RESEARCH ARTICLE

Default-mode network dynamics are restricted during high speed discrimination in healthy aging: Associations with neurocognitive status and simulated driving behavior

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Funding information

Fundación Caja Navarra, Grant number: FBCN 15/70757; University of Navarra Friends Association

Abstract

Numerous daily tasks, including car driving, require fine visuospatial tuning. One such visuospatial ability, speed discrimination, declines with aging but its neural underpinnings remain unknown. In this study, we use fMRI to explore the effect of aging during a high speed discrimination task and its neural underpinnings, along with a complete neuropsychological assessment and a simulated driving evaluation in order to examine how they interact with each other through a multivariate regression approach. Beyond confirming that high speed discrimination performance is diminished in the elderly, we found that this deficit might be partly due to a lack of modulation in the activity and connectivity of the default mode network (DMN) in this age group, as well as an over-recruitment of frontoparietal and cerebellar regions, possibly as a compensatory mechanism. In addition, younger adults tended to drive at faster speeds, a behavior that was associated to adequate DMN dynamics and executive functioning, an effect that seems to be lost in the elderly. In summary, these results reveal how age-related declines in fine visuospatial abilities, such as high speed discrimination, were distinctly mediated by DMN functioning, a mechanism also associated to speeding behavior in a driving simulator.

KEYWORDS

aging, default mode network, driving simulator, elderly, fMRI, functional connectivity, high speed discrimination, lasso

1 | INTRODUCTION

Speed discrimination can be defined as the ability to detect and recognize the differences in the speed of moving objects, a more complex task than speed detection and processing (McKee, 1981). Despite speed being the rate of change in spatial position, and therefore containing two measurable variables –time and space– it has been proposed that speed can be perceived as a separate attribute, subject to discrimination (Lappin, Bell, Harm, & Kottas, 1975).

Speed discrimination tasks are generally used to determine a subject's speed discrimination threshold. To this end, moving light bars (Orban, de Wolf, & Maes, 1984), random-dot patterns (de Bruyn & Orban, 1988; Orban et al., 1998) or moving grating patterns (Snowden & Kavanagh, 2006; Sinaert, Van Hecke, Marchal, & Orban, 2000) are presented as a two-alternative forced-choice procedure in order to detect the threshold where the subject is no longer able to differentiate

between two stimuli with different speeds, which can be as low as 5% (McKee, 1981).

Age-related differences in speed discrimination have shown mixed results. One of the first studies comparing speed discrimination in different age groups, Brown and Bowman (1987) did not find differences between young and older adults, with stimuli moving from 3 to 8.8°/s. In contrast, Norman, Ross, Hawkes, & Long (2003) found that in the elderly, the ability to discriminate between two moving stimuli is deteriorated by up to a 71%, with females presenting worse scores compared to males. This effect was further confirmed by Raghuram, Lakshminarayanan, & Khanna (2005) who found higher thresholds in older women in speed discrimination when shorter stimuli (500 ms) were presented.

Most studies have employed relatively slow stimuli, with only a few using higher speeds (>64°/s) (de Bruyn & Orban, 1988; Orban et al., 1984). At these speeds, the detectable Weber fraction seems to

increase by up to 15% in young adults, representing the ascending arm of an U-shaped speed function, where stimuli become harder to discriminate, a finding that leads us to think that the difference in the elderly could be even wider with a high speed discrimination (HSD) task. This is important to take into account, since naturalistic stimuli, like those found in everyday activities such as car driving, move at higher speeds and can comprise real life risks.

There has been little research exploring the neural correlates of speed discrimination. In one experiment, using fluorodeoxyglucose positron emission tomography (FDG-PET) in using a “speed identification” minus “detection” paradigm, found differential activation in the right cuneus, bilateral lingual gyri, along with the left anterior cingulate and bilateral frontal operculum (Orban et al., 1998). In a similar experiment with BOLD-fMRI and using a moving random texture pattern, Sunaert et al. (2000) replicated these findings, reporting activation in the cuneus bilaterally, left and right lingual gyri and the supplementary motor area (SMA). In another experiment where attention to speed was compared to coherence of motion, differential activity in the V3 and V3a cortices, posterior cingulate cortex (PCC), precuneus, inferior parietal lobule (IPL) and medial prefrontal cortex was found (Kau et al., 2013).

