et al., 2015). Specifically, it represents conscious feelings and body states related to interoceptive awareness (Craig, 2009; Uddin et al., 2017). Together with the ACC, this structure forms the "salience network" (SN; Seeley et al., 2007) that is activated in response to behaviorally relevant and novel stimuli rather than expected events (Corbetta et al., 2008). Furthermore, in a functional magnetic resonance study where a group of taxi drivers played a driving video game, Spiers & Maguire (2007) found increased activation in the medial occipital, posterior middle temporal, posterior parietal and lateral prefrontal cortices, ACC, precuneus, and insula when responding to road hazards. Effective

connectivity studies have also demonstrated that information enters the salience network via the insula, which acts as an "out-flow hub" regulating the interaction between large-scale networks (Ham et al., 2013; Sridharan et al., 2008). In other words, the insula serves as a final step in hierarchical information processing, integrating relevant sensory, interoceptive, emotional, and cognitive information (Kurth et al., 2010).

In summary, the evidence indicates that the IPL, ACC, and insula are activated during driving and these structures are also linked to attentional shifts based on stored information. These processes enable the interpretation of the environment, detection of errors, and monitoring of potential conflicts. Moreover, these brain regions are essential for integrating emotional and interoceptive information, allowing individuals to identify certain features of the environment that are relevant for anticipating unexpected or potentially threatening situations. In line with previous research (Duma et al., 2017), our findings support the existence of anticipatory brain activity in response to catastrophic events. Specifically, we observed that the IPL, ACC, and insula become active in the milliseconds (ms) preceding a simulated driving accident. Therefore, it seems that the activation of internal processes, including emotional, cognitive, and interoceptive awareness, forms the basis for anticipating unpredictable situations that cannot be avoided.

Post-accident period

The Accident-Baseline comparison revealed activation in several key brain regions, including the bilateral OFC/vmPFC, right IPL and bilateral ACC, and middle and superior frontal gyrus. Very similar activation patterns were found in the Accident-No-accident comparison. Previous studies have demonstrated the role of several frontal and parietal regions in the planning phases that predict good driving performance (Oba et al., 2022; Ware et al., 2020). Furthermore, in a computerized driving task where the outcome could

be a crash or successful pass, greater activation of the OFC, IPL, insula, and ACC was observed during the crash condition (Vorobyev et al., 2015). One of the main functions of the OFC/vmPFC is to integrate past and current information to affectively evaluate stimuli and guide the decision-making process (Knudsen & Wallis, 2022; Peters & Büchel, 2010). This region is involved in comparing real and expected outcomes, showing greater activation in response to highly unexpected outcomes (Ernst & Paulus, 2005). Activation of the premotor area (a6) could reflect unconscious voluntary motor planning (Drabant et al., 2011), while the ACC and premotor areas are jointly implicated in driving action in response to negative feedback (Klein et al., 2007). The ACC plays a pivotal role in task performance across all phases (Dosenbach et al., 2006) and serves as a part of the SN, contributing to error monitoring and the hierarchical initiation of control signals for activating prefrontal regions (Sridharan et al., 2008; Srinivasan et al., 2013). The superior frontal gyrus is a component of the cognitive control network responsible for inhibitory and attentional control, flexibility, and decision-making for behavioral self-regulation (Miller & Cohen, 2001; Niendam et al., 2012; Passingham & Lau, 2023). Moreover, some authors have reported changes in brain activity in the milliseconds following a simulated crash (Li et al., 2022; Sun et al., 2013). Taken together, these findings suggest that the activation of areas responsible for detecting relevant stimuli is sustained after an accident. Additionally, frontal regions responsible for the valuation of the present experience and initiating the control processes necessary for behavioral self-regulation are activated.

Effective connectivity

Pre-accident period

The Accident-Baseline comparison revealed a causal activation flow within LN nodes and between VAN and DAN nodes. Specifically, somatosensory regions of the VAN (left

areas 4 and 1/2/3) received information from the limbic region of the right insula and the temporal area of the DAN (left area 37). On the other hand, limbic regions of the right insula, parahippocampal (right area 35/36), and superior and inferior temporal (right areas 38 and 20) gyrus showed effective connectivity to the orbital region of the LN (left area 13). The VAN is typically activated during attentional orientation and plays a role in identifying salient or novel stimuli (Corbetta & Shulman, 2002; Petersen & Posner, 2012). Previous studies have shown the collaborative interaction between DAN and VAN in redirecting attention to unexpected stimuli (Vossel et al., 2014). The insula serves as the central node of the SN, which overlaps with the VAN (Menon & D'Esposito, 2022), playing a role in event anticipation, among other functions (see above). Area 13, part of the OFC, is responsible for the emotional valuation of stimuli by integrating information received from other brain areas (Knudsen & Wallis, 2022; Peters & Büchel, 2010; Rolls et al., 2023). This area is also responsible for the integration of past and current information and shows anticipatory activity before the presentation of stimuli (Seidel et al., 2015; Zhou et al., 2021). Other studies have demonstrated activation of the OFC when cognitive maps or sets of associations underlying a task are identified, which, in turn, facilitates behavioral learning (Schuck et al., 2016) and the prediction of rewards or punishments (Zhou et al., 2019). Therefore, the OFC appears to play a pivotal role in forming a representation of the structure of the environment to anticipate future outcomes. Additionally, anterior, inferior, and medial temporal regions are known to be involved in emotional processing, semantic representations, and episodic memory (Herlin et al., 2021; Wong & Gallate, 2012; Zhang et al., 2022). Previous research has also shown evidence of effective and structural connectivity between the insula and parahippocampal and temporal areas with the OFC (Fan et al., 2014; Lin et al., 2020; Rolls et al., 2022a). Our results on effective connectivity are consistent with those obtained on pre-accident

brain activity. Moreover, they are consistent with previous evidence and suggest that relevant environmental cues are integrated with information retrieved from memory, conceptual knowledge, and interoceptive information related to potential hazards. This integration process enables the brain to form a comprehensive representation of the structure and emotional value of the situation. Therefore, it seems that the anticipation of uncertain or unexpected situations, such as accidents, is strongly associated with the activation of affective mechanisms (Seidel et al., 2015).

Post-accident period

The increased effective connectivity between networks from the VAN to the SMN in the Accident-Baseline comparison is consistent with the findings reported by Duann et al. (2009) using an inhibitory control task. Their study revealed effective connectivity from the VAN to the SMN, where the VAN was involved in the attentional processing of novel information, and the SMN played a role in the inhibitory control of movement. These results parallel our findings and suggest that during driving, especially in the milliseconds following an accident, there is a shift in attention and an activation of control and inhibitory processes that facilitate behavioral adaptation to new environmental demands.

At the within-network level, the Accident-Baseline comparison revealed the involvement of all brain networks. Sensory nodes within the VN, SMN, and VAN transmitted information to frontal and orbitofrontal nodes belonging to the VAN, DAN, and FPN and to temporal and insular areas of the LN. Additionally, the cingulate regions of the DMN showed effective connectivity with orbitofrontal regions belonging to the FPN, DMN, and LN, while effective connectivity was observed between nodes belonging to the same networks. The accident-no accident comparison showed similar results, although with fewer significant differences. Vorobyev et al. (2015) also found increased activation in the lateral and medial occipital areas, the junction between temporal polar,

orbitofrontal, and insular cortices, and the posterior middle temporal cortex during accidents in a simulated driving task.

The occurrence of a crash (resulting in the fall of the motorcycle) leads to a complete alteration of the environmental characteristics of the driving simulator. This is reflected in the activation of occipital and parietal nodes of the VN (left occipital polar, left cuneus, left lateral occipital, left area 39, and left parietooccipital sulcus), all of which are involved in visual attention, object and motion processing, memory, and navigation (Grill-Spector et al., 2001; Malikovic et al., 2016; Rolls et al., 2022c). Previous studies have identified fixed and reciprocal connections between the VN and VAN, which facilitate spatial orientation to relevant stimuli (Vossel et al., 2012, 2014). The inferior frontal gyrus (IFG; area 44), which belongs to the VAN and the DAN (Corbetta et al., 2008), is responsible for the representation of the hierarchical sequential structure of ongoing events, using information received from precentral motor areas (Fiebach & Schubotz, 2006). These findings indicate that the connectivity from the VN and SMN to the VAN and DAN enables the formation of a representation of a sequence of events to facilitate an attentional shift from stimulus detection to goal-directed attention (Fox et al., 2006). The superior and inferior temporal regions of the LN (right areas 38 and 20) are involved in affective visual processing, semantic representations, and episodic memory (see above), and the anterior temporal cortex is part of the "meaning" network that facilitates the understanding of events for executive control (Jouen et al., 2018). Several investigations have found structural and effective connections between the occipitoparietal regions and the superior and inferior temporal cortices (Baker et al., 2018; Lin et al., 2020; Rolls et al., 2022c; Wu et al., 2016). These connections suggest the occurrence of an abstract representation of the current affective experience, which promotes adaptive behavior. These findings are consistent with the results of Choi et al.

(2020), who also identified effective connectivity from the VN to the inferior frontal, superior temporal, and inferior temporal gyrus during driving. Additionally, the insular region of the LN receives information from the superior temporal region of the VAN, which is involved in the auditory processing and perception of threatening information (Connolly et al., 2016; Rolls et al., 2022b), sending information to the temporal region of the DAN (area 37) for processing information from different sensory modalities (Hodgson et al., 2022). These patterns of effective connectivity are consistent with the idea that the insula plays a fundamental role in switching between different networks and shifting the focus from external to internal processes to facilitate the decision-making process (Lamichhane & Dhamala, 2015; Sridharan et al., 2008). In support of the above, our results suggest that, in the milliseconds following a crash, and following the notion of posterior-to-anterior patterns of information flow proposed by Mesulam (1998), the sensory association areas detect changes in the environment and relay this information to higher-order structures to initiate the information integration and cognitive control processes necessary to adapt behavior to the demands of the situation.

It is important to note that the areas of the LN that are influenced by the VN in the post-accident period (right areas 38 and 20 and temporal insular) are the same areas that influence the activation of the OFC in the pre-accident period. Before the accident, the visual scenes were identical for individuals who would later have an accident and those who would not. When the accident occurs, the limbic regions receive information from the sensory regions associated with an environment where negative consequences have occurred. This influx of new information could assist the OFC in making decisions related to the aversive consequences of the accident. In fact, in the post-accident period, the fronto-orbital areas (right areas 10, 11, 13, and 12/47) were influenced by different brain networks responsible for general task performance (Dosenbach et al., 2006), including

the visual network. Previous studies have identified effective connectivity from visual regions to the OFC/VPFC when presented with aversive stimuli (Dima et al., 2016; Rolls et al., 2023). Furthermore, the effective connectivity we observed from the cingulate regions of the DMN (right areas 32 and 24) to the orbitofrontal regions belonging to the FPN, DMN, and LN support the idea that the DMN and task-positive systems are not antagonistic (Cocchi et al., 2013). The DMN is responsible for self-referential processing and internal mental state monitoring (Greicius et al., 2003), while the FPN is involved in planning, inhibition, and cognitive flexibility, allowing for goal modification based on the environment and the changing demands of a task (Menon & D'Esposito, 2022; Woolgar et al., 2015). Studies of effective connectivity have revealed the cooperative interactions between the DMN and task-positive networks, with the DMN exerting an excitatory influence on the executive networks (De Pisapia et al., 2012; Pu et al., 2016; Uddin et al., 2009). In this context, the activation of orbital regions linked to cognitive control, through the influence of the cingulate cortex, can facilitate the decision-making process based on the valuation of the environment following an accident.

Conclusions

The primary objective of this study was to explore brain activity indicators related to the processing of unexpected and unavoidable catastrophic events (accidents that occurred while driving in a simulator). In summary, our results demonstrated changes in brain activation and effective connectivity patterns during different phases of this process. During the pre-accident period, we observed activation of LN regions and attentional networks, while in the post-accident period, involvement of all brain networks was evident, ranging from sensory association regions to higher-order processing areas. These findings suggest that the activation of salience-related processes and emotional processing allows anticipating the occurrence of accidents. However, once an accident

has already occurred, there is an integration and valuation of the new information, and control processes are initiated to adapt behavior to the new demands of the environment.

References

- Almahasneh, H., Kamel, N., & Khan, D. M. (2018). Variation in Brain's Effective Connectivity due to Driving using Partial Directed Coherence. *2018 IEEE International Conference on Automatic Control and Intelligent Systems (I2CACIS)*, 67-70. <https://doi.org/10.1109/I2CACIS.2018.8603692>
- Baker, C. M., Burks, J. D., Briggs, R. G., Conner, A. K., Glenn, C. A., Manohar, K., Milton, C. K., Sali, G., McCoy, T. M., Battiste, J. D., O'Donoghue, D. L., & Sughrue, M. E. (2018). A Connectomic Atlas of the Human Cerebrum-Chapter 8: The Posterior Cingulate Cortex, Medial Parietal Lobe, and Parieto-Occipital Sulcus. *Operative Neurosurgery*, *15*, S350-S371. <https://doi.org/10.1093/ons/opy262>
- Baltruschat, S., Cándido, A., Megías, A., Maldonado, A., & Catena, A. (2020). Risk proneness modulates the impact of impulsivity on brain functional connectivity. *Human Brain Mapping*, *41*(4), 943-951. <https://doi.org/10.1002/hbm.24851>
- Breska, A., & Ivry, R. B. (2018). Double dissociation of single-interval and rhythmic temporal prediction in cerebellar degeneration and Parkinson's disease. *Proceedings of the National Academy of Sciences*, *115*(48), 12283-12288. <https://doi.org/10.1073/pnas.1810596115>
- Calhoun, V. D., Pekar, J. J., McGinty, V. B., Adali, T., Watson, T. D., & Pearlson, G. D. (2002). Different activation dynamics in multiple neural systems during simulated driving. *Human Brain Mapping*, *16*(3), 158-167. <https://doi.org/10.1002/hbm.10032>

- Catena, A., Perales, J. C., Megías, A., Cándido, A., Jara, E., & Maldonado, A. (2012). The Brain Network of Expectancy and Uncertainty Processing. *PLOS ONE*, *7*(7), e40252. <https://doi.org/10.1371/journal.pone.0040252>
- Centanni, S. W., Janes, A. C., Haggerty, D. L., Atwood, B., & Hopf, F. W. (2021). Better living through understanding the insula: Why subregions can make all the difference. *Neuropharmacology*, *198*, 108765. <https://doi.org/10.1016/j.neuropharm.2021.108765>
- Chen, Q., Weidner, R., Vossel, S., Weiss, P. H., & Fink, G. R. (2012). Neural Mechanisms of Attentional Reorienting in Three-Dimensional Space. *Journal of Neuroscience*, *32*(39), 13352-13362. <https://doi.org/10.1523/JNEUROSCI.1772-12.2012>
- Choi, M.-H., Kim, H.-S., & Chung, S.-C. (2020). Evaluation of Effective Connectivity Between Brain Areas Activated During Simulated Driving Using Dynamic Causal Modeling. *Frontiers in Behavioral Neuroscience*, *14*. <https://doi.org/10.3389/fnbeh.2020.00158>
- Chung, S.-C., Choi, M.-H., Kim, H.-S., You, N.-R., Hong, S.-P., Lee, J.-C., Park, S.-J., Baek, J.-H., Jeong, U.-H., You, J.-H., Lim, D.-W., & Kim, H.-J. (2014). Effects of distraction task on driving: A functional magnetic resonance imaging study. *Bio-Medical Materials and Engineering*, *24*(6), 2971-2977. <https://doi.org/10.3233/BME-141117>
- Cocchi, L., Zalesky, A., Fornito, A., & Mattingley, J. B. (2013). Dynamic cooperation and competition between brain systems during cognitive control. *Trends in Cognitive Sciences*, *17*(10), 493-501. <https://doi.org/10.1016/j.tics.2013.08.006>

- Connolly, A. C., Sha, L., Swaroop Guntupalli, J., Oosterhof, N., Halchenko, Y. O., Nastase, S. A., Castello, M. V. O., Abdi, H., Jobst, B. C., Ida Gobbini, M., & Haxby, J. V. (2016). How the human brain represents perceived dangerousness or “predacity” of animals. *Journal of Neuroscience*, *36*(19), 5373-5384.
<https://doi.org/10.1523/JNEUROSCI.3395-15.2016>
- 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.
<https://doi.org/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.
<https://doi.org/10.1038/nrn755>
- Coull, J. T. (2009). Neural substrates of mounting temporal expectation. *PLoS Biology*, *7*(8), e1000166. <https://doi.org/10.1371/journal.pbio.1000166>
- Craig, A. D. (2009). How do you feel - now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, *10*(1), 59-70. <https://doi.org/10.1038/nrn2555>
- De Pisapia, N., Turatto, M., Lin, P., Jovicich, J., & Caramazza, A. (2012). Unconscious priming instructions modulate activity in default and executive networks of the human brain. *Cerebral Cortex*, *22*(3), 639-649.
<https://doi.org/10.1093/cercor/bhr146>
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9-21.
<https://doi.org/10.1016/j.jneumeth.2003.10.009>

- Di Stasi, L. L., Álvarez-Valbuena, V., Cañas, J. J., Maldonado, A., Catena, A., Antolí, A., & Candido, A. (2009). Risk behaviour and mental workload: Multimodal assessment techniques applied to motorbike riding simulation. *Transportation Research Part F: Traffic Psychology and Behaviour*, *12*(5), 361-370. <https://doi.org/10.1016/j.trf.2009.02.004>
- Dima, D., Roberts, R. E., & Frangou, S. (2016). Connectomic markers of disease expression, genetic risk and resilience in bipolar disorder. *Translational Psychiatry*, *6*(1), Article 1. <https://doi.org/10.1038/tp.2015.193>
- Dosenbach, N. U. F., Visscher, K. M., Palmer, E. D., Miezin, F. M., Wenger, K. K., Kang, H. C., Burgund, E. D., Grimes, A. L., Schlaggar, B. L., & Petersen, S. E. (2006). A Core System for the Implementation of Task Sets. *Neuron*, *50*(5), 799-812. <https://doi.org/10.1016/j.neuron.2006.04.031>
- Drabant, E. M., Kuo, J. R., Ramel, W., Blechert, J., Edge, M. D., Cooper, J. R., Goldin, P. R., Hariri, A. R., & Gross, J. J. (2011). Experiential, autonomic, and neural responses during threat anticipation vary as a function of threat intensity and neuroticism. *NeuroImage*, *55*(1), 401-410. <https://doi.org/10.1016/j.neuroimage.2010.11.040>
- Duann, J.-R., Ide, J. S., Luo, X., & Li, C.-S. R. (2009). Functional connectivity delineates distinct roles of the inferior frontal cortex and presupplementary motor area in stop signal inhibition. *Journal of Neuroscience*, *29*(32), 10171-10179. <https://doi.org/10.1523/JNEUROSCI.1300-09.2009>
- Duggan, M., & Tressoldi, P. (2018). Predictive physiological anticipatory activity preceding seemingly unpredictable stimuli: An update of Mossbridge et al's meta-analysis. *F1000Research*, *7*, 407. <https://doi.org/10.12688/f1000research.14330.2>

- Duma, G. M., Mento, G., Manari, T., Martinelli, M., & Tressoldi, P. (2017). Driving with Intuition: A Preregistered Study about the EEG Anticipation of Simulated Random Car Accidents. *PLOS ONE*, *12*(1), e0170370. <https://doi.org/10.1371/journal.pone.0170370>
- Ernst, M., & Paulus, M. P. (2005). Neurobiology of Decision Making: A Selective Review from a Neurocognitive and Clinical Perspective. *Biological Psychiatry*, *58*(8), 597-604. <https://doi.org/10.1016/j.biopsych.2005.06.004>
- Fan, L., Li, H., Zhuo, J., Zhang, Y., Wang, J., Chen, L., Yang, Z., Chu, C., Xie, S., Laird, A. R., Fox, P. T., Eickhoff, S. B., Yu, C., & Jiang, T. (2016). The Human Brainnetome Atlas: A New Brain Atlas Based on Connectional Architecture. *Cerebral Cortex*, *26*(8), 3508-3526. <https://doi.org/10.1093/cercor/bhw157>
- Fan, L., Wang, J., Zhang, Y., Han, W., Yu, C., & Jiang, T. (2014). Connectivity-Based Parcellation of the Human Temporal Pole Using Diffusion Tensor Imaging. *Cerebral Cortex*, *24*(12), 3365-3378. <https://doi.org/10.1093/cercor/bht196>
- Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149-1160. <https://doi.org/10.3758/BRM.41.4.1149>
- Fiebach, C. J., & Schubotz, R. I. (2006). Dynamic Anticipatory Processing of Hierarchical Sequential Events: A Common Role for Broca's Area and Ventral Premotor Cortex Across Domains? *Cortex*, *42*(4), 499-502. [https://doi.org/10.1016/S0010-9452\(08\)70386-1](https://doi.org/10.1016/S0010-9452(08)70386-1)
- Fox, M. D., Corbetta, M., Snyder, A. Z., Vincent, J. L., & Raichle, M. E. (2006). Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(26), 10046-10051. <https://doi.org/10.1073/pnas.0604187103>

- Friston, K. J. (2011). Functional and Effective Connectivity: A Review. *Brain Connectivity, 1*(1), 13-36. <https://doi.org/10.1089/brain.2011.0008>
- Gaudio, S., & Quattrocchi, C. C. (2012). Neural basis of a multidimensional model of body image distortion in anorexia nervosa. *Neuroscience & Biobehavioral Reviews, 36*(8), 1839-1847. <https://doi.org/10.1016/j.neubiorev.2012.05.003>
- Greicius, M. D., Krasnow, B., Reiss, A. L., & Menon, V. (2003). Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proceedings of the National Academy of Sciences, 100*(1), 253-258. <https://doi.org/10.1073/pnas.0135058100>
- Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research, 41*(10-11), 1409-1422. [https://doi.org/10.1016/s0042-6989\(01\)00073-6](https://doi.org/10.1016/s0042-6989(01)00073-6)
- Grupe, D. W., & Nitschke, J. B. (2013). Uncertainty and anticipation in anxiety: An integrated neurobiological and psychological perspective. *Nature Reviews Neuroscience, 14*(7), Article 7. <https://doi.org/10.1038/nrn3524>
- Guo, Z., Tan, X., Pan, Y., Liu, X., Zhao, G., Wang, L., & Peng, Z. (2019). Contingent negative variation during a modified cueing task in simulated driving. *PLOS ONE, 14*(11), e0224966. <https://doi.org/10.1371/journal.pone.0224966>
- Ham, T., Leff, A., de Boissezon, X., Joffe, A., & Sharp, D. J. (2013). Cognitive control and the salience network: An investigation of error processing and effective connectivity. *Journal of Neuroscience, 33*(16), 7091-7098. <https://doi.org/10.1523/JNEUROSCI.4692-12.2013>
- Herlin, B., Navarro, V., & Dupont, S. (2021). The temporal pole: From anatomy to function—A literature appraisal. *Journal of Chemical Neuroanatomy, 113*, 101925. <https://doi.org/10.1016/j.jchemneu.2021.101925>

- Hodgson, V. J., Lambon Ralph, M. A., & Jackson, R. L. (2022). The cross-domain functional organization of posterior lateral temporal cortex: Insights from ALE meta-analyses of 7 cognitive domains spanning 12,000 participants. *Cerebral Cortex*, bhac394. <https://doi.org/10.1093/cercor/bhac394>
- Jouen, A. L., Ellmore, T. M., Madden-Lombardi, C. J., Pallier, C., Dominey, P. F., & Ventre-Dominey, J. (2018). Beyond the word and image: II- Structural and functional connectivity of a common semantic system. *NeuroImage*, 166, 185-197. <https://doi.org/10.1016/j.neuroimage.2017.10.039>
- Kan, K., Schweizer, T. A., Tam, F., & Graham, S. J. (2013). Methodology for functional MRI of simulated driving. *Medical Physics*, 40(1). <https://doi.org/10.1118/1.4769107>
- Klein, T. A., Endrass, T., Kathmann, N., Neumann, J., von Cramon, D. Y., & Ullsperger, M. (2007). Neural correlates of error awareness. *NeuroImage*, 34(4), 1774-1781. <https://doi.org/10.1016/j.neuroimage.2006.11.014>
- Knudsen, E. B., & Wallis, J. D. (2022). Taking stock of value in the orbitofrontal cortex. *Nature Reviews Neuroscience*, 23(7), Article 7. <https://doi.org/10.1038/s41583-022-00589-2>
- Kotani, Y., Ohgami, Y., Ishiwata, T., Arai, J., Kiryu, S., & Inoue, Y. (2015). Source analysis of stimulus-preceding negativity constrained by functional magnetic resonance imaging. *Biological Psychology*, 111, 53-64. <https://doi.org/10.1016/j.biopsycho.2015.08.005>
- Kurth, F., Zilles, K., Fox, P. T., Laird, A. R., & Eickhoff, S. B. (2010). A link between the systems: Functional differentiation and integration within the human insula revealed by meta-analysis. *Brain Structure and Function*, 214(5), 519-534. <https://doi.org/10.1007/s00429-010-0255-z>