These neuroimaging studies have all examined speed discrimination in a young healthy population, and as of yet no work has been done on the elderly. Since this population is susceptible to changes in speed discrimination, a change in functional activity and connectivity can be expected. The default mode network (DMN), comprised of different frontal, parietal, and temporal structures is particularly affected in the elderly, showing differences in activation and connectivity across several cognitive tasks, which are usually represented as a lack of deactivation while executing a task (Grady et al., 2010; Park, Polk, Hebrank, & Jenkins, 2010) or as a decline in functional connectivity (Andrews-Hanna et al., 2007; Dørum et al., 2016; Persson, Pudas, Nilsson, & Nyberg, 2014) or efficiency, changes that can even be found in middle-aged adults (Siman-Tov et al., 2017).

Differences in simulated driving performance between young and older adults have been widely documented, where impairments in the elderly are usually observed (Bélanger, Gagnon, & Stinchcombe, 2015; Campagne, Pebayle, & Muzet, 2004; Lee, Cameron, & Lee, 2003; Stinchcombe, Gagnon, Zhang, Montembeault, & Bedard, 2011; Urwyler et al., 2015). Other studies have focused on the relationship between simulated driving performance in the elderly and cognitive processes such as visual attention (Cuenen et al., 2015; Hoffman, McDowd, Atchley, & Dubinsky, 2005), divided attention, mental workload (Cantin, Lavallière, Simoneau, & Teasdale, 2009), processing speed, visuospatial performance and executive functioning (Shanmugaratnam, Kass, & Arruda, 2010) suggesting either deficits in these abilities or the existence of a possible underlying compensatory effect (Andrews & Westerman, 2012). An extension on how speed estimation or speed discrimination influence real or simulated driving hasn't been fully explored, despite it being an ability affected by aging. In an attempt to link driving and speed estimation, participants seated in the passenger seat were asked to estimate on-going car changes in velocity (Scialfa, Guzy, Leibowitz, Garvey, & Tyrrell, 1991), finding that older adults

showed less sensitivity to changes in velocity, a finding that might be related to traffic accidents (Hills, 1980).

Hence, here we aim to explore the age-related changes on brain activity and functional connectivity during a HSD task, as well as how these brain dynamics are related with to driving performance, as measured in a driving simulator. Our hypothesis is then threefold: (1) that the elderly group will perform worse in the HSD task; (2) that HSD performance will be related to a change in activity and functional connectivity in the elderly when compared to a younger control group; (3) and that differences in driving performance between groups will be related to performance in the HSD task and their corresponding brain activity and connectivity patterns.

2 | MATERIALS AND METHODS

2.1 | Participants

A total of 49 volunteers were recruited and classified in two groups: 24 healthy young subjects (YS) and 25 healthy older subjects (OS). Seven participants were excluded from the study (2 YS, 5 OS) due to incomplete examinations (2), distress during the MRI scan (2), possible cognitive impairment (2) and an abnormal MRI scan (1). The final number of evaluated subjects was 22 for YS (11 males, 30.3 ± 4.3 years old [descriptive results will continue to be presented in the mean $\pm$ standard deviation format]) and 20 for OS (14 males, 67.4 ± 5.2 years old).

Inclusion criteria for the YS group included subjects aged from 20 to 40 years old with a valid driving license; for the OS group, an age of more than 60 years was required, along with a valid driving license. Exclusion criteria included those associated with MRI use (metallic implants, claustrophobia, etc.), the presence of cognitive dysfunction or another neurological disease, current central nervous system modulating treatment and abnormal findings on the subjects' structural MRI scan.

All participants were right-handed (mean dexterity score 47.4 ± 3.3 out of 50) as determined by the 10 item Edinburgh handedness inventory (Oldfield, 1971). Each item was scored from 1 to 5. The total score was calculated by adding the individual item scores. A total high score indicates right-handedness and a total low score, left-handedness.

Volunteer recruitment was mainly done at the University of Navarra, through its studentship and alumni. All but 2 YS were research-naïve, and had never participated in any study before. The experimental protocol was approved by the University of Navarra Research Ethics Committee. Subjects signed a written informed consent before participating in the study.

2.2 | Neuropsychological evaluation

Additionally, we were also interested in running a complementary neuropsychological examination to test for cognitive fitness in our populations, as well as to use these results to correlate them with neuroimaging data. This examination included the followings tests:

Mini-Mental Status Exam to rule out cognitive impairment; the Geriatric Depression Scale (GDS) to screen for depressive symptoms; Trail Making Test A and B (TMT-A, TMT-B) to evaluate visual attention and divided attention; Stroop Effect test for sustained attention and inhibition; the Digit Span, both forward and backward, to test for short-term and working memory; Ray Auditory Verbal Learning Test which examines verbal memory span, long-term memory, verbal learning, and verbal recognition; the Digit Symbol Coding (from the WAIS-IV) test for processing speed index; the Wechsler Memory Scale test for short and long-term visual reproduction; the Phonological and Semantic Fluency tests; the Block Design test that measures perceptual organization; and the "Zoo Map" or Behavioral Assessment of the Dysexecutive Syndrome (BADS) test that examines planning and problem solving abilities.