- Lamichhane, B., & Dhamala, M. (2015). The Salience Network and Its Functional Architecture in a Perceptual Decision: An Effective Connectivity Study. *Brain Connectivity, 5*(6), 362-370. <https://doi.org/10.1089/brain.2014.0282>
- Li, X., Yang, L., & Yan, X. (2022). An exploratory study of drivers' EEG response during emergent collision avoidance. *Journal of Safety Research, 82*, 241-250. <https://doi.org/10.1016/j.jsr.2022.05.015>
- Lin, Y.-H., Young, I. M., Conner, A. K., Glenn, C. A., Chakraborty, A. R., Nix, C. E., Bai, M. Y., Dhanaraj, V., Fonseka, R. D., Hormovas, J., Tanglay, O., Briggs, R. G., & Sughrue, M. E. (2020). Anatomy and White Matter Connections of the Inferior Temporal Gyrus. *World Neurosurgery, 143*, e656-e666. <https://doi.org/10.1016/j.wneu.2020.08.058>
- Liu, X., Hairston, J., Schrier, M., & Fan, J. (2011). Common and distinct networks underlying reward valence and processing stages: A meta-analysis of functional neuroimaging studies. *Neuroscience & Biobehavioral Reviews, 35*(5), 1219-1236. <https://doi.org/10.1016/j.neubiorev.2010.12.012>
- Liu, Z., Zhang, M., Xu, G., Huo, C., Tan, Q., Li, Z., & Yuan, Q. (2017). Effective Connectivity Analysis of the Brain Network in Drivers during Actual Driving Using Near-Infrared Spectroscopy. *Frontiers in Behavioral Neuroscience, 11*. <https://www.frontiersin.org/articles/10.3389/fnbeh.2017.00211>
- Malikovic, A., Amunts, K., Schleicher, A., Mohlberg, H., Kujovic, M., Palomero-Gallagher, N., Eickhoff, S. B., & Zilles, K. (2016). Cytoarchitecture of the human lateral occipital cortex: Mapping of two extrastriate areas hOc4la and hOc4lp. *Brain Structure and Function, 221*(4), 1877-1897. <https://doi.org/10.1007/s00429-015-1009-8>

- Megías, A., Cortes, A., Maldonado, A., & Cándido, A. (2017). Using negative emotional feedback to modify risky behavior of young moped riders. *Traffic Injury Prevention, 18*(4), 351-356. <https://doi.org/10.1080/15389588.2016.1205189>
- Menon, V., & D'Esposito, M. (2022). The role of PFC networks in cognitive control and executive function. *Neuropsychopharmacology, 47*(1), Article 1. <https://doi.org/10.1038/s41386-021-01152-w>
- Mento, G. (2017). The role of the P3 and CNV components in voluntary and automatic temporal orienting: A high spatial-resolution ERP study. *Neuropsychologia, 107*, 31-40. <https://doi.org/10.1016/j.neuropsychologia.2017.10.037>
- Mento, G., Tarantino, V., Vallesi, A., & Bisiacchi, P. S. (2015). Spatiotemporal Neurodynamics Underlying Internally and Externally Driven Temporal Prediction: A High Spatial Resolution ERP Study. *Journal of Cognitive Neuroscience, 27*(3), 425-439. https://doi.org/10.1162/jocn_a_00715
- Mesulam, M.-M. (1998). From sensation to cognition. *Brain, 121*(6), 1013-1052. <https://doi.org/10.1093/brain/121.6.1013>
- Miller, E. K., & Cohen, J. D. (2001). An Integrative Theory of Prefrontal Cortex Function. *Annual Review of Neuroscience, 24*(1), 167-202. <https://doi.org/10.1146/annurev.neuro.24.1.167>
- Mossbridge, J. A., Tressoldi, P., Utts, J., Ives, J. A., Radin, D., & Jonas, W. B. (2014). Predicting the unpredictable: Critical analysis and practical implications of predictive anticipatory activity. *Frontiers in Human Neuroscience, 8*. <https://doi.org/10.3389/fnhum.2014.00146>

- Niendam, T. A., Laird, A. R., Ray, K. L., Dean, Y. M., Glahn, D. C., & Carter, C. S. (2012). Meta-analytic evidence for a superordinate cognitive control network subserving diverse executive functions. *Cognitive, Affective and Behavioral Neuroscience, 12*(2), 241-268. <https://doi.org/10.3758/s13415-011-0083-5>
- Oba, K., Hamada, K., Tanabe-Ishibashi, A., Murase, F., Hirose, M., Kawashima, R., & Sugiura, M. (2022). Neural Correlates Predicting Lane-Keeping and Hazard Detection: An fMRI Study Featuring a Pedestrian-Rich Simulator Environment. *Frontiers in Human Neuroscience, 16*. <https://www.frontiersin.org/articles/10.3389/fnhum.2022.754379>
- Pascual-Marqui, R. D. (2002). Standardized low-resolution brain electromagnetic tomography (sLORETA): Technical details. *Methods and Findings in Experimental and Clinical Pharmacology, 24 Suppl D*, 5-12.
- Passingham, R. E., & Lau, H. (2023). Do we understand the prefrontal cortex? *Brain Structure and Function, 228*(5), 1095-1105. <https://doi.org/10.1007/s00429-022-02587-7>
- Peters, J., & Büchel, C. (2010). Neural representations of subjective reward value. *Behavioural Brain Research, 213*(2), 135-141. <https://doi.org/10.1016/j.bbr.2010.04.031>
- Petersen, S. E., & Posner, M. I. (2012). The Attention System of the Human Brain: 20 Years After. *Annual Review of Neuroscience, 35*(1), 73-89. <https://doi.org/10.1146/annurev-neuro-062111-150525>
- Pu, W., Luo, Q., Palaniyappan, L., Xue, Z., Yao, S., Feng, J., & Liu, Z. (2016). Failed cooperative, but not competitive, interaction between large-scale brain networks impairs working memory in schizophrenia. *Psychological Medicine, 46*(6), 1211-1224. <https://doi.org/10.1017/S0033291715002755>

- Radin, D. I., Vieten, C., Michel, L., & Delorme, A. (2011). Electrocortical Activity Prior to Unpredictable Stimuli in Meditators and Nonmeditators. *EXPLORE*, *7*(5), 286-299. <https://doi.org/10.1016/j.explore.2011.06.004>
- Rolls, E. T., Deco, G., Huang, C.-C., & Feng, J. (2022a). The effective connectivity of the human hippocampal memory system. *Cerebral Cortex*, *32*(17), 3706-3725. <https://doi.org/10.1093/cercor/bhab442>
- Rolls, E. T., Deco, G., Huang, C.-C., & Feng, J. (2022b). The human language effective connectome. *NeuroImage*, *258*, 119352. <https://doi.org/10.1016/j.neuroimage.2022.119352>
- Rolls, E. T., Deco, G., Huang, C.-C., & Feng, J. (2022c). The human posterior parietal cortex: Effective connectome, and its relation to function. *Cerebral Cortex*, bhac266. <https://doi.org/10.1093/cercor/bhac266>
- Rolls, E. T., Deco, G., Huang, C.-C., & Feng, J. (2023). The human orbitofrontal cortex, vmPFC, and anterior cingulate cortex effective connectome: Emotion, memory, and action. *Cerebral Cortex*, *33*(2), 330-356. <https://doi.org/10.1093/cercor/bhac070>
- Schuck, N. W., Cai, M. B., Wilson, R. C., & Niv, Y. (2016). Human Orbitofrontal Cortex Represents a Cognitive Map of State Space. *Neuron*, *91*(6), 1402-1412. <https://doi.org/10.1016/j.neuron.2016.08.019>
- Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., Reiss, A. L., & Greicius, M. D. (2007). Dissociable Intrinsic Connectivity Networks for Salience Processing and Executive Control. *Journal of Neuroscience*, *27*(9), 2349-2356. <https://doi.org/10.1523/JNEUROSCI.5587-06.2007>

- Seidel, E.-M., Pfabigan, D. M., Hahn, A., Sladky, R., Grahl, A., Paul, K., Kraus, C., Küblböck, M., Kranz, G. S., Hummer, A., Lanzenberger, R., Windischberger, C., & Lamm, C. (2015). Uncertainty during pain anticipation: The adaptive value of preparatory processes. *Human Brain Mapping, 36*(2), 744-755. <https://doi.org/10.1002/hbm.22661>
- Seth, A. K. (2010). Measuring autonomy and emergence via Granger causality. *Artificial Life, 16*(2), 179-196. <https://doi.org/10.1162/artl.2010.16.2.16204>
- Spiers, H. J., & Maguire, E. A. (2007). Neural substrates of driving behaviour. *NeuroImage, 36*(1), 245-255. <https://doi.org/10.1016/j.neuroimage.2007.02.032>
- Sridharan, D., Levitin, D. J., & Menon, V. (2008). A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. *Proceedings of the National Academy of Sciences, 105*(34), 12569-12574. <https://doi.org/10.1073/pnas.0800005105>
- Srinivasan, L., Asaad, W. F., Ginat, D. T., Gale, J. T., Dougherty, D. D., Williams, Z. M., Sejnowski, T. J., & Eskandar, E. N. (2013). Action Initiation in the Human Dorsal Anterior Cingulate Cortex. *PLOS ONE, 8*(2), e55247. <https://doi.org/10.1371/journal.pone.0055247>
- Sun, Y., Ajiboye, A. B., Brian, Yu, X., & Berilla, J. (2013). The Electroencephalographic Response during a Driving Process: Normal Driving, Turning and Collision. *2013 39th Annual Northeast Bioengineering Conference, 147-148*. <https://doi.org/10.1109/NEBEC.2013.143>
- Uddin, L. Q., Kelly, A. M., Biswal, B. B., Castellanos, F. X., & Milham, M. P. (2009). Functional connectivity of default mode network components: Correlation, anticorrelation, and causality. *Human Brain Mapping, 30*(2), 625-637. <https://doi.org/10.1002/hbm.20531>

- Uddin, L. Q., Nomi, J. S., Hébert-Seropian, B., Ghaziri, J., & Boucher, O. (2017). Structure and Function of the Human Insula. *Journal of Clinical Neurophysiology*, *34*(4), 300. <https://doi.org/10.1097/WNP.0000000000000377>
- Vorobyev, V., Kwon, M. S., Moe, D., Parkkola, R., & Hämäläinen, H. (2015). Risk-taking behavior in a computerized driving task: Brain activation correlates of decision-making, outcome, and peer influence in male adolescents. *PLoS ONE*, *10*(6). <https://doi.org/10.1371/journal.pone.0129516>
- Vossel, S., Geng, J. J., & Fink, G. R. (2014). Dorsal and ventral attention systems: Distinct neural circuits but collaborative roles. *Neuroscientist*, *20*(2), 150-159. <https://doi.org/10.1177/1073858413494269>
- Vossel, S., Weidner, R., Driver, J., Friston, K. J., & Fink, G. R. (2012). Deconstructing the architecture of dorsal and ventral attention systems with dynamic causal modeling. *Journal of Neuroscience*, *32*(31), 10637-10648. <https://doi.org/10.1523/JNEUROSCI.0414-12.2012>
- Ware, M., Feng, J., & Nam, C. S. (2020). Neuroergonomics Behind the Wheel: Neural Correlates of Driving. En C. S. Nam (Ed.), *Neuroergonomics: Principles and Practice* (pp. 353-388). Springer International Publishing. https://doi.org/10.1007/978-3-030-34784-0_18
- Wong, C., & Gallate, J. (2012). The function of the anterior temporal lobe: A review of the empirical evidence. *Brain Research*, *1449*, 94-116. <https://doi.org/10.1016/j.brainres.2012.02.017>
- Woolgar, A., Afshar, S., Williams, M. A., & Rich, A. N. (2015). Flexible Coding of Task Rules in Frontoparietal Cortex: An Adaptive System for Flexible Cognitive Control. *Journal of Cognitive Neuroscience*, *27*(10), 1895-1911. https://doi.org/10.1162/jocn_a_00827

- World Health Organization. (2021). *Global Plan for the Decade of Action for Road Safety 2021-2030*. <https://www.who.int/publications/m/item/global-plan-for-the-decade-of-action-for-road-safety-2021-2030>
- World Medical Association. (2013). World Medical Association Declaration of Helsinki: Ethical Principles for Medical Research Involving Human Subjects. *JAMA*, *310*(20), 2191-2194. <https://doi.org/10.1001/jama.2013.281053>
- Wu, Y., Sun, D., Wang, Y., Wang, Y., & Wang, Y. (2016). Tracing short connections of the temporo-parieto-occipital region in the human brain using diffusion spectrum imaging and fiber dissection. *Brain Research*, *1646*, 152-159. <https://doi.org/10.1016/j.brainres.2016.05.046>
- Yan, L., Wang, Y., Ding, C., Liu, M., Yan, F., & Guo, K. (2019). Correlation among behavior, personality, and electroencephalography revealed by a simulated driving experiment. *Frontiers in Psychology*, *10*. <https://doi.org/10.3389/fpsyg.2019.01524>
- Yeo, B. T. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., Roffman, J. L., Smoller, J. W., Zöllei, L., Polimeni, J. R., Fischl, B., Liu, H., & Buckner, R. L. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, *106*(3), 1125-1165. <https://doi.org/10.1152/jn.00338.2011>
- Yuen, N. H., Tam, F., Churchill, N. W., Schweizer, T. A., & Graham, S. J. (2021). Driving With Distraction: Measuring Brain Activity and Oculomotor Behavior Using fMRI and Eye-Tracking. *Frontiers in Human Neuroscience*, *15*. <https://doi.org/10.3389/fnhum.2021.659040>

- Zhang, L., Cao, G., Liu, Z., Bai, Y., Li, D., Liu, J., & Yin, H. (2022). The gray matter volume of bilateral inferior temporal gyrus in mediating the association between psychological stress and sleep quality among Chinese college students. *Brain Imaging and Behavior, 16*(2), 557-564. <https://doi.org/10.1007/s11682-021-00524-6>
- Zhang, X., & Yan, X. (2023). Predicting collision cases at unsignalized intersections using EEG metrics and driving simulator platform. *Accident Analysis & Prevention, 180*, 106910. <https://doi.org/10.1016/j.aap.2022.106910>
- Zhou, J., Gardner, M. P. H., Stalnaker, T. A., Ramus, S. J., Wikenheiser, A. M., Niv, Y., & Schoenbaum, G. (2019). Rat Orbitofrontal Ensemble Activity Contains Multiplexed but Dissociable Representations of Value and Task Structure in an Odor Sequence Task. *Current Biology, 29*(6), 897-907.e3. <https://doi.org/10.1016/j.cub.2019.01.048>
- Zhou, J., Gardner, M. P., & Schoenbaum, G. (2021). Is the core function of orbitofrontal cortex to signal values or make predictions? *Current Opinion in Behavioral Sciences, 41*, 1-9. <https://doi.org/10.1016/j.cobeha.2021.02.011>

ESTUDIO 3

Brain changes following mindfulness: Reduced caudate volume is associated with decreased positive urgency.

Mas-Cuesta, L., Baltruschat, S., Cándido, A., Verdejo-Lucas, C., Catena-Verdejo, E. y Catena, A. (2024). Brain changes following mindfulness: Reduced caudate volume is associated with decreased positive urgency. *Behavioural Brain Research*, 461, 114859. <https://doi.org/10.1016/j.bbr.2024.114859>

Abstract

Mindfulness training has been shown to improve psychological health and general well-being. However, it is unclear which brain and personality systems may be affected by this practice for improving adaptive behavior and quality of life. The present study explores the effects of a 5-week mindfulness-based intervention (MBI) at the neuroanatomical level and its relationship with dispositional mindfulness and impulsivity. Sixty-six risky drivers were quasi-randomly assigned to a mindfulness training group (MT) or a control group (N). Participants underwent magnetic resonance imaging and completed the Five Facet Mindfulness Questionnaire (FFMQ) and the UPPS-P impulsivity scale twice, at baseline and after receiving the MBI. We observed that MBI changes dispositional mindfulness in the non-reactivity and observing facets. Further, we observed that the magnitude of change in impulsivity was associated with the change in dispositional mindfulness. Whole-brain voxel-wise analysis revealed that the volume of the right caudate nucleus of the MT group (n=27) showed a reduction compared to that of the control group (n=33), which increased in terms of the pre-post measurement (MT=-1.76 mm³; N=6.31 mm³). We also observed that reduced caudate nucleus volume correlated with decreased positive urgency in the MT group. Taken together, our results show that MBI improves the skills of observing and non-reactivity to inner experience, while producing changes in the structure of the caudate nucleus. These structural changes are associated with a reduction in impulsivity levels, decreasing the tendency to act rashly in situations that generate positive emotions and thus facilitating more adaptive behavior.

Keywords: *Mindfulness, gray matter, caudate nucleus, positive urgency, FFMQ.*

Introduction

Mindfulness is the act of intentionally paying attention to the present moment with acceptance, openness, and non-judgment [1]. This ability is conceptualized as a momentary condition and a stable characteristic or natural tendency of each individual [2]. Dispositional mindfulness has been related to various cognitive and personality factors involved in mental health, such as neuroticism, coping strategies, rumination, executive functions, and impulsivity [3]. Although dispositional mindfulness is independent of mindfulness practice [4], it has been found that mindfulness skills training can produce more than short-term state changes, leading to an increase in trait characteristics [5] and modifications in brain anatomy [6–8]. In addition, mindfulness practice has been shown to produce improvements in psychological health and general well-being [9,10]. Although the beneficial effects of mindfulness have been widely studied, there is debate regarding which brain and personality systems may be affected by this practice to improve adaptive behavior and quality of life [11]. We aim to address this gap by further studying the effects of mindfulness training at the neuroanatomical level while exploring its relationship with certain personality traits, such as dispositional mindfulness and impulsivity.

As a personality trait, the UPPS model [12] proposes that impulsivity is a multidimensional construct characterized by the lack of premeditation and/or perseverance when acting, risk-taking or sensation-seeking behaviors, and the tendency to act rashly in highly emotional situations. At the brain level, the different dimensions of impulsivity have been related, both in a general and clinical population, to the brain networks responsible for response inhibition, reward valuation, and emotional regulation [13,14]. Nevertheless, previous studies on the association between gray matter volume (GMV) and impulsivity have yielded mixed results. For example, lack of perseverance

and sensation seeking have been negatively related to the anterior cingulate cortex (ACC) and amygdala, respectively [15]. However, both positive and negative associations between negative urgency, positive urgency and lack of premeditation with the frontal pole and striatum have been found [16–21]. So more research is still needed to clarify the neuroanatomical basis of impulsivity.

As a construct of considerable relevance for mental health, various impulsivity factors have been related to mindfulness and its facets. However, the results on the magnitude and direction of the associations vary across studies. It is generally observed that many of the dimensions of impulsivity are negatively associated with the different facets of mindfulness (e.g., negative urgency with non-reactivity or awareness with lack of perseverance), whereas others show no significant relationships (e.g., sensation seeking with non-reactivity) [22–25]. In addition, positive relationships have also been found between the different factors of both variables (e.g., observing with positive urgency and sensation seeking [24,25]). Despite the evidence concerning the association between mindfulness and impulsivity, studies that have investigated the effects of mindfulness-based interventions (MBI) on impulsivity are scarce and were designed to address very specific mental disorders, such as ADHD and addictive disorders [26,27]. For example, Davis et al. [28] found that young adults who received a Mindfulness-Based Relapse Prevention (MBRP) treatment showed significant reductions in all facets of impulsivity, except sensation seeking. However, Maddox [29] found that MBRP did not improve any of the dimensions of impulsivity. Therefore, further research is needed to determine how mindfulness training influences impulsivity.

Aside from modifying various cognitive and personality processes, MBIs can affect brain anatomy. Both increases and decreases in GMV have been observed in cortical (e.g. prefrontal, somatosensory, parietal and cingulate cortices) and subcortical

(e.g. amygdala, insula, caudate, thalamus, precuneus, hippocampus) structures after MBIs [30–36]. However, changes in the anatomical brain configuration after mindfulness training have been related to a lesser extent to the cognitive, emotional, or personality processes thought to underpin mindfulness skills. For example, Hölzel et al. [37] found that a reduction in perceived stress after an 8-week Mindfulness-Based Stress Reduction (MBSR) intervention correlated with a reduction in gray matter density in the amygdala. Fahmy et al. [30] found that increased prefrontal/ACC network volume after MBSR was associated with reduced negative urgency. In contrast, Yu et al. [35] found that brain structure changes after mindfulness training did not correlate with changes in different cognitive domains, such as attention or working memory.

Despite the evidence regarding the association between mindfulness and impulsivity and the changes of mindfulness practice on brain structure, there is a clear need to study further how these changes relate to cognitive or personality processes that influence mental health and general well-being. This study aimed to explore the effects of a mindfulness-based intervention on brain structure and determine how these effects relate to changes in impulsivity and trait mindfulness. We hypothesized that mindfulness training might reduce impulsivity levels, increase dispositional mindfulness and affect structures related to self-regulation and impulsivity Tang et al. [8].

Material and methods

Participants

Participants in this study were part of a larger study (ERPAT) to determine the brain basis of risk behavior in risky traffic scenarios. We used structural MRI from 66 participants (19 women, 34.2 years old, age range= [19, 63]). Six participants were discarded due to bad quality MRI images and missing data in questionnaires. None of the participants

reported a history of head injury nor a history of neurological disorders. All participants were scanned twice — at baseline and after receiving a mindfulness intervention devoted to correcting their risky behavior. All participants signed an informed consent form, were informed of their rights, and were treated according to the Helsinki Declaration [38]. All participants were paid for their participation in the study. The Ethics Committee of Human Research of the University of Granada approved this research (204/CEIH/2016). To have a power of 0.80, the sample size was calculated as 60 participants with G-power, with a partial R-square of 0.028 and 0.8 correlation between the repeated measures.

Procedure

Participants were risky individuals recruited from the traffic driving school of Granada where they were recovering points on their driver license (n=20) or from internet advertising (n=46). All of them were asked to complete a questionnaire on traffic violations. To establish whether a participant was risky we used the following self-reported inclusion criteria: attendance of a rehabilitation course for drivers at least once, a loss of points according to the Spanish penalty system for traffic rule violations, being fined at least twice for risky driving behavior (alcohol or drug use, not using a seat belt, or exceeding speed limits), or reporting as having usually exceeded speed limits by more than 20% of the permitted speed. Participants were assigned to two groups dependent on their weekly availability. The first was a control group (N, n=33, 33.3% females) that did not receive an intervention, while the second group received training in mindfulness meditation (MT, n=27, 33.3% females). To gather the largest number of participants for the training group, the availability of the participants was established prior to testing. At four different times over the 2-year period of data collection, we grouped the participants with the same availability, resulting in a quasi-randomized controlled trial.

The mindfulness meditation intervention was aimed at improving risky driving (see Baltruschat et al. [39], for more details) and was based on the Mindfulness-Based Stress Reduction program (MBSR; [40]) but adapted to a five weeks duration (3 hours sessions) due to the reduced availability of the participants. Sessions were prepared by a clinical psychologist (CVL) and were delivered by the clinical herself and another sanitary psychologist (ECV). Both were professionally accredited to deliver the MBSR program. However, neither of them was involved in the evaluation of data collection beyond the mindfulness programs. The sessions were designed to enhance situation awareness and included meditation (attention to breathing, body scanning, guided meditation) and yoga practice, groups discussion, as well as training in emotion regulation and the importance of focusing on what happens in the present moment, pausing to take a breath, observing both inside and outside and finally selecting the appropriate response. To ensure adherence to the intervention, participants were required to sign an attendance sheet and home practices were assigned after each session. The intervention was done immediately after the pre-test. The time elapsed between the pre and the post evaluations was around four months (mean = 143.07 days, SD = 69.68). There is no specific time interval after which the effects of mindfulness are evident [7], although previous studies have shown that mindfulness interventions (and others) have delayed effects on brain structure change [41–43].

Measures

The Spanish version of the Five Facet Mindfulness Questionnaire (FFMQ; [44,45]) measured dispositional mindfulness pre and post-intervention. This 39-item questionnaire has five scales and is rated on a 5-point Likert-type scale from 1 (never or very rarely true) to 5 (very often or always true). The questionnaire has good psychometric properties (Cronbach's: $\alpha = 0.88$ for the whole scale, minimum Cronbach's α for the subscales =

0.80), and measures five facets of mindfulness: Observing (the attention paid to sensations and perceptions of inner and external stimuli); Describing (labeling experience and perceptions with words); Acting with awareness (the attention paid to one's activities); Non-judging of inner experience (evaluation of one's thoughts and feelings); and Non-reactivity to inner experiences (the ability to let thoughts and feelings come and go without getting caught up in them).

The Spanish version of the UPPS-P [12,46] was used to measure impulsivity at pre and post-intervention. This scale assesses impulsivity across five facets: (lack of) premeditation, (lack of) perseverance, sensation seeking, and negative and positive urgency. In addition, the scale has good psychometric properties (min Cronbach's $\alpha = 0.61$).

MRI scanning was conducted with a Siemens 3T Trio system equipped with a 32-channel head coil at the Mind, Brain, and Behavior Research Center (University of Granada). Participants were instructed not to move during the scan. In addition, head restraint and foam padding around the head were used to limit head motion. A T1-weighted MPRAGE scan was obtained with a TR (repetition time) of 1900 ms, TE (echo time) of 2.52 ms, and a flip angle of 9° . For each volume, 176 slices of 1 mm thickness were obtained, which provide whole-brain coverage (voxel size = $1 \times 1 \times 1$ mm; FOV = 256 mm; 256×256 data acquisition matrix).

The MRI scans were submitted to the CAT12 toolbox (<http://www.neuro.uni-jena.de/cat/>) to obtain brain volumes, running under the umbrella of SPM12 (<https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>), using default parameters. In essence, CAT12 corrects for bias inhomogeneity, segmented into gray matter, white matter, and cerebrospinal fluid using the AMAP approach. The images were spatially normalized using the Diffeomorphic Anatomical Registration through Exponentiated Lie

algebra (DARTEL) algorithm. Volumes were then normalized to the MNI neurological space and multiplied by the Jacobian determinant to preserve volume. Gray matter volumes were then smoothed using an 8 mm FWHM Gaussian kernel.