In order to facilitate analysis, these tests were classified in six cognitive domains: (1) perceptual organization (block design test), (2) attention (TMT-a, TMT-b, stroop effect test), (3) verbal cognition (ray auditory verbal learning test and forward digit span test), (4) visual cognition (block design test and Wechsler Memory Scale test), (5) language (phonological and semantic fluency tests), and (6) executive (TMT-b, backwards digit span test, stroop effect test, digit symbol coding test and "Zoo Map" test). To facilitate visualization of differences between groups, t-tests results were normalized to z-scores. Also, a composite score was made for each domain by averaging individuals' scores in the corresponding tests in order to build a variable that could be evaluated during further multiple regression analyses.

2.3 | Driving simulator setup and evaluation

The driving simulator set-up used in this study (Signos, Prometeo Innovations C) consisted of a PC, a 40-inch TV, the Logitech G25 Driving Wheel, Pedals and Stick and a racing seat. The screen was positioned 1 m in front on the driver while seated and displayed a simulated first person view from the inside of a Toyota Yaris driver's seat. The driving session consisted of a 40-minute evaluation where participants had to follow a set of pre-defined verbal instructions, similar to a GPS system, (e.g. "at the roundabout, take the second exit") through a 3-stage circuit (Supporting Information Figure 1) while driving as they would in a real car. The first stage took place in an urban environment that included traffic lights, different speed limits, pedestrians crossing the street, slow traffic and roundabout crossing that lasted for approximately 2.4 km. The second stage was done on a highway where participants had to drive for 11.6 km (round trip) with a 120 km/h speed limit. In the third stage participants had to drive through a two-lane mountain road (9.6 km, roundtrip) with traffic and different speed limits. Prior to the examination, subjects were allowed to practice driving on "free mode" for up to 20 minutes, in order to get familiarized with the simulator's controls and sensitivity to steering, accelerating, and braking. Participants were continually monitored for simulator sickness symptoms during the whole evaluation.

A total of 26 telemetric parameters were registered during each driving evaluation, which were related to how fast the participant was driving (total session time, % of time moving, % of time above speed

limit, mean speed at 40, 50, 80, 100 and 120 km/h limit areas), pedal management (time with gas pedal pressed over 75%, % of time with gas pedal pressed over 75%, time braking, % of time braking, time with brake pedal pressed over 75%, % of time with brake pedal pressed over 75%, number of >5 second brakes, number of >10 second brakes), steering (number of 60°–90°, 90°–180°, 180°–270°, 270°–360° steers in 0.5 seconds) and traffic violations (two wheel sidewalk invasion, collision with other cars or objects, yellow or red traffic light skips and runovers). After each driving session a log file including these parameters was created, from which data was then extracted and analyzed.

2.4 | fMRI experimental setup and design

Subjects laid supine inside the scanner. Images were projected onto a screen and reflected by a mirror system attached to the head coil into the subjects' field of vision from which stimuli speeds were calculated. Motor finger responses were collected from a 4-key response pad (Current Designs, Inc.), placed on the subjects' abdomen. Stimuli design, presentation and data collection were done using PsychoPy2 v1.82.01 (Peirce, 2008) and Matlab (R2017b, The Mathworks Inc., Natick, MA, USA).

The objective of this experiment design was for the subject to discriminate between two visual stimuli presented sequentially with different high velocities. Thus, we asked individuals to answer which of them was faster. The experimental task consisted of a pseudo block event-related design which included rest, control and task conditions (Figure 1). Each cycle (13 in total) consisted of a Rest period, a Task block, a second Rest period and a Control block. During the Rest period subjects had to maintain visual fixation at the central cross during 8 seconds. Task blocks contained 4 trials each; a trial consisted of a white circle (2.5° radius) that crossed the screen horizontally from left to right in the superior visual hemifield followed by another white circle crossing horizontally from left to right in the inferior visual hemifield. One of the following eleven speeds was pseudorandomly assigned to each stimuli: 106°/s, 113°/s, 120°/s, 127°/s, 134°/s, 141°/s, 148°/s, 155°/s, 162°/s, 169°/s, 176°/s. Speed difference (SDF) was defined as the difference in speed between two stimuli, giving rise to either a positive (first stimulus faster than the second by 7°/s, 21°/s, 28°/s, 42°/s, 56°/s or 70°/s) or negative (second stimulus faster than the first by –14°/s, –21°/s, –28°/s, –36°/s, –42°/s, or –56°/s) value. Based on a pilot study, subjects were given 2,000 ms to indicate which of both stimuli was the fastest, by pressing the first button on the response pad if they thought it was the first stimulus or by pressing the second button if it was the second stimulus. They were not requested to answer as fast as they could, since this paradigm aimed to achieve maximum accuracy. Subsequently, another 8-second Rest period was displayed, followed by the Control block which contained 4 trials consisting of a single white square (2.5° per side) crossing the screen horizontally from left to right through the central axis at a speed of 106°/s after which the subject had to press any button in response to stimulus detection. Responses were recorded for further offline performance analysis. The duration of Task and Control blocks was of 16 seconds each, making