Data analyses

SPM 12 was used to conduct the whole-brain voxel-wise statistical analyses. Repeated measures factorial statistical analysis was used, in which comparisons between the two groups in the pre and post-intervention were made while controlling for age, gender, education level, and total gray matter volume. The significance threshold was cluster-wise corrected to $p_{FWE} < 0.05$ with a minimum cluster size of $k=200$ to handle the multiple comparison problem. FFMQ and UPPS-P scores were transformed to the behavior shift index (BSI; [47]), defined as the magnitude of change between baseline and post-intervention evaluation, using the formula $(\text{Post-Pre})/\text{Pre} * 100$. Previous studies have used the BSI to examine the effects of mindfulness in different domains [39,48]. The Pearson correlation coefficient was used to evaluate the associations between the FFMQ and the UPPS-P scores. SPSS v 24 (IBM SPSS Statistics for Windows, Version 24.0, Armonk, NY: IBM Corp.) was used to analyze the effects of the intervention on the FFMQ dimensions and UPPS-P scores, using an analysis of covariance approach in which we controlled for the effects of age, gender, and education level.

Results

Table 1 displays the means (standard errors) for the BSI and baseline scores for the FFMQ and the UPPS-P scales. At the baseline, no significant differences were found between the MT and N groups in either the FFMQ or the UPPS, when the multiple comparisons problem was taken into account. Regarding the BSI, for the FFMQ dimensions, only the non-reactivity to inner experience, $F(1,56)=7.65$, $p < 0.01$, which was greater for the MT (BSS= 6.5) than for the N (BSS=-5.1) group, and the observing dimension, $F(1,56)=5.24$,

$p < 0.026$, which was also greater for the MT (BSS=9.3) than for the N (BSS=-.9) group, were significant. There were gender differences in the awareness dimension, $F(1,56)=5.27$, $p < 0.01$, this score being higher for women (BSS= 7.9) than men (BSS=-3.2). There were neither main nor interaction effects on impulsivity scores ($p > 0.10$). However, there was an effect of education level on (lack of) perseverance, $F(1,56)=9.38$, $p < 0.01$, and (lack of) premeditation, $F(1,56)=6.30$, $p < 0.01$. In both cases, the higher the education level, the lower the impulsivity score.

Table 1. Behavioral Change ((post-pre)/pre*100) and baseline scores as a function of group and dimensions of the FFMQ and UPPS-P.

Group	BSI		Baseline	
	MT	N	MT	N
FFMQ				
Awareness	-1.15 (2.80)	2.01 (3.04)	25.8 (1.2)	28.8 (0.8)
Describing	4.61 (2.83)	2.11 (3.07)	28.0 (1.1)	27.9 (0.8)
Non Judgment	7.90 (5.71)	13.53 (6.20)	23.7 (1.3)	26.7 (1.1)
Non React	6.48 (2.96)	-5.10 (3.21)	23.1 (0.9)	22.7 (0.7)
Observing	9.34 (2.93)	-0.90 (3.19)	28.7 (0.8)	27.0 (0.7)
UPPS-P				
(Lack) Pers	0.50 (-11.10)	5.49 (11.09)	1.9 (0.1)	1.6 (0.1)
Lack) Prem	-1.46 (-3.12)	-0.40 (0.08)	1.9 (0.1)	1.8 (0.1)
Negat U	0.00 (3.05)	-3.96 (-12.18)	2.5 (0.1)	2.3 (0.1)
Pos U	0.70 (-11.09)	-2.77 (8.54)	2.6 (0.1)	2.5 (0.1)
Sens Seek	-2.07 (-11.39)	1.3 (8.95)	2.7 (0.1)	2.8 (0.1)

Note. MT: mindfulness training, N: control. Standard errors are between parentheses. Shaded cells indicate significant differences.

Table 2 summarizes the results obtained at the brain structural level (changes in GMV) in this study. We observed main effects of the intervention group in three clusters, one located in the left precuneus and the others located in the left temporal inferior and right fusiform, with GMV being larger for the MT group than for the N one group. We also observed an effect of the pre>post contrast in clusters located in the right superior temporal pole, and the right superior frontal, with GMV being greater in the pre than post-

measurement. There was also a significantly greater post-pre difference in volume in the cluster in the right hippocampus. The group by pre-post interaction was significant at a cluster in the right caudate (Figures 1 and 2), embracing parts of the right thalamus, with the post-pre difference being greater in the N (6.31 mm³) than in the MT (-1.76 mm³) group. Therefore, the right caudate appears to show a reduction in volume (compared with the control group) after the mindfulness intervention.

Table 2. Significant effects of the repeated measures factorial on brain structure.

Label	k	Peak T	X	Y	Z	pFWE
MT > N						
L Precuneus	325	4.73	-18	-51	65	0.001
L Temporal Inf	309	4.65	-32	-30	-20	0.001
R Fusiform	290	4.16	-47	-35	-21	0.001
Pre > Post						
R Temporal Pole Sup	301	3.77	-21	8	-32	0.001
R Frontal Sup	232	3.85	36	63	-9	0.005
Post > Pre						
R Hippocampus	405	4.60	21	-30	9	0.048
Group by Pre-Post						
R Caudate	417	5.03	15	-15	18	0.001

Note. K is the size of the cluster in voxels. X, Y, and Z: coordinates in MNI space. MT: mindfulness training, N: control. pFWE= cluster-wise corrected p-values.

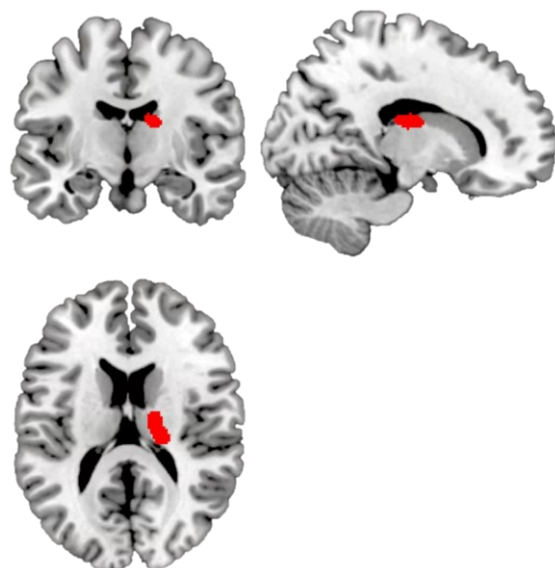


Figure 1. Post-pre comparison of the caudate cluster, showing reduced volume in the MT than the N group.

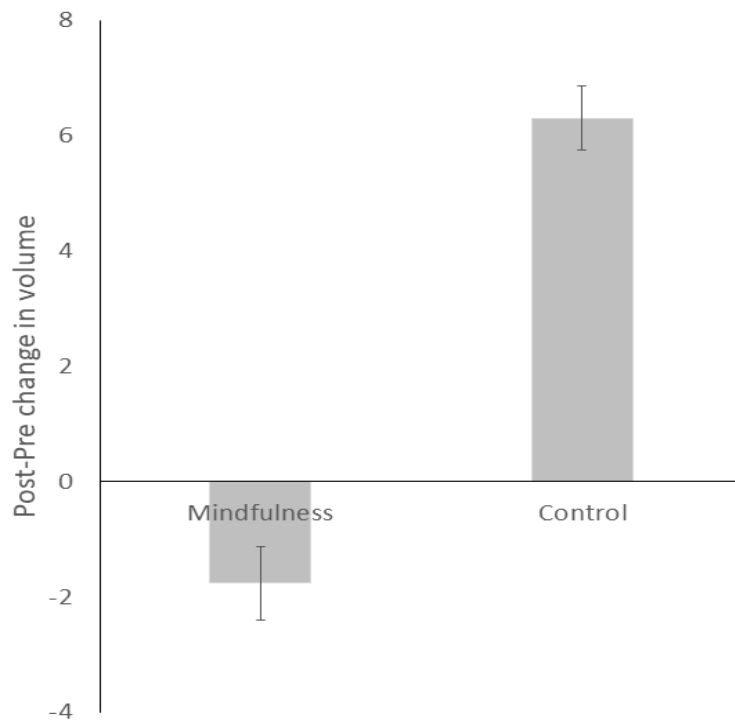


Figure 2. Post-Pre differences in volume (mm³) for MT and N group.

The post-pre change in the volume of the caudate cluster correlated negatively with the behavior shift index of impulsivity in the dimension of positive urgency in the MT group ($r=-0.46$, $z=-2.43$, $p=0.05$), with a marginal and positive correlation in the N group ($r=0.35$, $z=1.79$, $p=0.08$). The difference between these two correlations was also significant, using the Fisher Z score ($z=3.15$, $p=0.001$). The change in caudate volume in the MT group implies that a lower caudate volume is associated with lower impulsivity in the post than in the pre-assessment. No correlations were significant for this brain cluster and BSI indices in the FFMQ (all $p>0.10$).

The partial correlations, controlling for age, gender, and education level, between the BSI indices of the FMMQ and those of the UPPS-P, are displayed in Table 3, which shows that the BSI indices of positive urgency are positively associated with that of awareness and that sensation seeking is positively correlated with awareness and describing.

Table 3. Partial correlations between BSI indices for UPPS-P and FFMQ. Shaded cells indicate significant association.

	Awareness	Describe	Non-Judge	Non-React	Observing
(lack of) Perseverance	-0.11	-0.04	-0.23	-0.04	-0.20
(lack of) Premeditation	-0.01	-0.19	-0.19	-0.09	0.18
Negative Urgency	0.06	-0.26	0.01	-0.01	-0.15
Positive Urgency	0.31	-0.14	-0.17	0.08	-0.05
Sensation Seeking	0.36	0.39	0.13	0.17	0.03

Discussion

This study aimed to reveal the effects of mindfulness training in structural gray matter volumes and how these effects are related to impulsivity and dispositional mindfulness using a quasi-randomized pre-post mindfulness intervention design. We have observed that mindfulness training changes dispositional mindfulness as measured by the FFMQ questionnaire in the non-reactivity and observing facets. In both facets, the MT group scored higher in the post than in the pre-test compared with the control group. Further, we have observed that positive urgency was positively associated with change in awareness; the greater the change in positive urgency, the greater the change in awareness. Sensation seeking was also positively associated with awareness and describing. At the brain level, we found that the volume of the right caudate nucleus of the mindfulness training group was smaller than that of the control group in the post-measurement. We also observed that the change in caudate nucleus volume correlated with decreased positive urgency in the MT group.

After mindfulness training, we found an increase in observing and non-reactivity scores in the MT group. This implies that certain facets of dispositional mindfulness could be susceptible to change due to mindfulness training. Numerous studies have investigated the effect of mindfulness-based interventions on enhancing mindfulness skills, understood as personality traits. Although some studies have found that mindfulness-

based interventions have no specific effects on dispositional mindfulness [49–52], an increase in trait mindfulness is generally observed following such interventions [5,22,53–55]. This enhancement in dispositional mindfulness has been differentially attributed to one or more of the dimensions studied, depending on the characteristics of the intervention, the degree of control, and the population under study [5].

On the other hand, several investigations also conclude that the increase in the mindfulness trait is explained by an improvement in the abilities to observe or pay attention to one's perceptions and sensations and to let thoughts and emotions pass without clinging or reacting to them, observing an increase in the scores of these facets after various mindfulness-based interventions [34,56–58]. In addition, non-reactivity is the most significant contributor to overall well-being [59]. Therefore, our results are consistent with previous studies showing that mindfulness training improves dispositional mindfulness by increasing observing and non-reactivity abilities.

The dispositional mindfulness facets that improve after mindfulness training are those that show no significant relationships with the magnitude of change in the various dimensions of impulsivity. Previous research has also found inconsistent associations between the observing and non-reactivity facets with impulsivity [25,60–62]. Looking at the facets of mindfulness related to changes in impulsivity, we observed positive correlations between the BSI of awareness with positive urgency and sensation seeking and between the BSI of describing with sensation seeking. These results contrast with those obtained in previous studies, which found negative associations or no correlation between these variables [23–25,61], and indicate that people who tend to be aware of their current activities also tend to act rashly in the presence of positive emotions and seek out exciting activities. Impulsivity is a heterogeneous construct in which not all its factors are related, *per se*, to problematic behaviors [46]. In fact, and similar to our results, Vinci

et al. [61] observed that sensation seeking and positive urgency were positively related to the state of mindfulness. Our results also support the notion [24] that mindfulness and impulsivity are related constructs with varying associations between the different factors that make up the two traits.

In addition to improving dispositional mindfulness, mindfulness training produces changes at the brain structural level. Our results showed a GMV reduction of the caudate nucleus in the MT group compared to the control group. The caudate nucleus has previously been implicated in mindfulness meditation and dispositional mindfulness. In dispositional mindfulness, the right amygdala and the caudate volume correlated negatively with the MAAS score [63]. In stark contrast, other authors [64] observed, in a cross-sectional study, a greater volume in the left caudate nucleus in an intervention group that received an MBSR course compared with an untreated group. In the same vein, Fahmy et al. [30] have observed increased volumes of the left caudate in a group of opiate-dependent patients receiving a MBI compared with a treatment as usual group.

Further, a MBI in patients with Parkinson's disease demonstrated that an eight-week program increased the density of the caudate compared with usual treatment [32]. Our data agree with those of Taren et al. [63] but disagree with the rest of the research. One possible explanation for these discrepancies could lie in the fact that in two of these studies [30,32], participants were from special populations (opiod-dependent and people with Parkinson's disease), which could suggest that the structure was already damaged at baseline but still recovers to a more normal volume due to the mindfulness intervention. Another possibility concerns the sample size and the reliability of the results [65], which is very high in the Taren et al. [63] study but low in the remaining studies. Furthermore, in line with our results, other research has found that expert meditators, compared to groups with no meditation experience, had lower GMV in several cortical and subcortical

regions [66,67], including the caudate [67], although in the Korponay et al. [67] study these differences were not related to the total number of hours of practice.

The caudate has also been implicated in studies aimed at uncovering the brain's functionality and its association with mindfulness. Stillman et al. [68] found that the connectivity of the caudate with the medial temporal lobe (MTL) was negatively correlated with dispositional mindfulness during an implicit learning task. Given that the caudate-MTL connection is related to performance in implicit learning, this result suggests that greater dispositional mindfulness can hinder the acquisition of this type of learning and promote a more explicit learning mechanism. In this vein, an asymmetry has been found between the left and right caudate, in the sense that the left caudate is involved in the acquisition of habitual actions (mechanistic stimulus-response association) whereas the right caudate is involved in the acquisition of goal-directed actions [69–71]. Further, the caudate nucleus has shown to be a fundamental structure in acquiring stimulus-control associations, in which stimuli are associated with control states, such as heightened attentional selectivity [72]. In addition, Brefczynski-Lewis et al. [73] found that expert meditators had lower activation in the caudate, dorsolateral prefrontal cortex, and pulvinar when performing a task with distracting stimuli. In this vein, the right caudate might operate as a bottom-up controller [74], which is a more efficient behavioral control mechanism than the top-down processing initiated in the dorsolateral prefrontal or anterior cingulate cortex [75].

On the other hand, meditators have shown reduced activation of the caudate in anticipation of monetary rewards [76] and during positive emotional processing [77]. Moreover, the connectivity of this area with the posterior insula showed a negative association with dispositional mindfulness, [76]. As part of the reward processing network, it appears that the caudate — together with the amygdala — forms a microcircuit

in which the former seems to represent the incentives and process the magnitude of reward, mediated by activity of the amygdala [78,79]. In addition to being part of the reward network, the caudate is also involved in processing negative affect [80]. It has been observed that both expert meditators and people who had received a mindfulness-based intervention showed lower activation of the caudate when presented with negative images [81,82]. This reduced reactivity to emotional signals or stimuli — both aversive and reward-related — could be taken to indicate an improvement in affective self-regulation [83].

The above evidence suggests that reduced caudate volume can be an index of the evolving brain [84,85] that promotes a more effective neural computation and enhances adaptive behavior [86]. In this regard, it should be noted that the participants were risk-taking individuals and that the N group showed an increased GMV of the caudate nucleus without having received any type of intervention. Several investigations have also found greater GMV in the caudate and other subcortical structures in risk-takers [87–90]. Thus, the fact that, regarding the control group, there was a reduction of GMV in the MT group may be a sign of neural plasticity and imply a recovery of the normal evolution of the structure. In addition, previous studies have reported that the improvement of certain cognitive processes after training is associated with a decrease in brain gray matter volume [91,92]. We might thus speculate that a reduced caudate volume in the mindfulness group (compared with controls) may benefit the functioning of this structure and promote more efficient control and self-regulation mechanisms.

Deficits in functions that have been linked to the caudate nucleus, such as behavioral control and affect regulation, underlie urgent or impulsive behavior [12]. In this regard, our results show that the caudate volume was related to the BSI of positive urgency, finding that reductions in GMV in the MT group correlated with lower positive

urgency. Positive urgency, defined as the tendency to act impulsively in response to intense positive emotions, implies a difficulty in suppressing prepotent responses [93] and is strongly related to risk behavior, such as driving errors and reckless driving [94,95]. The caudate has been implicated in impulsivity considered as urgency to respond, either negative or positive [93,96]. Similar to our results, Tschernegg et al. [97] observed that caudate volume correlated positively with impulsivity, independent of age in a delay discounting task. More specifically, Owens et al. [20] found a positive relationship between caudate GMV and positive urgency in a sample of pre-adolescents. The caudate has also shown increased activation when engaging in risky behavior [98]. Research in adolescents has found that bilateral activation was highly correlated with the decision to engage in risky choices, but more so in the presence than the absence of peers [98]. This structure is sensitive to feedback related to risky choices, as taking more risks is associated with increased bilateral caudate activity [99]. Therefore, the caudate plays an important role in the processing of affective stimuli (both rewarding and aversive), inhibitory control, risk-taking, and impulsive behavior, and is part of the cortico-striatal circuit comprising structures such as the anterior and posterior cingulate cortex, the insula, the amygdala, the striatum and the frontal and orbitofrontal cortices [17,69,100,101]. In this sense, alterations of the caudate have been related to various mental disorders whose main component is impulsivity, such as substance use and ADHD [102,103], and this structure could be an important component of the neural circuit of impulsivity, with excessive activity of this area being linked to rash behavior. Thus, if we consider the volume-activity relationship [104], our data suggests that the volume reduction in the MT group (compared with the control group) could be linked to reduced activity, which could in turn be associated with making fewer impulsive choices when acting under the influence of positive emotions. This could be applied to adapt

mindfulness-based interventions to populations with high levels of impulsivity and emotion regulation difficulties.

However, more research is needed to confirm our findings. The quasi-randomization process may not have completely equalized the groups. Thus, complete randomized trials, with a greater number of participants, as well as study the long-term effects of the intervention are also needed to confirm that brain changes are maintained over time and are related to improved adaptive behavior.

In short, our results show that a mindfulness-based intervention produces changes in the structure of the caudate nucleus and improves dispositional mindfulness. In addition, reductions in caudate GMV in the MT group are related to lower positive urgency, and this impulsivity facet is associated with trait mindfulness. Therefore, it appears that a mindfulness-based intervention improves the skills of observing and non-reactivity to inner experience, while producing changes in the structure of the caudate nucleus. These structural changes are associated with a reduction in impulsivity levels, decreasing the tendency to act rashly in situations that generate positive emotions and thus facilitating more adaptive behavior.

References

- [1] J. Kabat-Zinn, *Coming to Our Senses: Healing Ourselves and the World Through Mindfulness*, Hachette Books, 2005.
- [2] K.W. Brown, R.M. Ryan, The benefits of being present: Mindfulness and its role in psychological well-being, *J. Pers. Soc. Psychol.* 84 (2003) 822–848. <https://doi.org/10.1037/0022-3514.84.4.822>.
- [3] E.R. Tomlinson, O. Yousaf, A.D. Vittersø, L. Jones, Dispositional Mindfulness and Psychological Health: a Systematic Review, *Mindfulness.* 9 (2018) 23–43. <https://doi.org/10.1007/s12671-017-0762-6>.

- [4] K.W. Brown, R.M. Ryan, J.D. Creswell, Mindfulness: Theoretical Foundations and Evidence for its Salutary Effects, *Psychol. Inq.* 18 (2007) 211–237. <https://doi.org/10.1080/10478400701598298>.
- [5] J.T. Quaglia, S.E. Braun, S.P. Freeman, M.A. McDaniel, K.W. Brown, Meta-Analytic Evidence for Effects of Mindfulness Training on Dimensions of Self-Reported Dispositional Mindfulness, *Psychol. Assess.* 28 (2016) 803–818. <https://doi.org/10.1037/PAS0000268>.
- [6] R.A. Gotink, R. Meijboom, M.W. Vernooij, M. Smits, M.G.M. Hunink, 8-week Mindfulness Based Stress Reduction induces brain changes similar to traditional long-term meditation practice – A systematic review, *Brain Cogn.* 108 (2016) 32–41. <https://doi.org/10.1016/J.BANDC.2016.07.001>.
- [7] C.R. Pernet, N. Belov, A. Delorme, A. Zammit, Mindfulness related changes in grey matter: a systematic review and meta-analysis, *Brain Imaging Behav.* 15 (2021) 2720–2730. <https://doi.org/10.1007/s11682-021-00453-4>.
- [8] Y.-Y. Tang, B.K. Hölzel, M.I. Posner, The neuroscience of mindfulness meditation, *Nat. Rev. Neurosci.* 16 (2015) 213–225. <https://doi.org/10.1038/nrn3916>.
- [9] J. Eberth, P. Sedlmeier, The Effects of Mindfulness Meditation: A Meta-Analysis, *Mindfulness.* 3 (2012) 174–189. <https://doi.org/10.1007/s12671-012-0101-x>.
- [10] J. Gu, C. Strauss, R. Bond, K. Cavanagh, How do mindfulness-based cognitive therapy and mindfulness-based stress reduction improve mental health and wellbeing? A systematic review and meta-analysis of mediation studies, *Clin. Psychol. Rev.* 37 (2015) 1–12. <https://doi.org/10.1016/J.CPR.2015.01.006>.

- [11] A. Chiesa, R. Calati, A. Serretti, Does mindfulness training improve cognitive abilities? A systematic review of neuropsychological findings, *Clin. Psychol. Rev.* 31 (2011) 449–464. <https://doi.org/10.1016/J.CPR.2010.11.003>.
- [12] S.P. Whiteside, D.R. Lynam, The Five Factor Model and impulsivity: using a structural model of personality to understand impulsivity, *Personal. Individ. Differ.* 30 (2001) 669–689. [https://doi.org/10.1016/S0191-8869\(00\)00064-7](https://doi.org/10.1016/S0191-8869(00)00064-7).
- [13] S. Baltruschat, A. Cándido, A. Megías, A. Maldonado, A. Catena, Risk proneness modulates the impact of impulsivity on brain functional connectivity, *Hum. Brain Mapp.* 41 (2020) 943–951. <https://doi.org/10.1002/hbm.24851>.
- [14] J. Golchert, J. Smallwood, E. Jefferies, F. Liem, J.M. Huntenburg, M. Falkiewicz, M.E. Lauckner, S. Oligschläger, A. Villringer, D.S. Margulies, In need of constraint: Understanding the role of the cingulate cortex in the impulsive mind, *NeuroImage.* 146 (2017) 804–813. <https://doi.org/10.1016/j.neuroimage.2016.10.041>.
- [15] H. Wang, B. Wen, J. Cheng, H. Li, Brain structural differences between normal and obese adults and their links with lack of perseverance, negative urgency, and sensation seeking, *Sci. Rep.* 7 (2017) 1–7. <https://doi.org/10.1038/srep40595>.
- [16] M.J. Hoptman, D. Antonius, C.J. Mauro, E.M. Parker, D.C. Javitt, Cortical Thinning, Functional Connectivity, and Mood-Related Impulsivity in Schizophrenia: Relationship to Aggressive Attitudes and Behavior, *Am. J. Psychiatry.* 171 (2014) 939–948. <https://doi.org/10.1176/appi.ajp.2014.13111553>.

- [17] N. Kakoschke, V. Lorenzetti, K. Caeyenberghs, A. Verdejo-García, Impulsivity and body fat accumulation are linked to cortical and subcortical brain volumes among adolescents and adults, *Sci. Rep.* 9 (2019) 2580. <https://doi.org/10.1038/s41598-019-38846-7>.
- [18] L. Moreno-López, A. Catena, M.J. Fernández-Serrano, E. Delgado-Rico, E.A. Stamatakis, M. Pérez-García, A. Verdejo-García, Trait impulsivity and prefrontal gray matter reductions in cocaine dependent individuals, *Drug Alcohol Depend.* 125 (2012) 208–214. <https://doi.org/10.1016/j.drugalcdep.2012.02.012>.
- [19] N. Muhlert, A.D. Lawrence, Brain structure correlates of emotion-based rash impulsivity, *NeuroImage.* 115 (2015) 138–146. <https://doi.org/10.1016/J.NEUROIMAGE.2015.04.061>.
- [20] M.M. Owens, C.S. Hyatt, J.C. Gray, J.D. Miller, D.R. Lynam, S. Hahn, N. Allgaier, A. Potter, H. Garavan, Neuroanatomical correlates of impulsive traits in children aged 9 to 10., *J. Abnorm. Psychol.* 129 (2020) 831–844. <https://doi.org/10.1037/abn0000627>.
- [21] C.M. Ruiz de Lara, J.F. Navas, C. Soriano-Mas, G. Sescousse, J.C. Perales, Regional grey matter volume correlates of gambling disorder, gambling-related cognitive distortions, and emotion-driven impulsivity, *Int. Gambl. Stud.* 18 (2018) 195–216. <https://doi.org/10.1080/14459795.2018.1448427>.
- [22] S. Deplus, J. Billieux, C. Scharff, P. Philippot, A Mindfulness-Based Group Intervention for Enhancing Self-Regulation of Emotion in Late Childhood and Adolescence: A Pilot Study, *Int. J. Ment. Health Addict.* 2016 145. 14 (2016) 775–790. <https://doi.org/10.1007/S11469-015-9627-1>.