FIGURE 1 Speed discrimination fMRI paradigm. At each Task trial subjects were instructed to answer which of the two stimuli was faster. ITI = inter-trial interval; RT = response time

up for a total of 48 seconds per cycle. The total run duration was 10 minutes and 24 seconds. All subjects executed a similar task (two fixed speeds, up to eight trials) before entering the scanner, in order to get familiarized with the experimental task.

2.5 | Speed discrimination performance data

In this study, two behavioral variables were assessed by subject: accuracy (AC), which was defined as the sum of all incorrect task responses; and response time (RT), defined as the average time it took participants to answer all correct Task trials. AC and RT values were averaged by groups to be compared between them; they were also analyzed by SDF in order to examine how the difference in speed between stimuli impacted performance.

2.6 | fMRI data acquisition and analysis

BOLD fMRI studies were performed on a 3.0 Tesla MR scanner (Siemens TRIO, Germany) using a 16-channel head coil. A total of 210 whole-brain functional volumes using a T2*-weighted gradient echo-planar imaging (EPI) sequence (repetition time/echo time [TR/TE] = 3000/30 ms, field of view [FOV] = $192 \times 192 \text{ mm}^2$, flip-angle = 30° , 48 slices, resolution = $3 \times 3 \times 3 \text{ mm}^3$) were acquired during each session in an interleaved fashion. A total of three “dummy” volumes were discarded due to scanner stabilization.

The anatomical image was obtained using a whole-brain T1-weighted MPRAGE sequence (TR/TE = 1620/3 ms, inversion time (TI) = 950 ms, FOV = $250 \times 187 \times 160 \text{ mm}^3$, flip-angle = 15° , 160 slices, resolution = $1 \times 1 \times 1 \text{ mm}^3$). No fat suppression was employed.

Mass univariate data analysis was done using SPM12 (r6225, Wellcome Department of Imaging Neuroscience, UCL, London). To detect severe motion or artifacts we completed preliminary visual checks. Conventional preprocessing pipeline steps were followed. First, EPI images were motion-corrected and realigned to the first volume of the series and co-registered to the anatomical image. Slice time correction followed, taking slice 25 (first) as the reference slice. Functional and

anatomical images were then normalized to the coordinates of the MNI (Montreal Neurological Institute) template, version ICBM-152. A three-dimensional Gaussian smoothing kernel of 8 mm full width at half maximum (FWHM) was applied to the EPI images.

Statistical analysis was performed following the General Linear Model (GLM) and modeled with the canonical double gamma hemodynamic response function (HRF). At the first-level analysis, two conditions (task, control) were modeled for all subjects in each Group (YS, OS). In both task and control, only the timeframe between the onset of each stimulus and its response time was modeled into the design matrix. Six motion regressors were included to the design matrix to control for any head movements generated during image acquisition. All subjects' task > control contrasts (contrast of interest) were obtained and exported for further analysis.

Second-level analyses comparing contrasts of interest between groups were done using two-sample t-tests, where differences in brain activity between Groups (YS > OS, OS > YS) and shared coactivation (global conjunction, positive and negative YS ∩ OS) were obtained using a primary threshold of $p < .001$ and corrected for multiple comparisons using the Family Wise Error (FWE, $p < .05$) method at the cluster level. Anatomical cerebral activations were defined at the peak activation maxima and percent signal change differences were extracted using the Anatomy toolbox (v2.0) for all significant clusters.

2.7 | ROI definition and functional connectivity analysis

Using Marsbar, two different sets of regions of interest (ROI) were created: one for the significant activation clusters in the conjunction analysis (positive YS ∩ OS) and the second for the significant deactivation clusters in the conjunction analysis (negative YS ∩ OS), where shared clusters between both groups were taken into account to test for differences in connectivity. Seeds were defined as 5 mm-spheres centered at the peak MNI coordinates for each resulting cluster. Also,

TABLE 1 Participant data and neuropsychological evaluation

	YS M ± SD	OS M ± SD	YS vs. OS W-test	p-Value	Effect size
Gender (male/female)	11/11	14/6	264	.198	0.200
Age	30.1 ± 4.3	67.4 ± 5.2	0.0	<.001 ^a	−1.000
Driving experience (years)	8.9 ± 4.6	45.1 ± 5.1	0.0	<.001 ^a	−1.000
MMSE	29.3 ± 0.7	28.9 ± 1.2	196.0	.308	0.086
GDS	2.1 ± 1.9	3.4 ± 2.3	126.0	.059	−0.302
Perceptual organization	50.5 ± 8.8	44.7 ± 10.3	245.0	.059	0.360
Attention	41.6 ± 5.7	55.4 ± 9.2	44.0	<.001^a	−0.780
Visual attention	20.6 ± 5.9	30 ± 8.5	72.0	<.001 ^a	−0.657
Sustained attention	60.6 ± 8.6	71.1 ± 8.5	96.0	.002 ^a	−0.543
Divided attention	45.8 ± 9.1	65.9 ± 20.7	70.0	<.001 ^a	−0.667
Verbal cognition	10.6 ± 0.7	9.6 ± 1.2	277.0	.005	0.532
Memory span	7.5 ± 1.9	6.1 ± 1.8	242.5	.068	0.343
Short-term memory	10.4 ± 2	10.8 ± 2.6	190.0	.607	−0.095
Long-term memory	13.8 ± 1.6	10.1 ± 2.8	314.0	<.001 ^a	0.740
Verbal learning	6.8 ± 2	6.3 ± 2.5	198.0	.615	0.097
Verbal recognition	14.8 ± 0.4	14.5 ± 0.8	212.0	.222	0.175
Visual Cognition	9.4 ± 1.5	7.9 ± 2.2	257.5	.025	0.427
Memory span	8.7 ± 0.7	8 ± 0.7	271.5	.004	0.504
Short-term memory	10.4 ± 1.9	9 ± 2.6	235.0	.108	0.302
Long-term memory	9.3 ± 2.6	6.6 ± 3.9	254.0	.032	0.407
Language	21.2 ± 3.8	21.8 ± 4.4	166.5	.693	−0.078
Phonological fluency	18.4 ± 5.4	19.8 ± 5.3	155.0	.464	−0.141
Semantic fluency	24.1 ± 3.5	23.8 ± 4.4	180.5	1.000	0.000
Executive functions	79.7 ± 13.9	112.2 ± 26.9	35.0	<.001^a	−0.806
Mental flexibility	43.9 ± 8.6	65.9 ± 20.7	63.0	<.001 ^a	−0.685
Planning	103.5 ± 63.8	134.4 ± 104.7	122.0	.493	−0.144
Problem solving	65.7 ± 52.1	119.1 ± 84.4	90.0	.008	−0.501
Working memory	8.6 ± 2.3	9 ± 2.7	200.5	.813	−0.045
Inhibition	99.2 ± 12	123.4 ± 16.6	50.5	<.001 ^a	−0.760
Processing speed	187.3 ± 23.1	228.9 ± 44.6	264.0	.002 ^a	−0.587

Note. MMSE = mini mental status examination; GDS = geriatric depression scale; YS = Young subjects; OS = older subjects. Mann-Whitney U test. Effect size by rank-biserial correlation.

^aSignificant values after Bonferroni correction.

individual beta values from these ROIs were extracted for further analyses (see next section).

Task > control data was analyzed using the CONN 16.b functional connectivity toolbox. Conventional analysis steps were followed: BOLD data smoothing (8 mm), despiking and bandpass filtering for low frequency signals (0.008–0.1 Hz). White matter and cerebrospinal fluid and movement parameters BOLD signals were regressed out. Also, task-related coactivations and effects were removed from the signal in order to avoid correlations.

We conducted a series of seed-to-voxel analyses for each ROI, corrected by false discovery rate (FDR $p < .05$) at the cluster level. This method allowed us to explore the positive and negative functional connectivity between the selected ROI and all voxels in our volumes. Finally, individual connectivity values within supra-threshold clusters from the seed-to-voxel analysis were extracted for further examination.

2.8 | Statistical analysis

Scores and variables from the HSD performance, neuropsychological and driving evaluations were compared between groups through Mann-Whitney U tests, due to non-normal data distribution of many variables, along with its effect size calculated by rank-biserial correlation. Post-hoc resulting neuropsychological tests (20 in total) and driving simulator telemetric variables (26 in total) were corrected for multiple comparisons using the Bonferroni method. Also, 2-way ANOVAs (with factors Group and SDF) were conducted to test for the effect of AC and RT when at different speeds.