- [23] G.G. Gallo, D.F. Curado, E.S. Opaleye, A.P.G. Donate, V.V. Scattone, A.R. Noto, Impulsivity and Mindfulness among Inpatients with Alcohol Use Disorder, *Subst. Use Misuse*. 56 (2021) 25–32. <https://doi.org/10.1080/10826084.2020.1833924>.
- [24] C. Murphy, J. MacKillop, Living in the here and now: Interrelationships between impulsivity, mindfulness, and alcohol misuse, *Psychopharmacology (Berl.)*. 219 (2012) 527–536. <https://doi.org/10.1007/s00213-011-2573-0>.
- [25] J.R. Peters, S.M. Erisman, B.T. Upton, R.A. Baer, L. Roemer, A Preliminary Investigation of the Relationships Between Dispositional Mindfulness and Impulsivity, *Mindfulness*. 2 (2011) 228–235. <https://doi.org/10.1007/s12671-011-0065-2>.
- [26] A. Zgierska, D. Rabago, N. Chawla, K. Kushner, R. Koehler, A. Marlatt, Mindfulness meditation for substance use disorders: a systematic review, *Subst. Abuse*. 30 (2009) 266–294. <https://doi.org/10.1080/08897070903250019>.
- [27] L. Zylowska, D.L. Ackerman, M.H. Yang, J.L. Futrell, N.L. Horton, T.S. Hale, C. Pataki, S.L. Smalley, Mindfulness Meditation Training in Adults and Adolescents With ADHD: A Feasibility Study, *J. Atten. Disord.* 11 (2007) 737–746. <https://doi.org/10.1177/1087054707308502>.
- [28] J.P. Davis, N. Barr, E.R. Dworkin, T.M. Dumas, B. Breyer, G. DiGuseppi, B.R. Cahn, Effect of Mindfulness-Based Relapse Prevention on Impulsivity Trajectories Among Young Adults in Residential Substance Use Disorder Treatment, *Mindfulness*. 10 (2019) 1997–2009. <https://doi.org/10.1007/s12671-019-01164-0>.

- [29] J. Maddox, The effects of mindfulness-based relapse prevention on impulsivity and mindfulness, Ph.D., 2011. <https://www.proquest.com/docview/904546466/abstract/9F0DBEFF4824ACDPQ/1> (accessed October 6, 2021).
- [30] R. Fahmy, M. Wasfi, R. Mamdouh, K. Moussa, A. Wahba, M. Wittemann, D. Hirjak, K.M. Kubera, N.D. Wolf, F. Sambataro, R.C. Wolf, Mindfulness-based interventions modulate structural network strength in patients with opioid dependence, *Addict. Behav.* 82 (2018) 50–56. <https://doi.org/10.1016/J.ADDBEH.2018.02.013>.
- [31] B.K. Hölzel, J. Carmody, M. Vangel, C. Congleton, S.M. Yerramsetti, T. Gard, S.W. Lazar, Mindfulness practice leads to increases in regional brain gray matter density, *Psychiatry Res. Neuroimaging.* 191 (2011) 36–43. <https://doi.org/10.1016/J.PSCYCHRESNS.2010.08.006>.
- [32] B.A. Pickut, W. Van Hecke, E. Kerckhofs, P. Mariën, S. Vanneste, P. Cras, P.M. Parizel, Mindfulness based intervention in Parkinson’s disease leads to structural brain changes on MRI: a randomized controlled longitudinal trial, *Clin. Neurol. Neurosurg.* 115 (2013) 2419–2425. <https://doi.org/10.1016/j.clineuro.2013.10.002>.
- [33] E. Santarnecchi, S. D’Arista, E. Egiziano, C. Gardi, R. Petrosino, G. Vatti, M. Reda, A. Rossi, Interaction between Neuroanatomical and Psychological Changes after Mindfulness-Based Training, *PLOS ONE.* 9 (2014) e108359. <https://doi.org/10.1371/JOURNAL.PONE.0108359>.

- [34] C.-C. Yang, A. Barrós-Loscertales, M. Li, D. Pinazo, V. Borchardt, C. Ávila, M. Walter, Alterations in Brain Structure and Amplitude of Low-frequency after 8 weeks of Mindfulness Meditation Training in Meditation-Naïve Subjects, *Sci. Rep.* 2019 91. 9 (2019) 1–10. <https://doi.org/10.1038/s41598-019-47470-4>.
- [35] J. Yu, I. Rawtaer, L. Feng, J. Fam, A.P. Kumar, I. Kee-Mun Cheah, W.G. Honer, W. Su, Y.K. Lee, E.C. Tan, E.H. Kua, R. Mahendran, Mindfulness intervention for mild cognitive impairment led to attention-related improvements and neuroplastic changes: Results from a 9-month randomized control trial, *J. Psychiatr. Res.* 135 (2021) 203–211. <https://doi.org/10.1016/J.JPSYCHIRES.2021.01.032>.
- [36] J.P. Yuan, C.G. Connolly, E. Henje, L.P. Sugrue, T.T. Yang, D. Xu, O. Tymofiyeva, Gray Matter Changes in Adolescents Participating in a Meditation Training, *Front. Hum. Neurosci.* 14 (2020) 319. <https://doi.org/10.3389/FNHUM.2020.00319>.
- [37] B.K. Hölzel, J. Carmody, K.C. Evans, E.A. Hoge, J.A. Dusek, L. Morgan, R.K. Pitman, S.W. Lazar, Stress reduction correlates with structural changes in the amygdala, *Soc. Cogn. Affect. Neurosci.* 5 (2010) 11–17. <https://doi.org/10.1093/SCAN/NSP034>.
- [38] World Medical Association, World Medical Association Declaration of Helsinki: Ethical Principles for Medical Research Involving Human Subjects, *JAMA.* 310 (2013) 2191–2194. <https://doi.org/10.1001/jama.2013.281053>.

- [39] S. Baltruschat, L. Mas-Cuesta, A. Cándido, A. Maldonado, C. Verdejo-Lucas, E. Catena-Verdejo, A. Catena, Repeat Traffic Offenders Improve Their Performance in Risky Driving Situations and Have Fewer Accidents Following a Mindfulness-Based Intervention, *Front. Psychol.* 11 (2021). <https://doi.org/10.3389/fpsyg.2020.567278>.
- [40] J. Kabat-Zinn, Mindfulness-Based Interventions in Context: Past, Present, and Future, *Clin. Psychol. Sci. Pract.* 10 (2003) 144–156. <https://doi.org/10.1093/CLIPSY.BPG016>.
- [41] W.T. Chien, H.Y. Cheng, T.W. McMaster, A.L.K. Yip, J.C.L. Wong, Effectiveness of a mindfulness-based psychoeducation group programme for early-stage schizophrenia: An 18-month randomised controlled trial, *Schizophr. Res.* 212 (2019) 140–149. <https://doi.org/10.1016/j.schres.2019.07.053>.
- [42] F.P. De Lange, A. Koers, J.S. Kalkman, G. Bleijenberg, P. Hagoort, J.W.M. Van Der Meer, I. Toni, Increase in prefrontal cortical volume following cognitive behavioural therapy in patients with chronic fatigue syndrome, *Brain.* 131 (2008) 2172–2180. <https://doi.org/10.1093/brain/awn140>.
- [43] J.J. Polcari, R.J. Cali, B.C. Nephew, S. Lu, M. Rashkovskii, J. Wu, F. Saadeh, E. Loucks, J.A. King, Effects of the Mindfulness-Based Blood Pressure Reduction (MB-BP) program on depression and neural structural connectivity, *J. Affect. Disord.* 311 (2022) 31–39. <https://doi.org/10.1016/j.jad.2022.05.059>.
- [44] R.A. Baer, Mindfulness Training as a Clinical Intervention: A Conceptual and Empirical Review, *Clin. Psychol. Sci. Pract.* 10 (2003) 125–143. <https://doi.org/10.1093/CLIPSY.BPG015>.

- [45] A. Cebolla, A. García-Palacios, J. Soler, V. Guillen, R. Baños, C. Botella, Psychometric properties of the Spanish validation of the five facets of mindfulness questionnaire (FFMQ), *Eur. J. Psychiatry*. 26 (2012) 118–126. <https://doi.org/10.4321/S0213-61632012000200005>.
- [46] A. Cándido, E. Orduña, J.C. Perales, A. Verdejo-García, J. Billieux, Validation of a short Spanish version of the UPPS-P impulsive behaviour scale, *Trastor. Adict.* 14 (2012) 73–78. [https://doi.org/10.1016/S1575-0973\(12\)70048-X](https://doi.org/10.1016/S1575-0973(12)70048-X).
- [47] T.S. Braver, J.L. Paxton, H.S. Locke, D.M. Barch, Flexible neural mechanisms of cognitive control within human prefrontal cortex, *Proc. Natl. Acad. Sci.* 106 (2009) 7351–7356. <https://doi.org/10.1073/pnas.0808187106>.
- [48] Y. Li, F. Liu, Q. Zhang, X. Liu, P. Wei, The Effect of Mindfulness Training on Proactive and Reactive Cognitive Control, *Front. Psychol.* 9 (2018). <https://www.frontiersin.org/articles/10.3389/fpsyg.2018.01002>
- [49] E.S. Barnert, S. Himelstein, S. Herbert, A. Garcia-Romeu, L.J. Chamberlain, Exploring an intensive meditation intervention for incarcerated youth, *Child Adolesc. Ment. Health*. 19 (2014) 69–73. <https://doi.org/10.1111/CAMH.12019>.
- [50] S.B. Goldberg, J. Wielgosz, C. Dahl, B. Schuyler, D.S. MacCoon, M. Rosenkranz, A. Lutz, C.A. Sebranek, R.J. Davidson, Does the five facet mindfulness questionnaire measure what we think it does? Construct validity evidence from an active controlled randomized clinical trial, *Psychol. Assess.* 28 (2016) 1009–1014. <https://doi.org/10.1037/pas0000233>.
- [51] I. Majore-Dusele, V. Karkou, I. Millere, The Development of Mindful-Based Dance Movement Therapy Intervention for Chronic Pain: A Pilot Study With Chronic Headache Patients, *Front. Psychol.* 12 (2021) 940. <https://doi.org/10.3389/FPSYG.2021.587923/BIBTEX>.

- [52] C. Noone, M.J. Hogan, A randomised active-controlled trial to examine the effects of an online mindfulness intervention on executive control, critical thinking and key thinking dispositions in a university student sample, *BMC Psychol.* 6 (2018) 1–18. <https://doi.org/10.1186/S40359-018-0226-3/TABLES/8>.
- [53] V.L. Ives-Deliperi, F. Howells, D.J. Stein, E.M. Meintjes, N. Horn, The effects of mindfulness-based cognitive therapy in patients with bipolar disorder: A controlled functional MRI investigation, *J. Affect. Disord.* 150 (2013) 1152–1157. <https://doi.org/10.1016/j.jad.2013.05.074>.
- [54] X. Liu, R. Xiao, F. Tang, S. Wu, Mindfulness-based intervention to reduce multiple health risk behaviors in Chinese undergraduates: a randomized controlled trial, *Curr. Psychol.* (2021) 1–12. <https://doi.org/10.1007/S12144-021-01372-9/FIGURES/2>.
- [55] Y. Wang, C. Fu, Y. Liu, D. Li, C. Wang, R. Sun, Y. Song, A study on the effects of mindfulness-based cognitive therapy and loving-kindness mediation on depression, rumination, mindfulness level and quality of life in depressed patients, *Am. J. Transl. Res.* 13 (2021) 4666–4675.
- [56] A. Giannandrea, L. Simione, B. Pescatori, K. Ferrell, M. Olivetti Belardinelli, S.D. Hickman, A. Raffone, Effects of the Mindfulness-Based Stress Reduction Program on Mind Wandering and Dispositional Mindfulness Facets, *Mindfulness.* 10 (2019) 185–195. <https://doi.org/10.1007/S12671-018-1070-5>.
- [57] F.Y. Huang, A.L. Hsu, Y.P. Chao, C.M.H. Shang, J.S. Tsai, C.W. Wu, Mindfulness-based cognitive therapy on bereavement grief: Alterations of resting-state network connectivity associate with changes of anxiety and mindfulness, *Hum. Brain Mapp.* 42 (2021) 510–520. <https://doi.org/10.1002/HBM.25240>.

- [58] A. Ninomiya, M. Sado, S. Park, D. Fujisawa, T. Kosugi, A. Nakagawa, J. Shirahase, M. Mimura, Effectiveness of mindfulness-based cognitive therapy in patients with anxiety disorders in secondary-care settings: A randomized controlled trial, *Psychiatry Clin. Neurosci.* 74 (2020) 132–139. <https://doi.org/10.1111/PCN.12960>.
- [59] A. Roemer, A. Sutton, C. Grimm, O.N. Medvedev, Differential Contribution of the Five Facets of Mindfulness to Well-being and Psychological Distress, *Mindfulness.* 12 (2021) 693–700. <https://doi.org/10.1007/S12671-020-01535-Y>.
- [60] M. Maltais, G. Bouchard, J. Saint-Aubin, Predicting mindfulness facets: An examination of executive control, neuroticism, and impulsivity, *Can. J. Behav. Sci. Rev. Can. Sci. Comport.* 52 (2020) 1–7. <https://doi.org/10.1037/cbs0000152>.
- [61] C. Vinci, M. Peltier, K. Waldo, J. Kinsaul, S. Shah, S.F. Coffey, A.L. Copeland, Examination of trait impulsivity on the response to a brief mindfulness intervention among college student drinkers, *Psychiatry Res.* 242 (2016) 365–374. <https://doi.org/10.1016/j.psychres.2016.04.115>.
- [62] L. Weiner, M. Wittmann, G. Bertschy, A. Giersch, Dispositional Mindfulness and Subjective Time in Healthy Individuals, *Front. Psychol.* 7 (2016) 786. <https://doi.org/10.3389/fpsyg.2016.00786>.
- [63] A.A. Taren, J.D. Creswell, P.J. Gianaros, Dispositional Mindfulness Co-Varies with Smaller Amygdala and Caudate Volumes in Community Adults, *PLoS ONE.* 8 (2013) e64574. <https://doi.org/10.1371/journal.pone.0064574>.
- [64] N.A.S. Farb, Z.V. Segal, A.K. Anderson, Mindfulness meditation training alters cortical representations of interoceptive attention, *Soc. Cogn. Affect. Neurosci.* 8 (2013) 15–26. <https://doi.org/10.1093/scan/nss066>.

- [65] R.A. Poldrack, C.I. Baker, J. Durnez, K.J. Gorgolewski, P.M. Matthews, M.R. Munafò, T.E. Nichols, J.-B. Poline, E. Vul, T. Yarkoni, Scanning the horizon: towards transparent and reproducible neuroimaging research, *Nat. Rev. Neurosci.* 18 (2017) 115–126. <https://doi.org/10.1038/nrn.2016.167>.
- [66] D.-H. Kang, H.J. Jo, W.H. Jung, S.H. Kim, Y.-H. Jung, C.-H. Choi, U.S. Lee, S.C. An, J.H. Jang, J.S. Kwon, The effect of meditation on brain structure: cortical thickness mapping and diffusion tensor imaging, *Soc. Cogn. Affect. Neurosci.* 8 (2013) 27–33. <https://doi.org/10.1093/SCAN/NSS056>.
- [67] C. Korponay, D. Denticò, T.R.A. Kral, M. Ly, A. Kruis, K. Davis, R. Goldman, A. Lutz, R.J. Davidson, The Effect of Mindfulness Meditation on Impulsivity and its Neurobiological Correlates in Healthy Adults, *Sci. Rep.* 2019 91. 9 (2019) 1–17. <https://doi.org/10.1038/s41598-019-47662-y>.
- [68] C.M. Stillman, X. You, K.L. Seaman, C.J. Vaidya, J.H. Howard, D.V. Howard, Task-related functional connectivity of the caudate mediates the association between trait mindfulness and implicit learning in older adults, *Cogn. Affect. Behav. Neurosci.* 16 (2016) 736–753. <https://doi.org/10.3758/s13415-016-0427-2>.
- [69] B.W. Balleine, M.R. Delgado, O. Hikosaka, The Role of the Dorsal Striatum in Reward and Decision-Making, *J. Neurosci.* 27 (2007) 8161–8165. <https://doi.org/10.1523/JNEUROSCI.1554-07.2007>.
- [70] H. Eryilmaz, A. Rodriguez-Thompson, A.S. Tanner, M. Giegold, F.C. Huntington, J.L. Roffman, Neural determinants of human goal-directed vs. habitual action control and their relation to trait motivation, *Sci. Rep.* 7 (2017) 1–11. <https://doi.org/10.1038/s41598-017-06284-y>.

- [71] J.A. Grahn, J.A. Parkinson, A.M. Owen, The cognitive functions of the caudate nucleus, *Prog. Neurobiol.* 86 (2008) 141–155. <https://doi.org/10.1016/J.PNEUROBIO.2008.09.004>.
- [72] Y.C. Chiu, J. Jiang, T. Egner, The Caudate Nucleus Mediates Learning of Stimulus–Control State Associations, *J. Neurosci.* 37 (2017) 1028–1038. <https://doi.org/10.1523/JNEUROSCI.0778-16.2016>.
- [73] J.A. Brefczynski-Lewis, A. Lutz, H.S. Schaefer, D.B. Levinson, R.J. Davidson, Neural correlates of attentional expertise in long-term meditation practitioners, *Proc. Natl. Acad. Sci.* 104 (2007) 11483–11488. <https://doi.org/10.1073/PNAS.0606552104>.
- [74] A.M. Graybiel, The basal ganglia: learning new tricks and loving it, *Curr. Opin. Neurobiol.* 15 (2005) 638–644. <https://doi.org/10.1016/J.CONB.2005.10.006>.
- [75] E.H. Schumacher, M. D’Esposito, Neural implementation of response selection in humans as revealed by localized effects of stimulus–response compatibility on brain activation, *Hum. Brain Mapp.* 17 (2002) 193–201. <https://doi.org/10.1002/HBM.10063>.
- [76] U. Kirk, K.W. Brown, J. Downar, Adaptive neural reward processing during anticipation and receipt of monetary rewards in mindfulness meditators, *Soc. Cogn. Affect. Neurosci.* 10 (2015) 752–759. <https://doi.org/10.1093/scan/nsu112>.
- [77] V.A. Taylor, J. Grant, V. Daneault, G. Scavone, E. Breton, S. Roffe-Vidal, J. Courtemanche, A.S. Lavarenne, M. Beauregard, Impact of mindfulness on the neural responses to emotional pictures in experienced and beginner meditators, *NeuroImage.* 57 (2011) 1524–1533. <https://doi.org/10.1016/J.NEUROIMAGE.2011.06.001>.

- [78] N. Watanabe, J.P. Bhanji, H. Ohira, M.R. Delgado, Reward-Driven Arousal Impacts Preparation to Perform a Task via Amygdala–Caudate Mechanisms, *Cereb. Cortex.* 29 (2019) 3010–3022. <https://doi.org/10.1093/CERCOR/BHY166>.
- [79] N. Watanabe, J.P. Bhanji, H.C. Tanabe, M.R. Delgado, Ventromedial prefrontal cortex contributes to performance success by controlling reward-driven arousal representation in amygdala, *NeuroImage.* 202 (2019) 116136. <https://doi.org/10.1016/J.NEUROIMAGE.2019.116136>.
- [80] L. Carretié, M. Ríos, B.S. de la Gándara, M. Tapia, J. Albert, S. López-Martín, J. Álvarez-Linera, The striatum beyond reward: caudate responds intensely to unpleasant pictures, *Neuroscience.* 164 (2009) 1615–1622. <https://doi.org/10.1016/J.NEUROSCIENCE.2009.09.031>.
- [81] T.M.C. Lee, M.-K. Leung, W.-K. Hou, J.C.Y. Tang, J. Yin, K.-F. So, C.-F. Lee, C.C.H. Chan, Distinct Neural Activity Associated with Focused-Attention Meditation and Loving-Kindness Meditation, *PLOS ONE.* 7 (2012) e40054. <https://doi.org/10.1371/JOURNAL.PONE.0040054>.
- [82] S. Opialla, J. Lutz, S. Scherpiet, A. Hittmeyer, L. Jäncke, M. Rufer, M.G. Holtforth, U. Herwig, A.B. Brühl, Neural circuits of emotion regulation: a comparison of mindfulness-based and cognitive reappraisal strategies, *Eur. Arch. Psychiatry Clin. Neurosci.* 265 (2014) 45–55. <https://doi.org/10.1007/S00406-014-0510-Z>.
- [83] M.R. Delgado, Reward-Related Responses in the Human Striatum, *Ann. N. Y. Acad. Sci.* 1104 (2007) 70–88. <https://doi.org/10.1196/ANNALS.1390.002>.

- [84] P. Coupé, G. Catheline, E. Lanuza, J.V. Manjón, Towards a unified analysis of brain maturation and aging across the entire lifespan: A MRI analysis, *Hum. Brain Mapp.* 38 (2017) 5501–5518. <https://doi.org/10.1002/HBM.23743>.
- [85] Y. Wang, Q. Xu, J. Luo, M. Hu, C. Zuo, Effects of age and sex on subcortical volumes, *Front. Aging Neurosci.* 11 (2019) 259. <https://doi.org/10.3389/FNAGI.2019.00259/BIBTEX>.
- [86] B. Larsen, V. Olafsson, F. Calabro, C. Laymon, B. Tervo-Clemmens, E. Campbell, D. Minhas, D. Montez, J. Price, B. Luna, Maturation of the human striatal dopamine system revealed by PET and quantitative MRI, *Nat. Commun.* 11 (2020) 1–10. <https://doi.org/10.1038/s41467-020-14693-3>.
- [87] S. Koehler, E. Hasselmann, T. Wüstenberg, A. Heinz, N. Romanczuk-Seiferth, Higher volume of ventral striatum and right prefrontal cortex in pathological gambling, *Brain Struct. Funct.* 220 (2015) 469–477. <https://doi.org/10.1007/s00429-013-0668-6>.
- [88] C.-S. Lin, H.-H. Lin, S.-Y. Wu, Functional and Structural Signatures of the Anterior Insula are associated with Risk-taking Tendency of Analgesic Decision-making, *Sci. Rep.* 6 (2016) 37816. <https://doi.org/10.1038/srep37816>.
- [89] Z. Nasiriavanaki, M. ArianNik, A. Abbassian, E. Mahmoudi, N. Roufigari, S. Shahzadi, M. Nasiriavanaki, B. Bahrami, Prediction of individual differences in risky behavior in young adults via variations in local brain structure, *Front. Neurosci.* 9 (2015). <https://doi.org/10.3389/fnins.2015.00359>.

- [90] R. Yokoyama, T. Nozawa, H. Takeuchi, Y. Taki, A. Sekiguchi, R. Nouchi, Y. Kotozaki, S. Nakagawa, C.M. Miyauchi, K. Iizuka, T. Shinada, Y. Yamamoto, S. Hanawa, T. Araki, H. Hashizume, K. Kunitoki, M. Hanihara, Y. Sassa, R. Kawashima, Association between gray matter volume in the caudate nucleus and financial extravagance: Findings from voxel-based morphometry, *Neurosci. Lett.* 563 (2014) 28–32. <https://doi.org/10.1016/j.neulet.2014.01.026>.
- [91] R. Kanai, G. Rees, The structural basis of inter-individual differences in human behaviour and cognition, *Nat. Rev. Neurosci.* 12 (2011) 231–242. <https://doi.org/10.1038/nrn3000>.
- [92] H. Takeuchi, Y. Taki, Y. Sassa, H. Hashizume, A. Sekiguchi, A. Fukushima, R. Kawashima, Working Memory Training Using Mental Calculation Impacts Regional Gray Matter of the Frontal and Parietal Regions, *PLOS ONE.* 6 (2011) e23175. <https://doi.org/10.1371/JOURNAL.PONE.0023175>.
- [93] S.L. Johnson, J.A. Tharp, A.D. Peckham, A.H. Sanchez, C.S. Carver, Positive urgency is related to difficulty inhibiting prepotent responses, *Emotion.* 16 (2016) 750–759. <https://doi.org/10.1037/emo0000182>.
- [94] J.W. Luk, R.S. Trim, K.A. Karyadi, I. Curry, C.J. Hopfer, J.K. Hewitt, M.C. Stallings, S.A. Brown, T.L. Wall, Unique and interactive effects of impulsivity facets on reckless driving and driving under the influence in a high-risk young adult sample, *Personal. Individ. Differ.* 114 (2017) 42–47. <https://doi.org/10.1016/J.PAID.2017.03.048>.
- [95] M.R. Pearson, E.M. Murphy, A.N. Doane, Impulsivity-like traits and risky driving behaviors among college students, *Accid. Anal. Prev.* 53 (2013) 142–148. <https://doi.org/10.1016/J.AAP.2013.01.009>.