To understand the relationship between the series of variables delivered by our driving simulator, we performed an exploratory factor analysis test which included the 26 telemetric variables in order to find the main factors that could better explain data variance. Specifically, we ran a parallel analysis, with orthogonal rotation (varimax) and a

FIGURE 2 Neuropsychological scores. Results were transformed to z-scores and classified by domains. Asterisk indicates significant differences between groups after Bonferroni correction. YS = young subjects; OS = older subjects [Color figure can be viewed at wileyonlinelibrary.com]

loading threshold of 0.6. All behavioral statistical analyses were conducted on the JASP software (JASP Team, 2017).

In order to evaluate how accuracy in the HSD task and simulated driving behavior were related to neuroimaging data (BOLD activation and connectivity) and neuropsychological status, lasso regression modeling was employed. This multiple regression method performs variable selection and regularization based on OLS (ordinary least squares) in a penalized fashion, where coefficients are decreased to null value if located under a tuning parameter lambda value which is estimated by cross-validation.

AC and the resulting driving factors for both YS and OS groups were treated as dependant variables for the lasso regression models. The independent variables to be evaluated included (a) the average BOLD activity beta values of all ROIs from the resulting positive YS<OS and negative YS>OS ROIs, (b) average connectivity values from the seed-to-voxel analysis; (c) the neuropsychological factor results; and (d) the AC values, which were used only for the driving factor models. Data were mean-centered and standardized before input.

Lasso regression was performed with a N -fold (where N is the number of subjects in each model, 22 for YS and 20 for OS) cross-validation using the function "lasso" implemented in Matlab for each of the dependant variables. To increase robustness in our results, this process was repeated 1,000 times, from which we extracted and reported the mean and standard deviation for each resulting coefficient, as well as the models' mean optimal lambda value

(defined as the largest lambda value within one standard error of the minimum squared error).

3 | RESULTS

3.1 | Demographic results

Demographic results are detailed in Table 1. Significant differences were found for age and driving experience but not for gender, nor the MMSE and GDS tests.

3.2 | Neuropsychological results

Neuropsychological results are shown in Figure 2 and detailed in Table 1. Perceptual organization was not significant between groups. However, differences in the Attention domain were significant between groups in all three visual, sustained and divided attention tests. In the verbal cognition domain, significant differences were found only for long-term memory but not for memory span, short-term memory, verbal learning nor verbal recognition. On visual cognition, significant differences between groups (that did not surpass Bonferroni correction) were found in memory span and long-term memory, but not for short-term memory. No differences were found for either phonological or semantic fluency in the Language domain. In the Executive domain, significant differences were found in mental flexibility, problem solving (did not surpass Bonferroni correction), inhibition and processing speed but not in planning nor working memory.

TABLE 2 Driving simulator factor and telemetry data

	YS M ± SD	OS M ± SD	YS vs. OS W-test	p-value	Effect size
Speed	-1,850.9 ± 248.6	-2251.9 ± 337	285	<.001^a	0.676
Total session time	2,043.3 ± 236	2426.5 ± 330	53	<.001 ^a	-0.688
% Time above speed limit	4.4 ± 3.6	1.7 ± 1.2	269	.003	0.582
Mean speed at 40km/h zone	31.6 ± 3.5	26.8 ± 6.2	256	.009	0.506
Mean speed at 50km/h zone	16.5 ± 3.1	14.4 ± 1.9	245	.023	0.441
Mean speed at 80km/h zone	49.9 ± 6.2	43.3 ± 5.8	268	.003	0.576
Mean speed at 120km/h zone	94 ± 12.8	76.1 ± 12	285	<.001 ^a	0.676
Yellow traffic light skips	1.8 ± 1.3	3.2 ± 2	88	.011	-0.482
Dexterity	92.1 ± 25.8	114.8 ± 81.1	150	.552	-0.118
270–360° steers in 0.5 seconds	0.1 ± 0.3	0.6 ± 1.3	144	.226	-0.153
180–270° steers in 0.5 seconds	2.7 ± 2.6	4.8 ± 8.3	143.5	.420	-0.156
90–180° steers in 0.5 seconds	37.8 ± 14.2	46.9 ± 37	157	.703	-0.076
60–90° steers in 0.5 seconds	58.1 ± 17.6	71 ± 42.3	134	.279	-0.212
Collision Risk	50.9 ± 53.8	40.3 ± 30.3	173	.939	0.018
Time w/gas pedal >75%	60.6 ± 63.8	48.4 ± 36.5	172.5	.951	0.015
% Time w/gas pedal >75%	1.6 ± 1.9	1 ± 0.8	188	.594	0.106
Collision w/other car	0.5 ± 0.9	0.4 ± 0.7	173.5	.910	0.021
Hard Braking	-54.8 ± 7.8	-53.2 ± 18.7	198	.402	0.165
% Time moving	87.7 ± 2.9	88.0 ± 5.6	128	.206	-0.247
Time w/brake pedal >75%	3.5 ± 7.5	5.3 ± 16.6	162	.800	-0.047
% Time w/brake pedal >75%	0.1 ± 0.2	0.1 ± 0.3	172	.959	0.012
Braking	257 ± 89.6	261.2 ± 153.3	188	.594	0.106
Time braking	253 ± 87.8	260.4 ± 154.6	186	.637	0.094
% Time braking	12.6 ± 4.8	10.7 ± 5.7	221	.124	0.300
>10 second brakes	6.4 ± 3	4.6 ± 3	231.5	.062	0.362
Mean speed at 100km/h zone	35.4 ± 21.8	37.6 ± 24.3	160	.772	-0.059
Two wheel sidewalk invasion	57.3 ± 24.7	71.6 ± 17.8	82	.008	-0.518
>5 second brakes	2.3 ± 1.9	1.8 ± 1.3	188	.584	0.106
Collision w/other objects	3.7 ± 3.8	5 ± 3.8	124.5	.167	-0.268
Red traffic light skips	1.9 ± 2.1	3.8 ± 6.5	123	.140	-0.276
Run overs	0.1 ± 0.5	0.2 ± 0.4	149	.329	-0.124

Note. YS = young subjects; OS = older subjects. Mann-Whitney *U* test. Effect size by rank-biserial correlation.

^aSignificant values after Bonferroni correction.

3.3 | Driving simulator results

Results on the driving simulator performance are detailed in Table 2. One YS and five OS participants were excluded from this analysis due to simulator sickness that impeded evaluation completion. Also, four YS and three OS subjects reported mild simulator sickness symptoms (i.e., eye strain, dizziness).

The exploratory factor analysis indicated that only 20 variables (with no cross-loadings) surpassed the loading threshold, which was

intentionally set high due to the relative small number of variables (Supporting Information Table 1). The Bartlett's Test of Sphericity was significant ($\chi^2(205) = 633.35, p < .001$) demonstrating the adequacy of our data. A total of five uncorrelated factors were identified and explained 71% of the variability in our data (Supporting Information Figure 2). The relationship between variables within each factor allowed for adequate labeling: driving Speed, which included variables related to the time it took the subject to finish the driving session, the speed

FIGURE 3 High speed discrimination performance results. (a) Accuracy (AC) and (b) response time (RT) compared by groups; boxes indicate median and the 25th to 75th percentile and whiskers the minimum and maximum values. (c) AC and (d) RT compared by SPD between stimuli and group. Upper and lower limits represent the standard error. YS = young subjects; OS = older subjects

while driving and yellow light skips; Dexterity, which included sudden steering at any angle; Collision Risk for gas pedal pressing parameters and collisions with other cars; and Hard Braking and Braking for hard brake pressing and time braking parameters respectively. From these factors and their variables, we created composite scores in order to compare these results between groups and to use them as covariates in our functional neuroimaging analysis. These scores were based on the sum of the mean value of every variable in each factor, weighted by the loading value.

When compared by factors, only speed was significantly different between groups, indicating that YS were faster during the driving session. Within this factor, YS had a lower total session time, less yellow traffic light skips, higher % of time above speed limit, and mean speed at 40 km/h, 50 km/h, 80 km/h, and 120 km/h zones. Besides these, only the number of two wheel sidewalk invasions variable was also significantly different between groups. From all these results, only the total session time and mean speed at 120 km/h zone variables surpassed the Bonferroni correction threshold.

3.4 | HSD performance results

Results from AC and RT mean values compared by group and by SDF are summed up in Figure 3. AC was significantly lower in the OS group. When errors in AC were analyzed by the speed difference between stimuli, main effects of Group and SDF and interactions were statistically significant. Further post-hoc analyses showed, as expected, that more errors were committed in both groups when the difference between speeds was minimal. Interestingly, OS committed most errors

when the second stimulus presented was faster (Figure 3c), being significantly higher than those on the YS group.

Alternatively, no differences between groups were found in mean RT. Factorial analysis showed that only the SDF factor was significant ($F[11,440]=5.44, p < 0.001$), with no main effect of Group nor interactions. An additional analysis comparing all stimuli with a positive or negative SDF between groups (when the first stimulus was faster than the second and vice versa, respectively) showed a significant main effect of Group, where RT was higher and more variable in stimuli with negative SDF only in OS (see Supporting Information Figure 3).