- [96] E.P. Zorrilla, G.F. Koob, Impulsivity derived from the dark side: Neurocircuits that contribute to negative urgency, *Front. Behav. Neurosci.* 13 (2019). <https://doi.org/10.3389/FNBEH.2019.00136>.
- [97] M. Tschernegg, B. Pletzer, P. Schwartenbeck, P. Ludersdorfer, U. Hoffmann, M. Kronbichler, Impulsivity relates to striatal gray matter volumes in humans: evidence from a delay discounting paradigm, *Front. Hum. Neurosci.* 9 (2015) 1–9. <https://doi.org/10.3389/fnhum.2015.00384>.
- [98] A.R. Smith, G.M. Rosenbaum, M.A. Botdorf, L. Steinberg, J.M. Chein, Peers influence adolescent reward processing, but not response inhibition, *Cogn. Affect. Behav. Neurosci.* 18 (2018) 284–295. <https://doi.org/10.3758/S13415-018-0569-5>.
- [99] E.M. McCormick, E.H. Telzer, Failure to retreat: Blunted sensitivity to negative feedback supports risky behavior in adolescents, *NeuroImage.* 147 (2017) 381–389. <https://doi.org/10.1016/j.neuroimage.2016.12.041>.
- [100] B. Besteher, C. Gaser, I. Nenadić, Brain structure and trait impulsivity: A comparative VBM study contrasting neural correlates of traditional and alternative concepts in healthy subjects, *Neuropsychologia.* 131 (2019) 139–147. <https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2019.04.021>.
- [101] X. Noël, D. Brevers, A. Bechara, A neurocognitive approach to understanding the neurobiology of addiction, *Curr. Opin. Neurobiol.* 23 (2013) 632–638. <https://doi.org/10.1016/j.conb.2013.01.018>.

- [102] J.R. Booth, D.D. Burman, J.R. Meyer, Z. Lei, B.L. Trommer, N.D. Davenport, W. Li, T.B. Parrish, D.R. Gitelman, M.M. Mesulam, Larger deficits in brain networks for response inhibition than for visual selective attention in attention deficit hyperactivity disorder (ADHD), *J. Child Psychol. Psychiatry.* 46 (2005) 94–111. <https://doi.org/10.1111/J.1469-7610.2004.00337.X>.
- [103] K.D. Ersche, G.B. Williams, T.W. Robbins, E.T. Bullmore, Meta-analysis of structural brain abnormalities associated with stimulant drug dependence and neuroimaging of addiction vulnerability and resilience, *Curr. Opin. Neurobiol.* 23 (2013) 615–624. <https://doi.org/10.1016/J.CONB.2013.02.017>.
- [104] M.P. Harms, L. Wang, J.G. Csernansky, D.M. Barch, Structure-function relationship of working memory activity with hippocampal and prefrontal cortex volumes, *Brain Struct. Funct.* 218 (2013) 173–186. <https://doi.org/10.1007/S00429-012-0391-8/TABLES/2>.

DISCUSIÓN

DISCUSIÓN

La toma de decisiones es un proceso complejo en el que distintas redes cerebrales trabajan de manera conjunta para asignar las preferencias de acción, controlar la conducta, valorar los resultados y aprender de la experiencia, con el fin último de adaptar el comportamiento futuro (Coutlee y Huettel, 2012; Ernst y Paulus, 2005). Sin embargo, no todas las decisiones son adaptativas, ya que algunas implican comportamientos que suponen un riesgo para el bienestar. Además, dado su carácter dinámico y subjetivo, existen diferencias individuales y contextuales que podrían afectar a la configuración e interacción de los sistemas neurocognitivos que intervienen en este tipo de conductas. Es por esto que el estudio 1 profundiza en las bases neuroanatómicas del comportamiento de riesgo en entornos de tráfico y en la de sus factores de personalidad asociados, como son la sensibilidad a las recompensas y castigos y la preferencia por las recompensas inmediatas, o impulsividad cognitiva. Nuestros resultados indican que existe una tendencia a presentar un menor volumen de materia gris total cuanto mayor es el nivel de riesgo. Además, encontramos que las personas que conducen de manera arriesgada muestran también un menor volumen en regiones que forman parte de las redes de control cognitivo y de recompensa cerebral, como por ejemplo: las cortezas frontal (superior, media, medial, inferior y orbital), parietal superior y temporal superior, los giros parahipocampal y fusiforme, la ínsula, el cerebelo y el estriado ventral. Investigaciones previas muestran que estas redes actúan como un sistema neurobiológico interactivo para modular el proceso de toma de decisiones (Edelson y Reyna, 2023; X. Li et al., 2020; McIlvain et al., 2020; Steinberg, 2010). Por lo tanto, nuestros resultados apoyan y complementan la evidencia del modelo dual del comportamiento de riesgo (Epstein, 1994; Evans, 2008; Frankish, 2010; Kahneman y Frederick, 2002; Loewenstein et al.,

2001; Reyna, 2004; Sanfey y Chang, 2008; Slovic et al., 2007), sugiriendo que, en personas arriesgadas, existe una alteración en la configuración de los circuitos neurales implicados en la valoración de las recompensas, implementación de la acción y regulación del comportamiento. Además, teniendo en cuenta la influencia del volumen cerebral en la actividad neural (Aydogan et al., 2021; Harms et al., 2013; Honey et al., 2007), las alteraciones estructurales que observamos en las personas que conducen de manera arriesgada podrían reflejar un patrón de activación también distinto, resultando en un procesamiento desadaptativo de la información y una toma de decisiones disfuncional. Por otro lado, observamos que el nivel de riesgo en conducción es el que modula cómo algunas de las regiones anteriores, junto con otras que también forman parte de las redes de control cognitivo y de recompensa, se relacionan con la impulsividad y la sensibilidad a las recompensas y castigos, incluso ante la ausencia de diferencias entre los grupos en las puntuaciones de estas variables. En personas con un menor nivel de riesgo, la preferencia por las recompensas inmediatas se asocia con el volumen del núcleo accumbens, la amígdala y las cortezas cingulada posterior y orbitofrontal. Por su parte, la sensibilidad a las recompensas se relaciona con el volumen de la corteza temporal superior, los giros fusiforme y postcentral, y la sensibilidad al castigo con el volumen de la ínsula, el giro precentral y la corteza frontal superior. Es decir, nuestros resultados sugieren que los factores de personalidad que se han demostrado como más influyentes en la valoración de las alternativas de conducta y selección de la acción, se sustentan en las mismas redes cerebrales que subyacen a estas etapas en el proceso de toma de decisiones. Sin embargo, las personas con tendencia a conducir de manera arriesgada muestran, en general, correlaciones absolutas más bajas, o incluso ausentes, entre los factores de personalidad y el volumen de materia gris cerebral. Estos resultados apuntan a que las funciones de las regiones implicadas en la impulsividad cognitiva y en la

sensibilidad a las recompensas y castigos están enmascaradas por los mecanismos propios del comportamiento de riesgo. Por lo tanto, parece que las alteraciones en los procesos neurocognitivos del descuento por demora, la sensibilidad a los reforzadores y la inhibición conductual podrían estar a la base de las decisiones de riesgo en conducción. Esto se podría aplicar en las intervenciones destinadas a mejorar el comportamiento de riesgo, en general, o en los cursos de sensibilización y reeducación vial en particular, de manera que adaptaran sus contenidos para trabajar específicamente los procesos cognitivos relacionados con el aplazamiento del refuerzo, la apropiada valoración de las recompensas y castigos futuros y la autorregulación conductual.

El sistema de control cognitivo y el socioemocional, o de recompensa cerebral, además de estar implicados en la formación de preferencias e implementación de la acción, ejercen un rol fundamental en la anticipación y valoración de los resultados de las decisiones y en la regulación de la conducta (Grupe y Nitschke, 2013; Gupta et al., 2011b; Knutson et al., 2003; McClure et al., 2004; Morelli et al., 2022). Sin embargo, existen situaciones donde las consecuencias son impredecibles y, en muchas ocasiones, repercuten de manera altamente negativa en la salud física y mental. El estudio 2 explora la participación e interacción entre las principales redes cerebrales (Yeo et al., 2011) durante el procesamiento de este tipo de eventos, utilizando, para ello, los accidentes de tráfico en contextos de conducción simulada. Los resultados indican que, durante los milisegundos previos a la ocurrencia de un accidente, se activan las cortezas parietal inferior y cíngula anterior y la ínsula. Además, se produce un flujo de activación causal, o conectividad efectiva entre los nodos de las redes atencionales ventral y dorsal (VAN y DAN), y dentro de los nodos de la red límbica (LN). Por otro lado, cuando el accidente acaba de ocurrir, las cortezas orbitofrontal, inferior parietal y cíngula anterior, y los giros frontal superior y medio se activan, y se produce una mayor conectividad efectiva

entre redes, desde la red atencional ventral (VAN) hasta la somatomotora (SMN), y entre nodos, desde nodos de la red visual (VN), VAN y red por defecto (DMN), hasta nodos de las redes frontoparietal (FPN), atencionales y límbica. Estos patrones de actividad cerebral y conectividad efectiva sugieren que, en el periodo previo a un accidente, se activan procesos internos, tanto afectivos como cognitivos e interoceptivos, que se integran con la información saliente del entorno. Esta integración permite la identificación de la estructura y del valor emocional de la situación y facilita la anticipación de la ocurrencia del evento. Además, una vez que el accidente ha ocurrido, se produce una agrupación y valoración de la nueva información y se inician los procesos de control necesarios para adaptar el comportamiento a las nuevas demandas del ambiente. En definitiva, parece que el sistema dual también interviene en las últimas etapas del proceso de toma de decisiones, desempeñando un rol fundamental en la anticipación y el procesamiento de los eventos catastróficos. Esta mejor comprensión del procesamiento neural que tiene lugar en los momentos temporales que preceden y prosiguen a los accidentes podría servir de guía en la mejora de los sistemas de vigilancia y de alerta del estado de las personas que trabajan en entornos peligrosos o son usuarias de la carretera, utilizando los patrones de actividad electroencefalográfica para agilizar y optimizar los métodos de asistencia.

Por último, dada la evidencia sobre los sistemas neurocognitivos que están a la base de la toma de decisiones disfuncionales, las intervenciones que se han demostrado eficaces para mejorar la conducta adaptativa podrían afectar a la configuración de estos sistemas y a los factores que intervienen en las distintas etapas del proceso de toma de decisiones. Es por esto que el estudio 3 examina cómo una intervención basada en mindfulness puede producir cambios en la estructura de las regiones cerebrales que se relacionan con los procesos cognitivos y de personalidad implicados en el

comportamiento de riesgo. Nuestros resultados indican que el entrenamiento en mindfulness afecta al mindfulness disposicional, mejorando las facetas de observación y no reactividad. Además, el cambio en las habilidades de atención plena, después de la intervención, se relaciona con cambios en los niveles de impulsividad. Asimismo, observamos que el entrenamiento en mindfulness produce cambios en el volumen del núcleo caudado que, su vez, se relaciona con una menor urgencia positiva. Es decir, nuestros resultados avalan la evidencia previa sobre los efectos de las intervenciones basadas en mindfulness en el mindfulness disposicional (Liu et al., 2021; Quaglia et al., 2016; M. Y. Wang et al., 2021; Zuo et al., 2023) y sugieren que estos efectos podrían estar explicados por una mejora en la habilidad de observación de las propias sensaciones y percepciones y en la capacidad para dejar pasar los pensamientos y las emociones, sin aferrarse ni dejarse llevar por su ocurrencia. Además, teniendo en cuenta que el núcleo caudado forma parte de la red de recompensa y desempeña funciones de regulación del afecto y control comportamental (Chiu et al., 2017; Delgado, 2007; Watanabe et al., 2019), la reducción en el volumen que se observa después de la intervención sugiere una evolución de la estructura (Coupé et al., 2017; Y. Wang et al., 2019) para un funcionamiento neural más eficaz. En este sentido, nuestros resultados muestran que la reducción del volumen del núcleo caudado se asocia con una menor urgencia positiva. Por lo tanto, si se tiene en cuenta la relación entre volumen y activación (Harms et al., 2013), los resultados sugieren una menor actividad del núcleo caudado cuando se actúa bajo la influencia de emociones positivas, lo que podría reflejarse en una toma de decisiones menos impulsiva. Esto podría aplicarse clínicamente para adaptar las intervenciones basadas en mindfulness a poblaciones que presenten altos niveles de impulsividad y dificultades en la regulación emocional.

Los estudios que componen la presente tesis doctoral profundizan en aspectos específicos del proceso de la toma de decisiones que, combinados entre sí, enriquecen el conocimiento y ofrecen nuevas claves para la investigación en este campo. En conjunto, nuestros resultados avalan la evidencia de los modelos duales y muestran que los sistemas cerebrales de control cognitivo, recompensa y procesamiento emocional actúan de manera interconectada en las diferentes etapas del proceso de toma de decisiones (figura 1), desde la formación de preferencias y selección de la acción (estudio 1) hasta la valoración de resultados (estudio 2) y la regulación de la conducta (estudio 3). Más concretamente, se observa una alteración en la estructura de las regiones que conforman los sistemas de recompensa cerebral y control cognitivo en aquellas personas con tendencia tomar decisiones arriesgadas al volante (estudio 1) y se evidencia que una intervención que facilita la toma de decisiones adaptativa, como el entrenamiento en mindfulness, produce cambios estructurales en el núcleo caudado, una región que también forma parte del sistema de recompensa cerebral y que influye en la autorregulación conductual (estudio 3). Así mismo, la participación e interacción entre las áreas y redes cerebrales que subyacen a los procesos de saliencia, procesamiento emocional y control comportamental permite la anticipación y el procesamiento de resultados catastróficos (estudio 2).

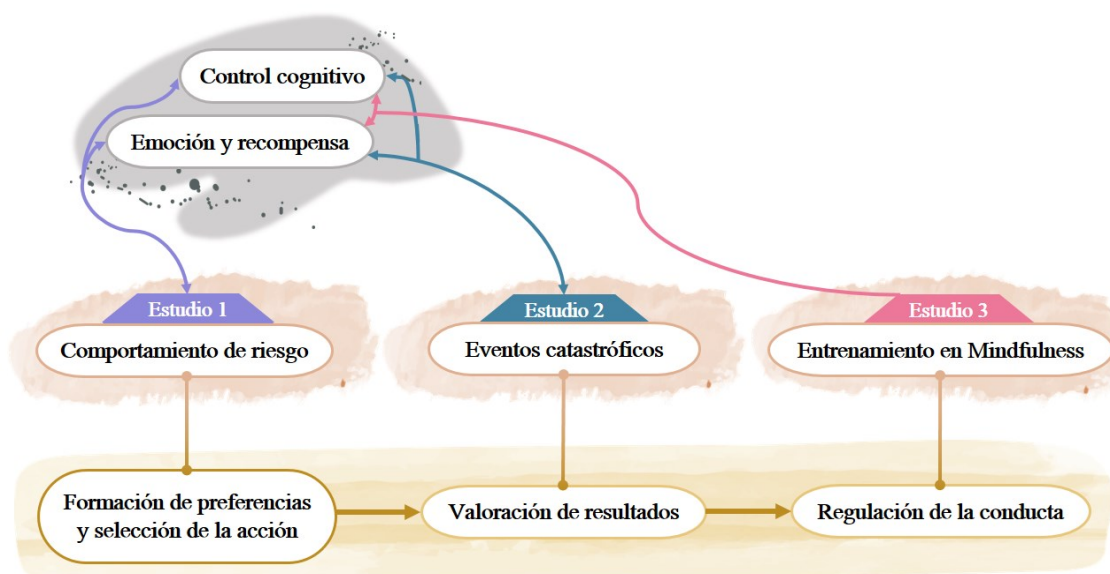


Figura 1. Estudios de la tesis sobre los sistemas cerebrales involucrados en el proceso de toma de decisiones.

La mayoría de las investigaciones de los modelos duales sobre la toma de decisiones se basan en los efectos de la edad, ya que las regiones corticales pertenecientes al sistema de control cognitivo se desarrollan más despacio y no maduran completamente hasta la mitad de la veintena, mientras que las áreas subcorticales relacionadas con el procesamiento emocional y de las recompensas ejercen una mayor influencia en la adolescencia y en las primeras etapas de la edad adulta, al madurar a edades más tempranas (Edelson y Reyna, 2023; Steinberg, 2010; Zhang, 2022, entre otros). Además, cuando se explora la toma de decisiones a lo largo de la vida, se observan cambios sustanciales relacionados con la edad, siendo de especial relevancia en edades avanzadas (Casey, 2015; Duell et al., 2018; Tymula et al., 2013). Debido a esto, y teniendo en cuenta que para 2050 se espera que más del 35% de las personas tengan 65 años o más (Eurostat, 2023) y que la población de los estudios de la tesis, aunque es variada, no supera en ningún caso los 68 años, futuras investigaciones podrían abordar el estudio de los

procesos neurocognitivos y de personalidad implicados en la toma de decisiones en personas mayores, además de estudiar la eficacia de las intervenciones basadas en mindfulness y sus efectos en los sistemas de control cognitivo y recompensa cerebral en este grupo de edad.

Por otro lado, nuestros resultados también muestran que algunos factores de personalidad que intervienen en el proceso de toma de decisiones, como la impulsividad y la sensibilidad a las recompensas y castigos, se relacionan con regiones que forman parte de los sistemas de control y recompensa (estudio 1). Sin embargo las relaciones observadas son diferentes en función del nivel de riesgo en conducción, por lo que, en personas arriesgadas parece que también existe una alteración en los mecanismos neurales que subyacen a estos rasgos de personalidad. Además, el entrenamiento en mindfulness afecta a otros rasgos de personalidad que intervienen en el proceso de decisión, mejorando la atención plena disposicional (estudio 3). Por último, los cambios a nivel de estructura cerebral que produce la práctica de mindfulness se relacionan con una menor urgencia positiva, lo que podría reflejarse en una toma de decisiones menos precipitada o impulsiva cuando se actúa ante la influencia de emociones positivas (estudio 3). En definitiva, nuestros resultados evidencian los correlatos neuroanatómicos de la inextricable asociación entre las decisiones arriesgadas, la atención plena disposicional, la sensibilidad a las recompensas y castigos y la impulsividad (figura 2). Las relaciones entre los factores de personalidad que intervienen en la toma de decisiones se han evidenciado en la literatura previa, considerando incluso la tendencia al riesgo como un rasgo de personalidad más (Baltruschat et al., 2020; Baltruschat, Cándido, et al., 2021; Megías-Robles et al., 2023; Tingaz et al., 2022; Zheng et al., 2023). Sin embargo, la mayoría de las investigaciones también han estudiado la relación entre los diferentes constructos de manera aislada. Por lo tanto, en investigaciones futuras se podría tener en

cuenta el peso relativo y conjunto de cada uno de estos factores, para determinar su influencia en la toma de decisiones y, de esta manera, facilitar el perfeccionamiento de las intervenciones destinadas a mejorar la conducta adaptativa y la calidad de vida.

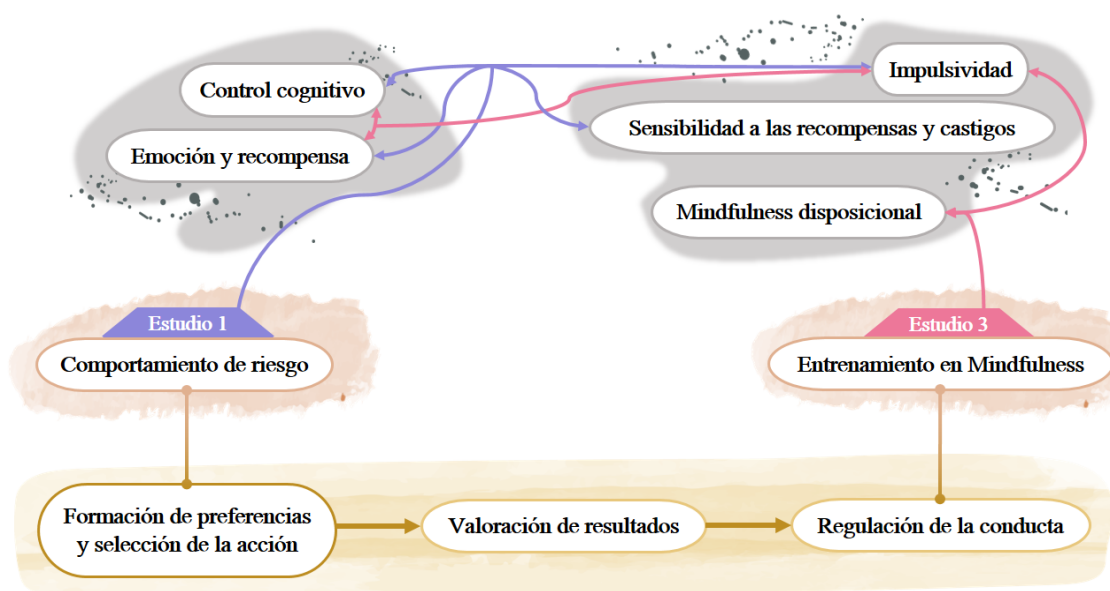


Figura 2. Estudios de la tesis sobre los factores de personalidad relacionados con la de toma de decisiones y sus correlatos neurales.

CONCLUSIONES / CONCLUSIONS

CONCLUSIONES

De los estudios que componen la presente tesis doctoral se derivan las siguientes conclusiones:

1. Las personas que conducen de manera arriesgada muestran un menor volumen de materia gris en regiones de las redes de control cognitivo y de recompensa cerebral, como la corteza frontal, parietal superior y temporal superior, los giros parahipocampal y fusiforme, la ínsula, el cerebelo y el estriado ventral. Además, existe una tendencia a presentar un menor volumen de materia gris total cuanto mayor es el nivel de riesgo en conducción.
2. La impulsividad y la sensibilidad a las recompensas y castigos se relacionan con diferentes regiones de las redes de control y recompensa cerebral. La impulsividad se asocia con el volumen del núcleo accumbens, la amígdala y las cortezas cingulada posterior y orbitofrontal. Por su parte, la sensibilidad a las recompensas se relaciona con el volumen de la corteza temporal superior y los giros fusiforme y postcentral, y la sensibilidad al castigo con el volumen de la ínsula, el giro precentral y la corteza frontal superior.
3. El comportamiento de riesgo en conducción modula cómo se relacionan la impulsividad y la sensibilidad a las recompensas y castigos con el volumen de materia gris cerebral, incluso ante la usencia de diferencias entre los diferentes niveles de riesgo en estos rasgos de personalidad.
4. La activación de redes cerebrales relacionadas con la saliencia y el procesamiento emocional permite anticipar resultados catastróficos e impredecibles. En el periodo previo a la ocurrencia de un accidente, en un contexto de conducción simulada, se activan las cortezas parietal inferior y cingulada anterior y la ínsula. Además, se

produce un flujo de activación causal, o conectividad efectiva entre los nodos de las redes atencionales ventral y dorsal, y dentro de los nodos de la red límbica.

5. La activación de redes cerebrales relacionadas con el control cognitivo y la regulación del comportamiento permiten procesar eventos catastróficos. Inmediatamente después de la ocurrencia de un accidente se activan las cortezas orbitofrontal, inferior parietal y cingulada anterior, y los giros frontal superior y medio. Además, se produce una mayor conectividad efectiva entre redes, desde la red atencional ventral hasta la somatomotora, y entre nodos, desde nodos de la red visual, atencional ventral y red por defecto, hasta nodos de las redes frontoparietal, atencionales y límbica.
6. Una intervención basada en mindfulness mejora la atención plena disposicional, incrementando la capacidad de observación de las propias sensaciones y percepciones, así como la habilidad para dejar pasar los pensamientos y las emociones, sin aferrarse ni dejarse llevar por su ocurrencia.
7. Una intervención basada en mindfulness produce cambios en el volumen del núcleo caudado, una estructura que forma parte de la red de recompensa y desempeña funciones de regulación del afecto y control comportamental.
8. Los cambios neuroanatómicos en el núcleo caudado después una intervención basada en mindfulness se relacionan con una menor urgencia positiva y, por lo tanto, con una menor tendencia a tomar decisiones impulsivas cuando se actúa bajo la influencia de emociones positivas.

CONCLUSIONS

The following conclusions can be drawn from the studies that make up the present doctoral thesis:

1. People who engage in risky driving show a reduced gray matter volume in regions of the cognitive control and reward brain networks, such as the frontal cortex, superior parietal and temporal cortices, parahippocampal and fusiform gyri, insula, cerebellum, and ventral striatum. Furthermore, there is a tendency to show a lower total gray matter volume as the level of risk in driving increases.
2. Impulsivity and sensitivity to rewards and punishments are related to different regions of the control and reward brain networks. Impulsivity is associated with the volume of the nucleus accumbens, amygdala, and posterior cingulate and orbitofrontal cortices. Sensitivity to rewards is related to the volume of the superior temporal cortex and fusiform and postcentral gyri, and sensitivity to punishment to the volume of the insula, precentral gyrus, and superior frontal cortex.
3. Risk-taking behavior in driving modulates how impulsivity and sensitivity to rewards and punishments are related to brain gray matter volume, even in the absence of differences between different levels of risk in these personality traits.
4. The activation of brain networks related to salience and emotional processing makes it possible to anticipate catastrophic and unpredictable outcomes. In the period before the occurrence of an accident, in a simulated driving context, the inferior parietal and anterior cingulate cortices and the insula are activated. In addition, there is a causal activation flow or effective connectivity between the

nodes of the ventral and dorsal attentional networks, and within the nodes of the limbic network.

5. The activation of brain networks related to cognitive control and behavioral regulation allows the processing of catastrophic events. Immediately after the occurrence of an accident, the orbitofrontal, inferior parietal, and anterior cingulate cortices and the superior and middle frontal gyri are activated. In addition, there is increased effective connectivity between networks, from the ventral attention network to the somatomotor network, and within nodes, from nodes in the visual, ventral attention, and default networks to nodes in the frontoparietal, attentional, and limbic networks.
6. A mindfulness-based intervention improves dispositional mindfulness, enhancing the capacity to observe one's own sensations and perceptions, as well as the ability to let thoughts and emotions pass without clinging or reacting to them.
7. A mindfulness-based intervention produces changes in the volume of the caudate nucleus, a structure that is part of the reward network and plays a role in affect regulation and behavioral control.
8. Neuroanatomical changes in the caudate nucleus after a mindfulness-based intervention are related to a reduced positive urgency and, therefore, to a decreased tendency to make impulsive decisions when acting under the influence of positive emotions.

REFERENCIAS

REFERENCIAS

- Adrián-Ventura, J., Costumero, V., Parcet, M. A. y Ávila, C. (2019a). Linking personality and brain anatomy: A structural MRI approach to Reinforcement Sensitivity Theory. *Social Cognitive and Affective Neuroscience*, *14*(3), 329-338. <https://doi.org/10.1093/scan/nsz011>
- Adrián-Ventura, J., Costumero, V., Parcet, M. A. y Ávila, C. (2019b). Reward network connectivity “at rest” is associated with reward sensitivity in healthy adults: A resting-state fMRI study. *Cognitive, Affective Behavioral Neuroscience*, *19*(3), 726-736. <https://doi.org/10.3758/s13415-019-00688-1>
- Adrián-Ventura, J., Fabregat-Nabás, J., Costumero, V. y Ávila, C. (2023). Underlying differences in resting-state activity metrics related to sensitivity to punishment. *Behavioural Brain Research*, *437*, 114152. <https://doi.org/10.1016/j.bbr.2022.114152>
- Aguerre, N. V., Gómez-Ariza, C. J. y Bajo, M. T. (2022). The relative role of executive control and personality traits in grit. *PLoS ONE*, *17*(6 June). <https://doi.org/10.1371/journal.pone.0269448>
- Ainslie, G. (1992). *Picoeconomics: The Strategic Interaction of Successive Motivational States within the Person*. Cambridge University Press.
- Aluja, A. y Blanch, A. (2011). Neuropsychological Behavioral Inhibition System (BIS) and Behavioral Approach System (BAS) Assessment: A Shortened Sensitivity to Punishment and Sensitivity to Reward Questionnaire Version (SPSRQ-20). *Journal of Personality Assessment*, *93*(6), 628-636. <https://doi.org/10.1080/00223891.2011.608760>

- Angie, A. D., Connelly, S., Waples, E. P. y Kligyte, V. (2011). The influence of discrete emotions on judgement and decision-making: A meta-analytic review. *Cognition and Emotion*, *25*(8), 1393-1422. <https://doi.org/10.1080/02699931.2010.550751>
- Aydogan, G., Daviet, R., Karlsson Linnér, R., Hare, T. A., Kable, J. W., Kranzler, H. R., Wetherill, R. R., Ruff, C. C., Koellinger, P. D., BIG BEAR Consortium y Nave, G. (2021). Genetic underpinnings of risky behaviour relate to altered neuroanatomy. *Nature Human Behaviour*, *5*(6), 787-794. <https://doi.org/10.1038/s41562-020-01027-y>
- Baer, R. A. (2003). Mindfulness Training as a Clinical Intervention: A Conceptual and Empirical Review. *Clinical Psychology: Science and Practice*, *10*(2), 125-143. <https://doi.org/10.1093/CLIPSY.BPG015>
- Baer, R. A., Smith, G. T., Hopkins, J., Krietemeyer, J. y Toney, L. (2006). Using self-report assessment methods to explore facets of mindfulness. *Assessment*, *13*(1), 27-45. <https://doi.org/10.1177/1073191105283504>
- Balleine, B. W. (2021). Emotional predictions and choice. *Nature Human Behaviour*, *5*(10), 1271-1272. <https://doi.org/10.1038/s41562-021-01208-3>
- Balleine, B. W., Delgado, M. R. y Hikosaka, O. (2007). The Role of the Dorsal Striatum in Reward and Decision-Making. *Journal of Neuroscience*, *27*(31), 8161-8165. <https://doi.org/10.1523/JNEUROSCI.1554-07.2007>
- Balleine, B. W. y Dezfouli, A. (2019). Hierarchical Action Control: Adaptive Collaboration Between Actions and Habits. *Frontiers in Psychology*, *10*. <https://www.frontiersin.org/articles/10.3389/fpsyg.2019.02735>
- Baltruschat, S. (2020). *Individual differences in risk-taking and behavioural modification* [Tesis Doctoral, Universidad de Granada]. <https://digibug.ugr.es/handle/10481/62264>

-
- Baltruschat, S., Cándido, A., Maldonado, A., Verdejo-Lucas, C., Catena-Verdejo, E. y Catena, A. (2021). There Is More to Mindfulness Than Emotion Regulation: A Study on Brain Structural Networks. *Frontiers in Psychology, 12*, 659403. <https://doi.org/10.3389/fpsyg.2021.659403>
- Baltruschat, S., Cándido, A., Megías, A., Maldonado, A. y Catena, A. (2020). Risk proneness modulates the impact of impulsivity on brain functional connectivity. *Human Brain Mapping, 41*(4), 943-951. <https://doi.org/10.1002/hbm.24851>
- Baltruschat, S., Mas-Cuesta, L., Cándido, A., Maldonado, A., Verdejo-Lucas, C., Catena-Verdejo, E. y Catena, A. (2021). Repeat Traffic Offenders Improve Their Performance in Risky Driving Situations and Have Fewer Accidents Following a Mindfulness-Based Intervention. *Frontiers in Psychology, 11*. <https://doi.org/10.3389/fpsyg.2020.567278>
- Baltruschat, S., Megías-Robles, A., Cándido, A., Maldonado, A. y Catena, A. (2021). Social and Non-social Brain Areas in Risk Behaviour: The Role of Social Context. *Neuroscience, 465*, 177-186. <https://doi.org/10.1016/j.neuroscience.2021.04.029>
- Barrós-Loscertales, A., Meseguer, V., Sanjuán, A., Belloch, V., Parcet, M. A., Torrubia, R. y Ávila, C. (2006a). Behavioral Inhibition System activity is associated with increased amygdala and hippocampal gray matter volume: A voxel-based morphometry study. *NeuroImage, 33*(3), 1011-1015. <https://doi.org/10.1016/j.neuroimage.2006.07.025>
- Barrós-Loscertales, A., Meseguer, V., Sanjuán, A., Belloch, V., Parcet, M. A., Torrubia, R. y Ávila, C. (2006b). Striatum gray matter reduction in males with an overactive behavioral activation system. *The European Journal of Neuroscience, 24*(7), 2071-2074. <https://doi.org/10.1111/j.1460-9568.2006.05084.x>

- Bartra, O., McGuire, J. T. y Kable, J. W. (2013). The valuation system: A coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. *NeuroImage*, 76, 412-427. <https://doi.org/10.1016/j.neuroimage.2013.02.063>
- Bechara, A. (2002). The neurology of social cognition. *Brain: A Journal of Neurology*, 125(Pt 8), 1673-1675. <https://doi.org/10.1093/brain/awf169>
- Bernhardt, B. C., Smallwood, J., Tusche, A., Ruby, F. J. M., Engen, H. G., Steinbeis, N. y Singer, T. (2014). Medial prefrontal and anterior cingulate cortical thickness predicts shared individual differences in self-generated thought and temporal discounting. *NeuroImage*, 90, 290-297. <https://doi.org/10.1016/j.neuroimage.2013.12.040>
- Bickel, W. K., Koffarnus, M. N., Moody, L. y Wilson, A. G. (2014). The Behavioral- and Neuro-Economic Process of Temporal Discounting: A Candidate Behavioral Marker of Addiction. *Neuropharmacology*, 76(0 0), 10.1016/j.neuropharm.2013.06.013. <https://doi.org/10.1016/j.neuropharm.2013.06.013>
- Bjork, J. M., Momenan, R. y Hommer, D. W. (2009). Delay discounting correlates with proportional lateral frontal cortex volumes. *Biological Psychiatry*, 65(8), 710-713. <https://doi.org/10.1016/j.biopsych.2008.11.023>
- Black, D. S., Sussman, S., Johnson, C. A. y Milam, J. (2012). Trait Mindfulness Helps Shield Decision-Making From Translating Into Health-Risk Behavior. *Journal of Adolescent Health*, 51(6), 588-592. <https://doi.org/10.1016/j.jadohealth.2012.03.011>

-
- Breska, A. y Ivry, R. B. (2018). Double dissociation of single-interval and rhythmic temporal prediction in cerebellar degeneration and Parkinson's disease. *Proceedings of the National Academy of Sciences*, *115*(48), 12283-12288. <https://doi.org/10.1073/pnas.1810596115>
- Brevet-Aeby, C., Brunelin, J., Iceta, S., Padovan, C. y Poulet, E. (2016). Prefrontal cortex and impulsivity: Interest of noninvasive brain stimulation. *Neuroscience & Biobehavioral Reviews*, *71*, 112-134. <https://doi.org/10.1016/j.neubiorev.2016.08.028>
- Brown, K. W. y Ryan, R. M. (2003). The benefits of being present: Mindfulness and its role in psychological well-being. *Journal of Personality and Social Psychology*, *84*(4), 822-848. <https://doi.org/10.1037/0022-3514.84.4.822>
- Bursky, M., Egglefield, D. A., Schiff, S. G., Premnath, P. y Sneed, J. R. (2022). Mindfulness-Enhanced Computerized Cognitive Training for Depression: An Integrative Review and Proposed Model Targeting the Cognitive Control and Default-Mode Networks. *Brain Sciences*, *12*(5). <https://doi.org/10.3390/brainsci12050663>
- Cairncross, M. y Miller, C. J. (2020). The Effectiveness of Mindfulness-Based Therapies for ADHD: A Meta-Analytic Review. *Journal of Attention Disorders*, *24*(5), 627-643. <https://doi.org/10.1177/1087054715625301>
- Cándido, A. (2000). *Introducción a la psicología del aprendizaje asociativo*. Biblioteca Nueva.

- Carroll, A. L., Damme, K. S. F., Alloy, L. B., Bart, C. P., Ng, T. H., Titone, M. K., Chein, J., Cichocki, A. C., Armstrong, C. C. y Nusslock, R. (2022). Risk for bipolar spectrum disorders associated with positive urgency and orbitofrontal cortical grey matter volume. *NeuroImage: Clinical*, 36. <https://doi.org/10.1016/j.nicl.2022.103225>
- Casey, B. J. (2015). Beyond Simple Models of Self-Control to Circuit-Based Accounts of Adolescent Behavior. *Annual Review of Psychology*, 66(1), 295-319. <https://doi.org/10.1146/annurev-psych-010814-015156>
- Cavicchioli, M., Movalli, M. y Maffei, C. (2018). The Clinical Efficacy of Mindfulness-Based Treatments for Alcohol and Drugs Use Disorders: A Meta-Analytic Review of Randomized and Nonrandomized Controlled Trials. *European Addiction Research*, 24(3), 137-162. <https://doi.org/10.1159/000490762>
- Chiu, Y. C., Jiang, J. y Egner, T. (2017). The Caudate Nucleus Mediates Learning of Stimulus–Control State Associations. *Journal of Neuroscience*, 37(4), 1028-1038. <https://doi.org/10.1523/JNEUROSCI.0778-16.2016>
- Cosenza, M., Griffiths, M. D., Nigro, G. y Ciccarelli, M. (2017). Risk-Taking, Delay Discounting, and Time Perspective in Adolescent Gamblers: An Experimental Study. *Journal of Gambling Studies*, 33(2), 383-395. <https://doi.org/10.1007/s10899-016-9623-9>
- Coull, J. T. (2009). Neural substrates of mounting temporal expectation. *PLoS Biology*, 7(8), e1000166. <https://doi.org/10.1371/journal.pbio.1000166>
- Coupé, P., Catheline, G., Lanuza, E. y Manjón, J. V. (2017). Towards a unified analysis of brain maturation and aging across the entire lifespan: A MRI analysis. *Human Brain Mapping*, 38(11), 5501-5518. <https://doi.org/10.1002/HBM.23743>

- Coutlee, C. G. y Huettel, S. A. (2012). The functional neuroanatomy of decision making: Prefrontal control of thought and action. *Brain Research*, *1428*, 3-12.
<https://doi.org/10.1016/j.brainres.2011.05.053>
- Cui, L., Ye, M., Sun, L., Zhang, S. y He, G. (2022). Common and distinct neural correlates of intertemporal and risky decision-making: Meta-analytical evidence for the dual-system theory. *Neuroscience and Biobehavioral Reviews*, *141*.
<https://doi.org/10.1016/j.neubiorev.2022.104851>
- Dalley, J. W. y Robbins, T. W. (2017). Fractionating impulsivity: Neuropsychiatric implications. *Nature Reviews Neuroscience*, *18*(3), Article 3.
<https://doi.org/10.1038/nrn.2017.8>
- Dantas, A. M., Sack, A. T., Bruggen, E., Jiao, P. y Schuhmann, T. (2023). The functional relevance of right DLPFC and VMPFC in risk-taking behavior. *Cortex*, *159*, 64-74. <https://doi.org/10.1016/j.cortex.2022.11.009>
- Davis, C., Patte, K., Tweed, S. y Curtis, C. (2007). Personality traits associated with decision-making deficits. *Personality and Individual Differences*, *42*(2), 279-290.
<https://doi.org/10.1016/j.paid.2006.07.006>
- Davis, J. P., Barr, N., Dworkin, E. R., Dumas, T. M., Berey, B., DiGuseppi, G. y Cahn, B. R. (2019). Effect of Mindfulness-Based Relapse Prevention on Impulsivity Trajectories Among Young Adults in Residential Substance Use Disorder Treatment. *Mindfulness*, *10*(10), 1997-2009. <https://doi.org/10.1007/s12671-019-01164-0>
- Delgado, M. R. (2007). Reward-Related Responses in the Human Striatum. *Annals of the New York Academy of Sciences*, *1104*(1), 70-88.
<https://doi.org/10.1196/ANNALS.1390.002>

- Dir, A. L., Coskunpinar, A. y Cyders, M. A. (2014). A meta-analytic review of the relationship between adolescent risky sexual behavior and impulsivity across gender, age, and race. *Clinical Psychology Review*, *34*(7), 551-562. <https://doi.org/10.1016/j.cpr.2014.08.004>
- Dosenbach, N. U. F., Visscher, K. M., Palmer, E. D., Miezin, F. M., Wenger, K. K., Kang, H. C., Burgund, E. D., Grimes, A. L., Schlaggar, B. L. y Petersen, S. E. (2006). A Core System for the Implementation of Task Sets. *Neuron*, *50*(5), 799-812. <https://doi.org/10.1016/j.neuron.2006.04.031>
- Duell, N., Steinberg, L., Icenogle, G., Chein, J., Chaudhary, N., Di Giunta, L., Dodge, K. A., Fanti, K. A., Lansford, J. E., Oburu, P., Pastorelli, C., Skinner, A. T., Sorbring, E., Tapanya, S., Uribe Tirado, L. M., Alampay, L. P., Al-Hassan, S. M., Takash, H. M. S., Bacchini, D. y Chang, L. (2018). Age Patterns in Risk Taking Across the World. *Journal of Youth and Adolescence*, *47*(5), 1052-1072. <https://doi.org/10.1007/s10964-017-0752-y>
- Duggan, M. y Tressoldi, P. (2018). Predictive physiological anticipatory activity preceding seemingly unpredictable stimuli: An update of Mossbridge et al's meta-analysis. *F1000Research*, *7*, 407. <https://doi.org/10.12688/f1000research.14330.2>
- Eberth, J. y Sedlmeier, P. (2012). The Effects of Mindfulness Meditation: A Meta-Analysis. *Mindfulness*, *3*(3), 174-189. <https://doi.org/10.1007/s12671-012-0101-x>
- Edelson, S. M. y Reyna, V. F. (2023). Dual and multi-process models of adolescent risk taking. En B. Halpern-Felsher (Ed.), *Encyclopedia of Child and Adolescent Health (First Edition)* (pp. 284-293). Academic Press. <https://doi.org/10.1016/B978-0-12-818872-9.00150-3>

- Engelmann, J. B. y Hare, T. A. (2018). Emotions can bias decision-making processes by promoting specific behavioral tendencies. En *The nature of emotion: Fundamental questions* (pp. 355-359). Oxford University Press.
<https://www.zora.uzh.ch/id/eprint/165573>
- Epstein, S. (1994). Integration of the cognitive and the psychodynamic unconscious. *American Psychologist*, 49(8), 709-724. <https://doi.org/10.1037/0003-066X.49.8.709>
- Ernst, M. y Paulus, M. P. (2005). Neurobiology of Decision Making: A Selective Review from a Neurocognitive and Clinical Perspective. *Biological Psychiatry*, 58(8), 597-604. <https://doi.org/10.1016/j.biopsych.2005.06.004>
- Eurostat. (2023). *EUROPOP2023—Population projections at national level (2022-2100)*.
https://ec.europa.eu/eurostat/cache/metadata/en/proj_23n_esms.htm
- Evans, J. St. B. T. (2008). Dual-Processing Accounts of Reasoning, Judgment, and Social Cognition. *Annual Review of Psychology*, 59(1), 255-278.
<https://doi.org/10.1146/annurev.psych.59.103006.093629>
- Fahmy, R., Wasfi, M., Mamdouh, R., Moussa, K., Wahba, A., Wittemann, M., Hirjak, D., Kubera, K. M., Wolf, N. D., Sambataro, F. y Wolf, R. C. (2018). Mindfulness-based interventions modulate structural network strength in patients with opioid dependence. *Addictive Behaviors*, 82, 50-56.
<https://doi.org/10.1016/J.ADDBEH.2018.02.013>
- Frankish, K. (2010). Dual-Process and Dual-System Theories of Reasoning. *Philosophy Compass*, 5(10), 914-926. <https://doi.org/10.1111/j.1747-9991.2010.00330.x>
- Frederick, S., Loewenstein, G. y O'Donoghue, T. (2002). Time Discounting and Time Preference: A Critical Review. *Journal of Economic Literature*, 40(2), 351-401.
<http://www.jstor.org/stable/2698382>

- Fuentes, P., Barrós-Loscertales, A., Bustamante, J. C., Rosell, P., Costumero, V. y Ávila, C. (2012). Individual differences in the Behavioral Inhibition System are associated with orbitofrontal cortex and precuneus gray matter volume. *Cognitive, Affective and Behavioral Neuroscience*, 12(3), 491-498.
<https://doi.org/10.3758/s13415-012-0099-5>
- Gallo, G. G., Curado, D. F., Opaleye, E. S., Donate, A. P. G., Scattone, V. V. y Noto, A. R. (2021). Impulsivity and Mindfulness among Inpatients with Alcohol Use Disorder. *Substance Use and Misuse*, 56(1), 25-32.
<https://doi.org/10.1080/10826084.2020.1833924>
- Garland, E. L., Hanley, A. W., Goldin, P. R. y Gross, J. J. (2017). Testing the mindfulness-to-meaning theory: Evidence for mindful positive emotion regulation from a reanalysis of longitudinal data. *PLOS ONE*, 12(12), e0187727.
<https://doi.org/10.1371/journal.pone.0187727>
- Goh, J. O. S., Su, Y.-S., Tang, Y.-J., McCarrey, A. C., Tereshchenko, A., Elkins, W. y Resnick, S. M. (2016). Frontal, Striatal, and Medial Temporal Sensitivity to Value Distinguishes Risk-Taking from Risk-Aversive Older Adults during Decision Making. *Journal of Neuroscience*, 36(49), 12498-12509.
<https://doi.org/10.1523/JNEUROSCI.1386-16.2016>
- Golchert, J., Smallwood, J., Jefferies, E., Liem, F., Huntenburg, J. M., Falkiewicz, M., Lauckner, M. E., Oligschläger, S., Villringer, A. y Margulies, D. S. (2017). In need of constraint: Understanding the role of the cingulate cortex in the impulsive mind. *NeuroImage*, 146, 804-813.
<https://doi.org/10.1016/j.neuroimage.2016.10.041>

- Gold, J. I. y Heekeren, H. R. (2014). Chapter 19—Neural Mechanisms for Perceptual Decision Making. En P. W. Glimcher & E. Fehr (Eds.), *Neuroeconomics (Second Edition)* (pp. 355-372). Academic Press. <https://doi.org/10.1016/B978-0-12-416008-8.00019-X>
- Gold, J. I. y Shadlen, M. N. (2007). The Neural Basis of Decision Making. *Annual Review of Neuroscience*, *30*(1), 535-574. <https://doi.org/10.1146/annurev.neuro.29.051605.113038>
- Gotink, R. A., Meijboom, R., Vernooij, M. W., Smits, M. y Hunink, M. G. M. (2016). 8-week Mindfulness Based Stress Reduction induces brain changes similar to traditional long-term meditation practice – A systematic review. *Brain and Cognition*, *108*, 32-41. <https://doi.org/10.1016/J.BANDC.2016.07.001>
- Gray, J. A. (1970). The psychophysiological basis of introversion-extraversion. *Behaviour Research and Therapy*, *8*(3), 249-266. [https://doi.org/10.1016/0005-7967\(70\)90069-0](https://doi.org/10.1016/0005-7967(70)90069-0)
- Grupe, D. W. y Nitschke, J. B. (2013). Uncertainty and anticipation in anxiety: An integrated neurobiological and psychological perspective. *Nature Reviews Neuroscience*, *14*(7), 488-501. <https://doi.org/10.1038/nrn3524>
- Gu, J., Strauss, C., Bond, R. y Cavanagh, K. (2015). How do mindfulness-based cognitive therapy and mindfulness-based stress reduction improve mental health and wellbeing? A systematic review and meta-analysis of mediation studies. *Clinical Psychology Review*, *37*, 1-12. <https://doi.org/10.1016/J.CPR.2015.01.006>
- Gupta, R., Kosciak, T. R., Bechara, A. y Tranel, D. (2011a). The amygdala and decision-making. *Neuropsychologia*, *49*(4), 760-766. <https://doi.org/10.1016/j.neuropsychologia.2010.09.029>

- Gupta, R., Koscik, T. R., Bechara, A. y Tranel, D. (2011b). The amygdala and decision-making. *Neuropsychologia*, *49*(4), 760-766.
<https://doi.org/10.1016/j.neuropsychologia.2010.09.029>
- Hamilton, K. R., Mitchell, M. R., Wing, V. C., Balodis, I. M., Bickel, W. K., Fillmore, M., Lane, S. D., Lejuez, C. W., Littlefield, A. K., Luijten, M., Mathias, C. W., Mitchell, S. H., Napier, T. C., Reynolds, B., Schütz, C. G., Setlow, B., Sher, K. J., Swann, A. C., Tedford, S. E., ... Moeller, F. G. (2015). Choice impulsivity: Definitions, measurement issues, and clinical implications. *Personality Disorders: Theory, Research, and Treatment*, *6*(2), 182-198.
<https://doi.org/10.1037/per0000099>
- Han, Y., Gao, F., Wang, X., Xia, J., Du, H., Liu, X., Cai, S., Tan, C., Fan, J. y Zhu, X. (2024). Neural correlates of risk taking in patients with obsessive-compulsive disorder during risky decision-making. *Journal of Affective Disorders*, *345*, 192-199. <https://doi.org/10.1016/j.jad.2023.10.099>
- Harms, M. P., Wang, L., Csernansky, J. G. y Barch, D. M. (2013). Structure-function relationship of working memory activity with hippocampal and prefrontal cortex volumes. *Brain Structure and Function*, *218*(1), 173-186.
<https://doi.org/10.1007/S00429-012-0391-8/TABLES/2>
- Hayes, S. C., Strosahl, K. D., Strosahl, K. y Wilson, K. G. (2003). *Acceptance and Commitment Therapy: An Experiential Approach to Behavior Change*. Guilford Publications.
- Heffner, J., Son, J.-Y. y FeldmanHall, O. (2021). Emotion prediction errors guide socially adaptive behaviour. *Nature Human Behaviour*, *5*(10), Article 10.
<https://doi.org/10.1038/s41562-021-01213-6>

- Helfinstein, S. M., Schonberg, T., Congdon, E., Karlsgodt, K. H., Mumford, J. A., Sabb, F. W., Cannon, T. D., London, E. D., Bilder, R. M. y Poldrack, R. A. (2014). Predicting risky choices from brain activity patterns. *Proceedings of the National Academy of Sciences*, *111*(7), 2470-2475. <https://doi.org/10.1073/pnas.1321728111>
- Holmes, A. J., Lee, P. H., Hollinshead, M. O., Bakst, L., Roffman, J. L., Smoller, J. W. y Buckner, R. L. (2012). Individual Differences in Amygdala-Medial Prefrontal Anatomy Link Negative Affect, Impaired Social Functioning, and Polygenic Depression Risk. *The Journal of Neuroscience*, *32*(50), 18087-18100. <https://doi.org/10.1523/JNEUROSCI.2531-12.2012>
- Hölzel, B. K., Carmody, J., Vangel, M., Congleton, C., Yerramsetti, S. M., Gard, T. y Lazar, S. W. (2011). Mindfulness practice leads to increases in regional brain gray matter density. *Psychiatry Research: Neuroimaging*, *191*(1), 36-43. <https://doi.org/10.1016/J.PSCYCHRESNS.2010.08.006>
- Honey, C. J., Kötter, R., Breakspear, M. y Sporns, O. (2007). Network structure of cerebral cortex shapes functional connectivity on multiple time scales. *Proceedings of the National Academy of Sciences*, *104*(24), 10240-10245. <https://doi.org/10.1073/pnas.0701519104>
- Hoptman, M. J., Antonius, D., Mauro, C. J., Parker, E. M. y Javitt, D. C. (2014). Cortical Thinning, Functional Connectivity, and Mood-Related Impulsivity in Schizophrenia: Relationship to Aggressive Attitudes and Behavior. *American Journal of Psychiatry*, *171*(9), 939-948. <https://doi.org/10.1176/appi.ajp.2014.13111553>

- Iidaka, T., Matsumoto, A., Ozaki, N., Suzuki, T., Iwata, N., Yamamoto, Y., Okada, T. y Sadato, N. (2006). Volume of left amygdala subregion predicted temperamental trait of harm avoidance in female young subjects. A voxel-based morphometry study. *Brain Research*, *1125*(1), 85-93. <https://doi.org/10.1016/j.brainres.2006.09.015>
- Izakson, L., Gal, S., Shahar, M., Tavor, I. y Levy, D. J. (2023). Similar functional networks predict performance in both perceptual and value-based decision tasks. *Cerebral Cortex*, *33*(6), 2669-2681. <https://doi.org/10.1093/cercor/bhac234>
- Kabat-Zinn, J. (2005). *Coming to Our Senses: Healing Ourselves and the World Through Mindfulness*. Hachette Books.
- Kabat-Zinn, J., Massion, A. O., Kristeller, J., Peterson, L. G., Fletcher, K. E., Pbert, L., Lenderking, W. R. y Santorelli, S. F. (1992). Effectiveness of a meditation-based stress reduction program in the treatment of anxiety disorders. *The American Journal of Psychiatry*, *149*(7), 936-943. <https://doi.org/10.1176/ajp.149.7.936>
- Kable, J. W. y Glimcher, P. W. (2007). The neural correlates of subjective value during intertemporal choice. *Nature Neuroscience*, *10*(12), Article 12. <https://doi.org/10.1038/nn2007>
- Kahneman, D. y Frederick, S. (2002). Representativeness Revisited: Attribute Substitution in Intuitive Judgment. En D. Griffin, D. Kahneman y T. Gilovich (Eds.), *Heuristics and Biases: The Psychology of Intuitive Judgment* (pp. 49-81). Cambridge University Press. <https://doi.org/10.1017/CBO9780511808098.004>
- Kahneman, D. y Tversky, A. (1979). Prospect Theory: An Analysis of Decision under Risk. *Econometrica*, *47*(2), 263-291. <https://doi.org/10.2307/1914185>

- Kakoschke, N., Lorenzetti, V., Caeyenberghs, K. y Verdejo-García, A. (2019). Impulsivity and body fat accumulation are linked to cortical and subcortical brain volumes among adolescents and adults. *Scientific Reports*, *9*(1), 2580. <https://doi.org/10.1038/s41598-019-38846-7>
- Kirby, K. N. y Maraković, N. N. (1996). Delay-discounting probabilistic rewards: Rates decrease as amounts increase. *Psychonomic Bulletin & Review*, *3*(1), 100-104. <https://doi.org/10.3758/BF03210748>
- Knutson, B. y Cooper, J. C. (2005). Functional magnetic resonance imaging of reward prediction. *Current Opinion in Neurology*, *18*(4), 411-417. <https://doi.org/10.1097/01.wco.0000173463.24758.f6>
- Knutson, B., Fong, G. W., Bennett, S. M., Adams, C. M. y Hommer, D. (2003). A region of mesial prefrontal cortex tracks monetarily rewarding outcomes: Characterization with rapid event-related fMRI. *NeuroImage*, *18*(2), 263-272. [https://doi.org/10.1016/s1053-8119\(02\)00057-5](https://doi.org/10.1016/s1053-8119(02)00057-5)
- Kohler, R., Lichtenstein, S. D., Cheng, A., Holmes, A., Bzdok, D., Pearlson, G. y Yip, S. W. (2023). Identification of a composite latent dimension of reward and impulsivity across clinical, behavioral and neurobiological domains among youth. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging*. <https://doi.org/10.1016/j.bpsc.2023.11.008>
- Koppel, S., Bugeja, L., Hua, P., Osborne, R., Stephens, A. N., Young, K. L., Chambers, R. y Hassed, C. (2019). Do mindfulness interventions improve road safety? A systematic review. *Accident; Analysis and Prevention*, *123*, 88-98. <http://dx.doi.org/10.1016/j.aap.2018.11.013>

- Koppel, S., Stephens, A. N., Kaviani, F., Peiris, S., Young, K. L., Chambers, R. y Hased, C. (2022). It's all in the mind: The relationship between mindfulness and nomophobia on technology engagement while driving and aberrant driving behaviours. *Transportation Research Part F: Traffic Psychology and Behaviour*, *86*, 252-262. <https://doi.org/10.1016/j.trf.2022.03.002>
- Koppel, S., Stephens, A. N., Young, K. L., Hua, P., Chambers, R. y Hased, C. (2018). What is the relationship between self-reported aberrant driving behaviors, mindfulness, and self-reported crashes and infringements? *Traffic Injury Prevention*, *19*(5), 480-487. <https://doi.org/10.1080/15389588.2018.1440083>
- Kotani, Y., Ohgami, Y., Ishiwata, T., Arai, J., Kiryu, S. y Inoue, Y. (2015). Source analysis of stimulus-preceding negativity constrained by functional magnetic resonance imaging. *Biological Psychology*, *111*, 53-64. <https://doi.org/10.1016/j.biopsycho.2015.08.005>
- Krain, A. L., Wilson, A. M., Arbuckle, R., Castellanos, F. X. y Milham, M. P. (2006). Distinct neural mechanisms of risk and ambiguity: A meta-analysis of decision-making. *NeuroImage*, *32*(1), 477-484. <https://doi.org/10.1016/j.neuroimage.2006.02.047>
- Lakey, C. E., Campbell, W. K., Brown, K. W. y Goodie, A. S. (2007). Dispositional mindfulness as a predictor of the severity of gambling outcomes. *Personality and Individual Differences*, *43*(7), 1698-1710. <https://doi.org/10.1016/j.paid.2007.05.007>
- Lambert, A. E., Simons-Morton, B. G., Cain, S. A., Weisz, S. y Cox, D. J. (2014). Considerations of a Dual-Systems Model of Cognitive Development and Risky Driving. *Journal of Research on Adolescence*, *24*(3), 541-550. <https://doi.org/10.1111/jora.12126>

- Lee, D., Park, J., Namkoong, K., Kim, I. Y. y Jung, Y.-C. (2018). Gray matter differences in the anterior cingulate and orbitofrontal cortex of young adults with Internet gaming disorder: Surface-based morphometry. *Journal of Behavioral Addictions*, 7(1), 21-30. <https://doi.org/10.1556/2006.7.2018.20>
- Lerner, J. S., Li, Y., Valdesolo, P. y Kassam, K. S. (2015). Emotion and Decision Making. *Annual Review of Psychology*, 66(1), 799-823. <https://doi.org/10.1146/annurev-psych-010213-115043>
- Levita, L., Bois, C., Healey, A., Smyllie, E., Papakonstantinou, E., Hartley, T. y Lever, C. (2014). The Behavioural Inhibition System, anxiety and hippocampal volume in a non-clinical population. *Biology of Mood and Anxiety Disorders*, 4(1). <https://doi.org/10.1186/2045-5380-4-4>
- Levy, I. (2017). Neuroanatomical Substrates for Risk Behavior. *Neuroscientist*, 23(3), 275-286. <https://doi.org/10.1177/1073858416672414>
- Levy, I., Snell, J., Nelson, A. J., Rustichini, A. y Glimcher, P. W. (2010). Neural Representation of Subjective Value Under Risk and Ambiguity. *Journal of Neurophysiology*, 103(2), 1036-1047. <https://doi.org/10.1152/jn.00853.2009>
- Li, M., Wei, D., Yang, W., Zhang, J. y Qiu, J. (2019). Neuroanatomical correlates of extraversion: A test-retest study implicating gray matter volume in the caudate nucleus. *NeuroReport*, 30(14), 953-959. <https://doi.org/10.1097/WNR.0000000000001306>
- Li, X., Hu, P. y Liu, J. (2019). The neuroanatomical correlates of individual differences in delay discounting: A voxel-based morphometry study. *Journal of Pacific Rim Psychology*, 13. <https://doi.org/10.1017/prp.2019.22>

- Li, X., Xu, S., Fang, Z. y Smith, A. (2020). Individual intelligence and brain neural correlates associated with outcome expectancies for risk behaviors in adults. *Neuroscience Letters*, 725. <https://doi.org/10.1016/j.neulet.2019.134720>
- Linehan, M. M. (1993). *Skills training manual for treating borderline personality disorder* (pp. xii, 180). Guilford Press.
- Liu, X., Xiao, R., Tang, F. y Wu, S. (2021). Mindfulness-based intervention to reduce multiple health risk behaviors in Chinese undergraduates: a randomized controlled trial. *Current Psychology*, 1-12. <https://doi.org/10.1007/S12144-021-01372-9/FIGURES/2>
- Loewenstein, G. F., Hsee, C. K., Weber, E. U. y Welch, N. (2001). Risk as Feelings. *Psychological Bulletin*, 127(2), 267-286. <https://doi.org/10.1037/0033-2909.127.2.267>
- Loganathan, K. y Tiego, J. (2023). Value-based decision-making network functional connectivity correlates with substance use and delay discounting behaviour among young adults. *NeuroImage: Clinical*, 38. <https://doi.org/10.1016/j.nicl.2023.103424>
- Luna, B., Padmanabhan, A. y O'Hearn, K. (2010). What has fMRI told us about the Development of Cognitive Control through Adolescence? *Brain and Cognition*, 72(1), 101-113. <https://doi.org/10.1016/j.bandc.2009.08.005>
- MacKillop, J., Amlung, M. T., Few, L. R., Ray, L. A., Sweet, L. H. y Munafò, M. R. (2011). Delayed reward discounting and addictive behavior: A meta-analysis. *Psychopharmacology*, 216(3), 305-321. <https://doi.org/10.1007/s00213-011-2229-0>

- Maddox, J. (2011). *The effects of mindfulness-based relapse prevention on impulsivity and mindfulness* [PhD., Institute of Transpersonal Psychology].
<https://www.proquest.com/docview/904546466/abstract/9F0DBEFF4824ACDPQ/1>
- Maldonado, A., Serra, S., Catena, A., Cándido, A. y Megías, A. (2016). Modifying Evaluations and Decisions in Risky Situations. *The Spanish Journal of Psychology*, 19, E53. <https://doi.org/10.1017/sjp.2016.51>
- Marlatt, G. A. y Witkiewitz, K. (2002). Harm reduction approaches to alcohol use: Health promotion, prevention, and treatment. *Addictive Behaviors*, 27(6), 867-886. [https://doi.org/10.1016/s0306-4603\(02\)00294-0](https://doi.org/10.1016/s0306-4603(02)00294-0)
- McClure, S. M., Laibson, D. I., Loewenstein, G. y Cohen, J. D. (2004). Separate Neural Systems Value Immediate and Delayed Monetary Rewards. *Science*, 306(5695), 503-507. <https://doi.org/10.1126/science.1100907>
- McIlvain, G., Clements, R. G., Magoon, E. M., Spielberg, J. M., Telzer, E. H. y Johnson, C. L. (2020). Viscoelasticity of reward and control systems in adolescent risk taking. *NeuroImage*, 215. <https://doi.org/10.1016/j.neuroimage.2020.116850>
- Meade, C. S., Bell, R. P., Towe, S. L. y Hall, S. A. (2020). Cocaine-related alterations in fronto-parietal gray matter volume correlate with trait and behavioral impulsivity. *Drug and Alcohol Dependence*, 206. <https://doi.org/10.1016/j.drugalcdep.2019.107757>
- Megías, A., Cándido, A., Catena, A., Molinero, S. y Maldonado, A. (2014). The Passenger Effect: Risky Driving is a Function of the Driver-Passenger Emotional Relationship. *Applied Cognitive Psychology*, 28(2), 254-258. <https://doi.org/10.1002/acp.2989>

- Megías, A., Cándido, A., Maldonado, A. y Catena, A. (2018). Neural correlates of risk perception as a function of risk level: An approach to the study of risk through a daily life task. *Neuropsychologia*, *119*, 464-473. <https://doi.org/10.1016/j.neuropsychologia.2018.09.012>
- Megías, A., Cortes, A., Maldonado, A. y Cándido, A. (2017). Using negative emotional feedback to modify risky behavior of young moped riders. *Traffic Injury Prevention*, *18*(4), 351-356. <https://doi.org/10.1080/15389588.2016.1205189>
- Megías, A., Di Stasi, L. L., Maldonado, A., Catena, A. y Cándido, A. (2014). Emotion-laden stimuli influence our reactions to traffic lights. *Transportation Research Part F: Traffic Psychology and Behaviour*, *22*, 96-103. <https://doi.org/10.1016/j.trf.2013.09.017>
- Megías, A., López-Riañez, M. y Cándido, A. (2013). Conductas urgentes y evaluativas en función del nivel de riesgo en situaciones de conducción. *Anales de Psicología*, *29*(3), Article 3. <https://doi.org/10.6018/analesps.29.3.145451>
- Megías, A., Maldonado, A., Cándido, A. y Catena, A. (2011). Emotional modulation of urgent and evaluative behaviors in risky driving scenarios. *Accident Analysis & Prevention*, *43*(3), 813-817. <https://doi.org/10.1016/j.aap.2010.10.029>
- Megías, A., Navas, J. F., Petrova, D., Cándido, A., Maldonado, A., Garcia-Retamero, R. y Catena, A. (2015). Neural mechanisms underlying urgent and evaluative behaviors: An fMRI study on the interaction of automatic and controlled processes. *Human Brain Mapping*, *36*(8), 2853-2864. <https://doi.org/10.1002/hbm.22812>

- Megías, A., Torres, M. A., Catena, A., Cándido, A. y Maldonado, A. (2018). Electrophysiological brain indices of risk behavior modification induced by contingent feedback. *International Journal of Psychophysiology*, *124*, 43-53. <https://doi.org/10.1016/j.ijpsycho.2018.01.003>
- Megías-Robles, A., Cándido, A., Maldonado, A., Baltruschat, S. y Catena, A. (2022). Differences between risk perception and risk-taking are related to impulsivity levels. *International Journal of Clinical and Health Psychology*, *22*(3). <https://doi.org/10.1016/j.ijchp.2022.100318>
- Megías-Robles, A., Sánchez-López, M. T., Gómez-Leal, R., Cabello, R., Gutiérrez-Cobo, M. J. y Fernández-Berrocal, P. (2023). Impulsivity and sensitivity to reward as mediating factors of the negative relationship between emotional intelligence and health-related risk-taking: Evidence from a sample of university students. *BMC Psychology*, *11*(1), 386. <https://doi.org/10.1186/s40359-023-01417-7>
- Melis, M., Blommaert, J., Radwan, A., Smeets, A., Van der Gucht, K., Deprez, S. y Sunaert, S. (2023). Structural Brain Changes After a Mindfulness-Based Intervention in Breast Cancer Survivors with Cognitive Complaints. *Mindfulness*, *14*(7), 1606-1621. <https://doi.org/10.1007/s12671-023-02140-5>
- Menon, V. y D'Esposito, M. (2022). The role of PFC networks in cognitive control and executive function. *Neuropsychopharmacology*, *47*(1), Article 1. <https://doi.org/10.1038/s41386-021-01152-w>
- Mento, G., Tarantino, V., Vallesi, A. y Bisiacchi, P. S. (2015). Spatiotemporal Neurodynamics Underlying Internally and Externally Driven Temporal Prediction: A High Spatial Resolution ERP Study. *Journal of Cognitive Neuroscience*, *27*(3), 425-439. https://doi.org/10.1162/jocn_a_00715

- Miglin, R., Bounoua, N., Goodling, S., Sheehan, A., Spielberg, J. M. y Sadeh, N. (2019). Cortical thickness links impulsive personality traits and risky behavior. *Brain Sciences*, *9*(12), 373. <https://doi.org/10.3390/brainsci9120373>
- Mischel, W. y Shoda, Y. (1995). A cognitive-affective system theory of personality: Reconceptualizing situations, dispositions, dynamics, and invariance in personality structure. *Psychological Review*, *102*(2), 246-268. <https://doi.org/10.1037/0033-295x.102.2.246>
- Mohammadi, B., Hammer, A., Miedl, S. F., Wiswede, D., Marco-Pallarés, J., Herrmann, M. y Münte, T. F. (2016). Intertemporal choice behavior is constrained by brain structure in healthy participants and pathological gamblers. *Brain Structure and Function*, *221*(6), 3157-3170. <https://doi.org/10.1007/s00429-015-1093-9>
- Morelli, M., Casagrande, M. y Forte, G. (2022). Decision Making: A Theoretical Review. *Integrative Psychological and Behavioral Science*, *56*(3), 609-629. <https://doi.org/10.1007/s12124-021-09669-x>
- Moreno-López, L., Catena, A., Fernández-Serrano, M. J., Delgado-Rico, E., Stamatakis, E. A., Pérez-García, M. y Verdejo-García, A. (2012). Trait impulsivity and prefrontal gray matter reductions in cocaine dependent individuals. *Drug and Alcohol Dependence*, *125*(3), 208-214. <https://doi.org/10.1016/j.drugalcdep.2012.02.012>
- Moreno-López, L., Soriano-Mas, C., Delgado-Rico, E., Rio-Valle, J. S. y Verdejo-García, A. (2012). Brain Structural Correlates of Reward Sensitivity and Impulsivity in Adolescents with Normal and Excess Weight. *PLoS ONE*, *7*(11). <https://doi.org/10.1371/journal.pone.0049185>

- Mossbridge, J., Tressoldi, P. E., Utts, J., Ives, J., Radin, D. y Jonas, W. (2014). Predicting the unpredictable: Critical analysis and practical implications of predictive anticipatory activity. *Frontiers in Human Neuroscience*, 8. <https://doi.org/10.3389/fnhum.2014.00146>
- Muhlert, N. y Lawrence, A. D. (2015). Brain structure correlates of emotion-based rash impulsivity. *NeuroImage*, 115, 138-146. <https://doi.org/10.1016/J.NEUROIMAGE.2015.04.061>
- Murphy, C. y MacKillop, J. (2012). Living in the here and now: Interrelationships between impulsivity, mindfulness, and alcohol misuse. *Psychopharmacology*, 219(2), 527-536. <https://doi.org/10.1007/s00213-011-2573-0>
- Nasirivanaki, Z., ArianNik, M., Abbassian, A., Mahmoudi, E., Roufigari, N., Shahzadi, S., Nasirivanaki, M. y Bahrami, B. (2015). Prediction of individual differences in risky behavior in young adults via variations in local brain structure. *Frontiers in Neuroscience*, 9. <https://doi.org/10.3389/fnins.2015.00359>
- Navas, J. F., Billieux, J., Perandrés-Gómez, A., López-Torrecillas, F., Cándido, A. y Perales, J. C. (2017). Impulsivity traits and gambling cognitions associated with gambling preferences and clinical status. *International Gambling Studies*, 17(1), 102-124. <https://doi.org/10.1080/14459795.2016.1275739>
- Navas, J. F., Martín-Pérez, C., Petrova, D., Verdejo-García, A., Cano, M., Sagripanti-Mazuquín, O., Perandrés-Gómez, A., López-Martín, Á., Cordovilla-Guardia, S., Megías, A., Perales, J. C. y Vilar-López, R. (2019). Sex differences in the association between impulsivity and driving under the influence of alcohol in young adults: The specific role of sensation seeking. *Accident Analysis & Prevention*, 124, 174-179. <https://doi.org/10.1016/j.aap.2018.12.024>

- Niendam, T. A., Laird, A. R., Ray, K. L., Dean, Y. M., Glahn, D. C. y Carter, C. S. (2012). Meta-analytic evidence for a superordinate cognitive control network subserving diverse executive functions. *Cognitive, Affective and Behavioral Neuroscience*, *12*(2), 241-268. <https://doi.org/10.3758/s13415-011-0083-5>
- Nogueira, R., Abolafia, J. M., Drugowitsch, J., Balaguer-Ballester, E., Sanchez-Vives, M. V. y Moreno-Bote, R. (2017). Lateral orbitofrontal cortex anticipates choices and integrates prior with current information. *Nature Communications*, *8*. <https://doi.org/10.1038/ncomms14823>
- Novoa, A. M., Pérez, K., Santamariña-Rubio, E., Marí-Dell'Olmo, M., Ferrando, J., Peiró, R., Tobías, A., Zori, P. y Borrell, C. (2010). Impact of the Penalty Points System on Road Traffic Injuries in Spain: A Time–Series Study. *American Journal of Public Health*, *100*(11), 2220-2227. <https://doi.org/10.2105/AJPH.2010.192104>
- Owens, M. M., Gray, J. C., Amlung, M. T., Oshri, A., Sweet, L. H. y MacKillop, J. (2017). Neuroanatomical foundations of delayed reward discounting decision making. *NeuroImage*, *161*, 261-270. <https://doi.org/10.1016/j.neuroimage.2017.08.045>
- Owens, M. M., Hyatt, C. S., Gray, J. C., Miller, J. D., Lynam, D. R., Hahn, S., Allgaier, N., Potter, A. y Garavan, H. (2020). Neuroanatomical correlates of impulsive traits in children aged 9 to 10. *Journal of Abnormal Psychology*, *129*(8), 831-844. <https://doi.org/10.1037/abn0000627>
- Parcet, M. A., Adrián-Ventura, J., Costumero, V. y Ávila, C. (2020). Individual Differences in Hippocampal Volume as a Function of BMI and Reward Sensitivity. *Frontiers in Behavioral Neuroscience*, *14*. <https://doi.org/10.3389/fnbeh.2020.00053>

- Paulus, M. P., Hozack, N. E., Zauscher, B. E., Frank, L., Brown, G. G., McDowell, J. y Braff, D. L. (2002). Parietal dysfunction is associated with increased outcome-related decision-making in schizophrenia patients. *Biological Psychiatry*, *51*(12), 995-1004. [https://doi.org/10.1016/S0006-3223\(01\)01358-0](https://doi.org/10.1016/S0006-3223(01)01358-0)
- Pehlivanova, M., Wolf, D. H., Sotiras, A., Kaczkurkin, A. N., Moore, T. M., Ciric, R., Cook, P. A., Garza, A. G. de L., Rosen, A. F. G., Ruparel, K., Sharma, A., Shinohara, R. T., Roalf, D. R., Gur, R. C., Davatzikos, C., Gur, R. E., Kable, J. W. y Satterthwaite, T. D. (2018). Diminished Cortical Thickness Is Associated with Impulsive Choice in Adolescence. *Journal of Neuroscience*, *38*(10), 2471-2481. <https://doi.org/10.1523/JNEUROSCI.2200-17.2018>
- Perales, J. C., Verdejo-Garcia, A., Moya, M., Lozano, Ó. y Pérez-Garcia, M. (2009). Bright and dark sides of impulsivity: Performance of women with high and low trait impulsivity on neuropsychological tasks. *Journal of Clinical and Experimental Neuropsychology*, *31*(8), 927-944. <https://doi.org/10.1080/13803390902758793>
- Pernet, C. R., Belov, N., Delorme, A. y Zammit, A. (2021). Mindfulness related changes in grey matter: A systematic review and meta-analysis. *Brain Imaging and Behavior*, *15*, 2720-2730. <https://doi.org/10.1007/s11682-021-00453-4>
- Peters, J. y Büchel, C. (2010). Neural representations of subjective reward value. *Behavioural Brain Research*, *213*(2), 135-141. <https://doi.org/10.1016/j.bbr.2010.04.031>
- Peters, J. y Büchel, C. (2011). The neural mechanisms of inter-temporal decision-making: Understanding variability. *Trends in Cognitive Sciences*, *15*(5), 227-239. <https://doi.org/10.1016/j.tics.2011.03.002>

- Peters, J. R., Erisman, S. M., Upton, B. T., Baer, R. A. y Roemer, L. (2011). A Preliminary Investigation of the Relationships Between Dispositional Mindfulness and Impulsivity. *Mindfulness*, 2(4), 228-235. <https://doi.org/10.1007/s12671-011-0065-2>
- Pickut, B. A., Van Hecke, W., Kerckhofs, E., Mariën, P., Vanneste, S., Cras, P. y Parizel, P. M. (2013). Mindfulness based intervention in Parkinson's disease leads to structural brain changes on MRI: A randomized controlled longitudinal trial. *Clinical Neurology and Neurosurgery*, 115(12), 2419-2425. <https://doi.org/10.1016/j.clineuro.2013.10.002>
- Poudel, R., Riedel, M. C., Salo, T., Flannery, J. S., Hill-Bowen, L. D., Eickhoff, S. B., Laird, A. R. y Sutherland, M. T. (2020). Common and distinct brain activity associated with risky and ambiguous decision-making. *Drug and Alcohol Dependence*, 209, 107884. <https://doi.org/10.1016/j.drugalcdep.2020.107884>
- Quaglia, J. T., Braun, S. E., Freeman, S. P., McDaniel, M. A. y Brown, K. W. (2016). Meta-Analytic Evidence for Effects of Mindfulness Training on Dimensions of Self-Reported Dispositional Mindfulness. *Psychological Assessment*, 28(7), 803-818. <https://doi.org/10.1037/PAS0000268>
- Rangel, A., Camerer, C. y Montague, P. R. (2008). A framework for studying the neurobiology of value-based decision making. *Nature Reviews Neuroscience*, 9(7), Article 7. <https://doi.org/10.1038/nrn2357>
- Reniers, R. L. E. P., Murphy, L., Lin, A., Bartolomé, S. P. y Wood, S. J. (2016). Risk Perception and Risk-Taking Behaviour during Adolescence: The Influence of Personality and Gender. *PLOS ONE*, 11(4), e0153842. <https://doi.org/10.1371/journal.pone.0153842>

- Rescorla, R. A. (1994). Control of instrumental performance by Pavlovian and instrumental stimuli. *Journal of Experimental Psychology. Animal Behavior Processes*, 20(1), 44-50. <https://doi.org/10.1037/0097-7403.20.1.44>
- Reyna, V. F. (2004). How People Make Decisions That Involve Risk: A Dual-Processes Approach. *Current Directions in Psychological Science*, 13(2), 60-66. <https://doi.org/10.1111/j.0963-7214.2004.00275.x>
- Reyna, V. F. y Farley, F. (2006). Risk and Rationality in Adolescent Decision Making: Implications for Theory, Practice, and Public Policy. *Psychological Science in the Public Interest*, 7(1), 1-44. <https://doi.org/10.1111/j.1529-1006.2006.00026.x>
- Reynolds, B., Ortengren, A., Richards, J. B. y de Wit, H. (2006). Dimensions of impulsive behavior: Personality and behavioral measures. *Personality and Individual Differences*, 40(2), 305-315. <https://doi.org/10.1016/j.paid.2005.03.024>
- Rilling, J. K. y Sanfey, A. G. (2011). The Neuroscience of Social Decision-Making. *Annual Review of Psychology*, 62(1), 23-48. <https://doi.org/10.1146/annurev.psych.121208.131647>
- Roemer, L., Williston, S. K. y Rollins, L. G. (2015). Mindfulness and emotion regulation. *Current Opinion in Psychology*, 3, 52-57. <https://doi.org/10.1016/j.copsyc.2015.02.006>
- Rolls, E. T. (2023). Emotion, motivation, decision-making, the orbitofrontal cortex, anterior cingulate cortex, and the amygdala. *Brain Structure and Function*, 228(5), 1201-1257. <https://doi.org/10.1007/s00429-023-02644-9>
- Royuela-Colomer, E., Fernández-González, L. y Orue, I. (2021). Longitudinal Associations between Internalizing Symptoms, Dispositional Mindfulness, Rumination and Impulsivity in Adolescents. *Journal of Youth and Adolescence*, 50(10), 2067-2078. <https://doi.org/10.1007/s10964-021-01476-2>

- Ruiz de Lara, C. M., Navas, J. F., Soriano-Mas, C., Sescousse, G. y Perales, J. C. (2018). Regional grey matter volume correlates of gambling disorder, gambling-related cognitive distortions, and emotion-driven impulsivity. *International Gambling Studies*, *18*(2), 195-216. <https://doi.org/10.1080/14459795.2018.1448427>
- Sadeh, N., Miglin, R., Bounoua, N., Sheehan, A. y Spielberg, J. M. (2023). Development of a cortical delay discounting assay: A potential biomarker of externalizing disorders. *Psychological Medicine*, *53*(4), 1143-1150. <https://doi.org/10.1017/S003329172100252X>
- Sanfey, A. G. y Chang, L. J. (2008). Multiple Systems in Decision Making. *Annals of the New York Academy of Sciences*, *1128*(1), 53-62. <https://doi.org/10.1196/annals.1399.007>
- Santarnecchi, E., D'Arista, S., Egiziano, E., Gardi, C., Petrosino, R., Vatti, G., Reda, M. y Rossi, A. (2014). Interaction between Neuroanatomical and Psychological Changes after Mindfulness-Based Training. *PLOS ONE*, *9*(10), e108359. <https://doi.org/10.1371/JOURNAL.PONE.0108359>
- Scott-Parker, B. y Weston, L. (2017). Sensitivity to reward and risky driving, risky decision making, and risky health behaviour: A literature review. *Transportation Research Part F: Traffic Psychology and Behaviour*, *49*, 93-109. <https://doi.org/10.1016/j.trf.2017.05.008>
- Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., Reiss, A. L. y Greicius, M. D. (2007). Dissociable Intrinsic Connectivity Networks for Salience Processing and Executive Control. *Journal of Neuroscience*, *27*(9), 2349-2356. <https://doi.org/10.1523/JNEUROSCI.5587-06.2007>
- Segal, Z. V., Williams, J. M. G. y Teasdale, J. D. (2002). *Mindfulness-based cognitive therapy for depression: A new approach to preventing relapse*. Guilford Press.

- Shook, N. J., Delaney, R. K., Strough, J., Wilson, J. M., Sevi, B. y Altman, N. (2021). Playing it safe: Dispositional mindfulness partially accounts for age differences in health and safety risk-taking propensity. *Current Psychology*, *40*(5), 2142-2152. <https://doi.org/10.1007/s12144-019-0137-3>
- Si, Y., Wu, X., Li, F., Zhang, L., Duan, K., Li, P., Song, L., Jiang, Y., Zhang, T., Zhang, Y., Chen, J., Gao, S., Biswal, B., Yao, D. y Xu, P. (2019). Different Decision-Making Responses Occupy Different Brain Networks for Information Processing: A Study Based on EEG and TMS. *Cerebral Cortex*, *29*(10), 4119-4129. <https://doi.org/10.1093/cercor/bhy294>
- Siew, S. y Yu, J. (2023). Mindfulness-based randomized controlled trials led to brain structural changes: An anatomical likelihood meta-analysis. *Scientific Reports*, *13*(1), Article 1. <https://doi.org/10.1038/s41598-023-45765-1>
- Slovic, P., Finucane, M. L., Peters, E. y MacGregor, D. G. (2004). Risk as Analysis and Risk as Feelings: Some Thoughts about Affect, Reason, Risk, and Rationality. *Risk Analysis*, *24*(2), 311-322. <https://doi.org/10.1111/j.0272-4332.2004.00433.x>
- Slovic, P., Finucane, M. L., Peters, E. y MacGregor, D. G. (2007). The affect heuristic. *European Journal of Operational Research*, *177*(3), 1333-1352. <https://doi.org/10.1016/j.ejor.2005.04.006>
- Smith, K. E., Mason, T. B., Crosby, R. D., Engel, S. G. y Wonderlich, S. A. (2019). A multimodal, naturalistic investigation of relationships between behavioral impulsivity, affect, and binge eating. *Appetite*, *136*, 50-57. <https://doi.org/10.1016/j.appet.2019.01.014>
- Sokolov, A. A., Miall, R. C. y Ivry, R. B. (2017). The Cerebellum: Adaptive Prediction for Movement and Cognition. *Trends in cognitive sciences*, *21*(5), 313-332. <https://doi.org/10.1016/j.tics.2017.02.005>

- Steinberg, L. (2008). A social neuroscience perspective on adolescent risk-taking. *Developmental Review, 28*(1), 78-106. <https://doi.org/10.1016/j.dr.2007.08.002>
- Steinberg, L. (2010). A dual systems model of adolescent risk-taking. *Developmental Psychobiology, 52*(3), 216-224. <https://doi.org/10.1002/dev.20445>
- Stephens, A. N., Koppel, S., Young, K. L., Chambers, R. y Hased, C. (2018). Associations between self-reported mindfulness, driving anger and aggressive driving. *Transportation Research Part F: Traffic Psychology and Behaviour, 56*, 149-155. <https://doi.org/10.1016/j.trf.2018.04.011>
- Story, G., Vlaev, I., Seymour, B., Darzi, A. y Dolan, R. (2014). Does temporal discounting explain unhealthy behavior? A systematic review and reinforcement learning perspective. *Frontiers in Behavioral Neuroscience, 8*. <https://doi.org/10.3389/fnbeh.2014.00076>
- Tang, Y.-Y., Hölzel, B. K. y Posner, M. I. (2015). The neuroscience of mindfulness meditation. *Nature Reviews. Neuroscience, 16*(4), 213-225. <https://doi.org/10.1038/nrn3916>
- Tingaz, E. O., Ekiz, M. A. y Çakmak, S. (2022). Examination of mindfulness and impulsiveness in university student-athletes in terms of sports injury development history. *Current Psychology, 41*(8), 5134-5142. <https://doi.org/10.1007/s12144-020-01024-4>
- Tomlinson, E. R., Yousaf, O., Vittersø, A. D. y Jones, L. (2018). Dispositional Mindfulness and Psychological Health: A Systematic Review. *Mindfulness, 9*(1), 23-43. <https://doi.org/10.1007/s12671-017-0762-6>

- Torres, A., Catena, A., Megías, A., Maldonado, A., Cándido, A., Verdejo-García, A. y Perales, J. (2013). Emotional and non-emotional pathways to impulsive behavior and addiction. *Frontiers in Human Neuroscience*, 7. <https://www.frontiersin.org/articles/10.3389/fnhum.2013.00043>
- Torrubia, R., Ávila, C., Moltó, J. y Caseras, X. (2001). The Sensitivity to Punishment and Sensitivity to Reward Questionnaire (SPSRQ) as a measure of Gray's anxiety and impulsivity dimensions. *Personality and Individual Differences*, 31(6), 837-862. [https://doi.org/10.1016/S0191-8869\(00\)00183-5](https://doi.org/10.1016/S0191-8869(00)00183-5)
- Tremblay, S., Sharika, K. M. y Platt, M. L. (2017). Social Decision-Making and the Brain: A Comparative Perspective. *Trends in Cognitive Sciences*, 21(4), 265-276. <https://doi.org/10.1016/j.tics.2017.01.007>
- Tschernegg, M., Pletzer, B., Schwartenbeck, P., Ludersdorfer, P., Hoffmann, U. y Kronbichler, M. (2015). Impulsivity relates to striatal gray matter volumes in humans: Evidence from a delay discounting paradigm. *Frontiers in Human Neuroscience*, 9, 1-9. <https://doi.org/10.3389/fnhum.2015.00384>
- Tymula, A., Rosenberg Belmaker, L. A., Ruderman, L., Glimcher, P. W. y Levy, I. (2013). Like cognitive function, decision making across the life span shows profound age-related changes. *Proceedings of the National Academy of Sciences*, 110(42), 17143-17148. <https://doi.org/10.1073/pnas.1309909110>
- Urošević, S., Collins, P., Muetzel, R., Schissel, A., Lim, K. O. y Luciana, M. (2015). Effects of reward sensitivity and regional brain volumes on substance use initiation in adolescence. *Social Cognitive and Affective Neuroscience*, 10(1), 106-113. <https://doi.org/10.1093/scan/nsu022>

- van der Pligt, J. (2015). Decision Making, Psychology of. En J. D. Wright (Ed.), *International Encyclopedia of the Social & Behavioral Sciences (Second Edition)* (pp. 917-922). Elsevier. <https://doi.org/10.1016/B978-0-08-097086-8.24014-2>
- Van Leijenhorst, L., Moor, B. G., Op de Macks, Z. A., Rombouts, S. A. R. B., Westenberg, P. M. y Crone, E. A. (2010). Adolescent risky decision-making: Neurocognitive development of reward and control regions. *NeuroImage*, *51*(1), 345-355. <https://doi.org/10.1016/j.neuroimage.2010.02.038>
- Vanzhula, I. A. y Levinson, C. A. (2020). Mindfulness in the Treatment of Eating Disorders: Theoretical Rationale and Hypothesized Mechanisms of Action. *Mindfulness*, *11*(5), 1090-1104. <https://doi.org/10.1007/s12671-020-01343-4>
- Verdejo-Garcia, A., Chong, T. T.-J., Stout, J. C., Yücel, M. y London, E. D. (2018). Stages of dysfunctional decision-making in addiction. *Pharmacology Biochemistry and Behavior*, *164*, 99-105. <https://doi.org/10.1016/j.pbb.2017.02.003>
- Verdejo-Garcia, A., Tiego, J., Kakoschke, N., Moskovsky, N., Voigt, K., Anderson, A., Koutoulogenis, J., Lubman, D. I. y Bellgrove, M. A. (2021). A unified online test battery for cognitive impulsivity reveals relationships with real-world impulsive behaviours. *Nature Human Behaviour*, *5*(11), 1562-1577. <https://doi.org/10.1038/s41562-021-01127-3>
- Vidrine, J. I., Spears, C. A., Heppner, W. L., Reitzel, L. R., Marcus, M. T., Cinciripini, P. M., Waters, A. J., Li, Y., Nguyen, N. T. T., Cao, Y., Tindle, H. A., Fine, M., Safranek, L. V. y Wetter, D. W. (2016). Efficacy of mindfulness-based addiction treatment (MBAT) for smoking cessation and lapse recovery: A randomized clinical trial. *Journal of Consulting and Clinical Psychology*, *84*(9), 824-838. <https://doi.org/10.1037/ccp0000117>

- Von Neumann, J. y Morgenstern, O. (1944). *Theory of games and economic behavior*. Princeton University Press.
- Von Siebenthal, Z., Boucher, O., Lazzouni, L., Taylor, V., Martinu, K., Roy, M., Rainville, P., Lepore, F. y Nguyen, D. K. (2020). Expected value and sensitivity to punishment modulate insular cortex activity during risky decision making. *Scientific Reports*, *10*(1), 11920. <https://doi.org/10.1038/s41598-020-68644-5>
- Wang, H., Wen, B., Cheng, J. y Li, H. (2017). Brain structural differences between normal and obese adults and their links with lack of perseverance, negative urgency, and sensation seeking. *Scientific Reports*, *7*(40595), 1-7. <https://doi.org/10.1038/srep40595>
- Wang, M. Y., Bailey, N. W., Payne, J. E., Fitzgerald, P. B. y Fitzgibbon, B. M. (2021). A Systematic Review of Pain-Related Neural Processes in Expert and Novice Meditator. *Mindfulness*, *12*, 799-814. <https://doi.org/10.1007/s12671-020-01558-5>/Published
- Wang, Q., Chen, C., Cai, Y., Li, S., Zhao, X., Zheng, L., Zhang, H., Liu, J., Chen, C. y Xue, G. (2016). Dissociated neural substrates underlying impulsive choice and impulsive action. *NeuroImage*, *134*, 540-549. <https://doi.org/10.1016/j.neuroimage.2016.04.010>
- Wang, Q., Wang, Y., Wang, P., Peng, M., Zhang, M., Zhu, Y., Wei, S., Chen, C., Chen, X., Luo, S. y Bai, X. (2021). Neural representations of the amount and the delay time of reward in intertemporal decision making. *Human Brain Mapping*, *42*(11), 3450-3469. <https://doi.org/10.1002/hbm.25445>
- Wang, Y., Xu, Q., Luo, J., Hu, M. y Zuo, C. (2019). Effects of age and sex on subcortical volumes. *Frontiers in Aging Neuroscience*, *11*, 259. <https://doi.org/10.3389/FNAGI.2019.00259/BIBTEX>

- Watanabe, N., Bhanji, J. P., Tanabe, H. C. y Delgado, M. R. (2019). Ventromedial prefrontal cortex contributes to performance success by controlling reward-driven arousal representation in amygdala. *NeuroImage*, *202*, 116136. <https://doi.org/10.1016/J.NEUROIMAGE.2019.116136>
- Weber, E. U., Blais, A. y Betz, N. E. (2002). A domain-specific risk-attitude scale: Measuring risk perceptions and risk behaviors. *Journal of Behavioral Decision Making*, *15*(4), 263-290. <https://doi.org/10.1002/bdm.414>
- Weder, B. J. (2022). Mindfulness in the focus of the neurosciences—The contribution of neuroimaging to the understanding of mindfulness. *Frontiers in Behavioral Neuroscience*, *16*. <https://doi.org/10.3389/fnbeh.2022.928522>
- Wesley, M. J. y Bickel, W. K. (2014). Remember the future II: Meta-analyses and functional overlap of working memory and delay discounting. *Biological Psychiatry*, *75*(6), 435-448. <https://doi.org/10.1016/j.biopsych.2013.08.008>
- Whiteside, S. P. y Lynam, D. R. (2001). The Five Factor Model and impulsivity: Using a structural model of personality to understand impulsivity. *Personality and Individual Differences*, *30*(4), 669-689. [https://doi.org/10.1016/S0191-8869\(00\)00064-7](https://doi.org/10.1016/S0191-8869(00)00064-7)
- Woolgar, A., Afshar, S., Williams, M. A. y Rich, A. N. (2015). Flexible Coding of Task Rules in Frontoparietal Cortex: An Adaptive System for Flexible Cognitive Control. *Journal of Cognitive Neuroscience*, *27*(10), 1895-1911. https://doi.org/10.1162/jocn_a_00827
- World Health Organization. (2023). Global status report on road safety 2023. <https://www.who.int/publications-detail-redirect/978924008651>

- Xie, C., Ma, L., Jiang, N., Huang, R., Li, L., Gong, L., He, C., Xiao, C., Liu, W., Xu, S. y Zhang, Z. (2017). Imbalanced functional link between reward circuits and the cognitive control system in patients with obsessive-compulsive disorder. *Brain Imaging and Behavior*, *11*(4), 1099-1109. <https://doi.org/10.1007/s11682-016-9585-7>
- Xue, F., Drouman, V., Barkley-Levenson, E. E., Smith, B. J., Xue, G., Miller, L. C., Bechara, A., Lu, Z.-L. y Read, S. J. (2018). The role of the dorsal anterior insula in sexual risk: Evidence from an erotic Go/NoGo task and real-world risk-taking. *Human Brain Mapping*, *39*(4), 1555-1562. <https://doi.org/10.1002/hbm.23931>
- Yang, C.-C., Barrós-Loscertales, A., Li, M., Pinazo, D., Borchardt, V., Ávila, C. y Walter, M. (2019). Alterations in Brain Structure and Amplitude of Low-frequency after 8 weeks of Mindfulness Meditation Training in Meditation-Naïve Subjects. *Scientific Reports* *2019 9:1*, *9*(1), 1-10. <https://doi.org/10.1038/s41598-019-47470-4>
- Yang, J., Liu, Z., Liu, S., Li, L., Zheng, L. y Guo, X. (2019). The emotional stability of elders with tai chi experience in the sequential risk-taking task. *PsyCh Journal*, *8*(4), 491-502. <https://doi.org/10.1002/pchj.279>
- Yao, Y.-W., Song, K.-R., Schuck, N. W., Li, X., Fang, X.-Y., Zhang, J.-T., Heekeren, H. R. y Bruckner, R. (2023). The dorsomedial prefrontal cortex represents subjective value across effort-based and risky decision-making. *NeuroImage*, *279*. <https://doi.org/10.1016/j.neuroimage.2023.120326>
- Yates, J. F. (Ed.). (1992). *Risk-taking behavior*. John Wiley & Sons.

- Yeo, B. T. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., Roffman, J. L., Smoller, J. W., Zöllei, L., Polimeni, J. R., Fischl, B., Liu, H. y Buckner, R. L. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, *106*(3), 1125-1165. <https://doi.org/10.1152/jn.00338.2011>
- Yu, J., Rawtaer, I., Feng, L., Fam, J., Kumar, A. P., Kee-Mun Cheah, I., Honer, W. G., Su, W., Lee, Y. K., Tan, E. C., Kua, E. H. y Mahendran, R. (2021). Mindfulness intervention for mild cognitive impairment led to attention-related improvements and neuroplastic changes: Results from a 9-month randomized control trial. *Journal of Psychiatric Research*, *135*, 203-211. <https://doi.org/10.1016/J.JPSYCHIRES.2021.01.032>
- Yuan, J. P., Connolly, C. G., Henje, E., Sugrue, L. P., Yang, T. T., Xu, D. y Tymofiyeva, O. (2020). Gray Matter Changes in Adolescents Participating in a Meditation Training. *Frontiers in Human Neuroscience*, *14*, 319. <https://doi.org/10.3389/FNHUM.2020.00319>
- Zhang, Z. (2022). Functionally similar yet distinct neural mechanisms underlie different choice behaviors: ALE meta-analyses of decision-making under risk in adolescents and adults. *Developmental Review*, *66*, 101052. <https://doi.org/10.1016/j.dr.2022.101052>
- Zheng, Y., Guan, C., Wang, Z., Yang, W. y Gao, B. (2023). Electrocortical correlates of hypersensitivity to large immediate rewards in sensation seeking. *NeuroImage*, *284*, 120456. <https://doi.org/10.1016/j.neuroimage.2023.120456>
- Zuckerman, M. y Kuhlman, D. M. (2000). Personality and Risk-Taking: Common Bisocial Factors. *Journal of Personality*, *68*(6), 999-1029. <https://doi.org/10.1111/1467-6494.00124>

Zuo, X., Tang, Y., Chen, Y. y Zhou, Z. (2023). The efficacy of mindfulness-based interventions on mental health among university students: A systematic review and meta-analysis. *Frontiers in Public Health*, 11. <https://doi.org/10.3389/fpubh.2023.1259250>

AGRADECIMIENTOS

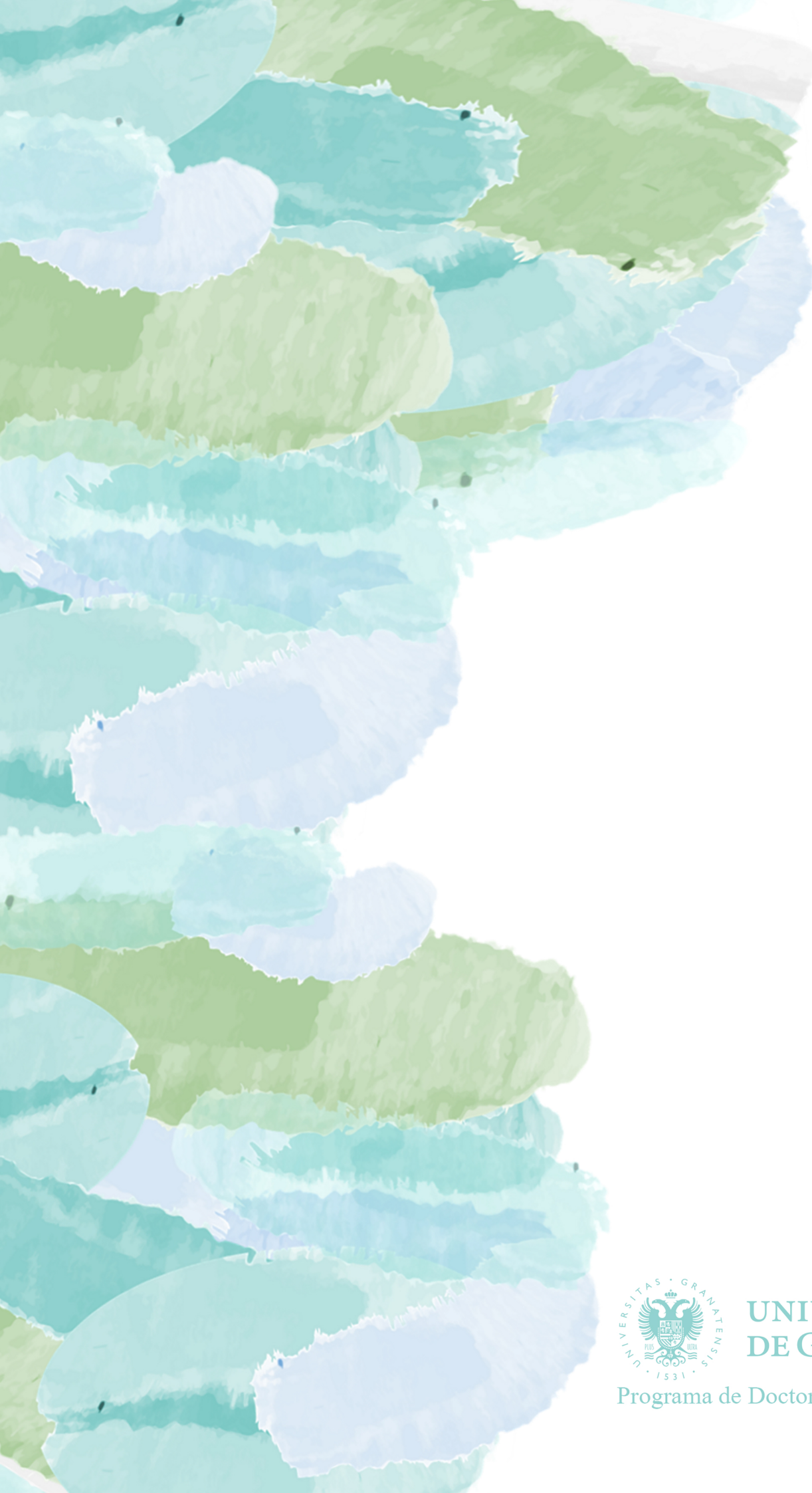
Todas las personas dependemos de la generosidad de las demás. No hay una sola situación en la que no hayamos contado con la ayuda de alguien para conseguir lo que necesitamos. Incluso cuando pensamos que estamos solas, hay algún ser generoso que, con su esfuerzo, nos facilita la existencia. Y escribir una tesis es un ejemplo precioso de generosidad infinita.

Sin mis directores, Andrés y Antonio, esta tesis no estaría escrita. Ellos me abrieron las puertas y me dejaron pasar y han sido las personas que más me han beneficiado en este proceso.

Sin mi Mami y mi Papi esta tesis, desde luego, no estaría escrita. De hecho, no habría tesis, ni alegría, ni vida, ni nada. Perquè tot el que sóc és gràcies a vosaltres.

Sin las personas que me han arropado el corazón y que me sostienen, desde mis primeros pasos, hasta el día de hoy, esta tesis tampoco estaría escrita. Porque cuando alguien te quiere, siempre recibes mucho más de lo que das. Y yo estoy repleta de amor, por todas partes.

Y a las demás personas, que lo han hecho todo más fácil, cómodo y bonito: las que han participado en los estudios, las que limpian las instalaciones, las que hacen funcionar los equipos, las que resuelven las dudas administrativas, las que arreglan los problemas técnicos, las que te enseñan otro idioma, las que te hacen el café, las que vienen a saludarte, las que encuadernan las ideas, las que te sonríen en el pasillo, las que riegan las flores, those who welcome you on the other side of the world. A todas, gracias, sin vosotras estas tesis no estaría escrita.



UNIVERSIDAD
DE GRANADA

Programa de Doctorado en Psicología