When evaluating the effect of sex in AC (Supporting Information Figure 4), significant main effects of Group and Sex were found but no interactions. Post-hoc comparisons showed that only in our OS group women made more errors than men ($W_{OS}: 14.5 \pm 3.73, M_{OS}: 9.43 \pm 3.29, t = 4.46, p = .016$).

3.5 | Neuroimaging results

3.5.1 | Global activity

Maps of differential and conjunction activation analysis are summarized in Tables 3 and 4, respectively. The OS > YS contrast revealed a widespread hyperactivation pattern (Figure 4), peaking in the SMA, right insula, precuneus, left dorsolateral prefrontal cortex (DLPFC), fusiform gyri, left temporal pole, left thalamus, left angular gyrus and cerebellum (see Supporting Information Figure 5 for changes in percent signal change). The YS > OS contrast did not reveal any significant activation.

The positive YS > OS contrast showed shared activity in the DMPFC, right DLPFC, bilateral intraparietal sulcus and bilateral insulae.

TABLE 3 Hyperactivation clusters in OS

Region	BA	Cluster size	MNI Coordinates			T-value
			x	y	z	
Left precentral gyrus	6	40,497	-22	-22	66	7.23
Left PRECENTRAL GYRUS	6		-38	4	38	6.27
Right SMA	6		4	-4	54	6.19
Left insula	13		-32	-24	4	6.09
Right superior frontal gyrus	6		34	-4	66	6.06
Left middle frontal gyrus	6		-28	2	58	6.04
Right SMA	6		-12	2	70	5.97
Right precuneus	7		6	-58	52	5.96
Cerebellar lobule I-IV (Vermis)	N/A		0	-52	-22	5.94
Left fusiform gyrus	19		-34	-66	-18	5.94
Left cerebellum lobule VI	19		-24	-70	-18	5.93
Left IFG p. triangularis	45	308	-54	18	-2	4.39
Left temporal pole	22		-50	10	-10	3.98
Left temporal pole	22		-54	8	-8	3.96
Left temporal pole	47		-42	20	-16	3.91

Note. BA = Broadmann area; OS = older subjects.

The negative YS $\cap$ OS contrast showed activity in areas that configure the DMN, including the medial prefrontal cortex, precuneus, PPC, left middle temporal gyrus and left angular gyrus.

3.5.2 | Functional connectivity results

Results from the functional connectivity analyses are shown in Figure 5 and detailed in Table 4. In the positive YS $\cap$ OS analysis, the YS group showed an increased connectivity between the right precentral gyrus with nearby right frontal areas, mostly SMA. OS was found to have higher connectivity than YS in two ROIs: the right insula with the contralateral putamen and insula; the right SMA with right posterior parietal (angular gyrus, supramarginal gyrus), lateral occipital and temporal cortex (inferior, middle and superior temporal gyrus) and also with the left thalamus.

In the negative YS $\cap$ OS, the YS group showed a generalized higher connectivity than OS between DMN regions: the superior medial gyrus with the precuneus and PCC; the middle cingulate cortex (MCC) connected with frontal medial cortex, PCC, precuneus, periculate and left middle temporal cortex (MT); the PCC with the precuneus, frontal medial cortex and left MT; the precuneus with the frontal medial cortex, left MT, lateral occipital cortex, both angular gyri and both temporal poles; the MT connected with the precuneus, PCC and right and left cuneal cortices; and finally the left angular gyrus was connected to the anterior cingulate cortex (ACC), precuneus, left paracingulate and lingual gyri. Also, YS had a stronger connectivity between the left mid orbital gyrus the left frontal cortex and pole. On the inverse contrast, OS only revealed a higher connectivity than YS between the left MT and left frontal pole.

3.6 | Behavioral regression analysis

Independent variables included to the 6 lasso regression models analyzed (AC and 5 driving factors) included 24 ROIs from the positive and negative conjunction analysis for each group (Table 4), 21 seed-to-voxel connectivity values for YS and 6 for OS, 6 values from each of the obtained neuropsychological factors and the AC score (only in the driving factor models), making up for a total of 52 variables for YS and 37 for OS.

This analysis revealed a robust relationship only within the AC and the Speed models for the YS group (Table 5). AC in YS showed a strong relationship with activation in the right insula and right inferior parietal lobule and connectivity between the left middle temporal gyrus and the left PCC and precuneus. Additionally, the speed driving factor in YS was associated with activation in regions mainly from the negative conjunction analysis (left midorbital gyrus, right superior medial gyrus, right PCC, left angular gyrus and left middle temporal gyrus) as well as the precentral gyrus; with functional connectivity from within-DMN regions (right superior medial gyrus and right precuneus, left middle temporal gyrus and left precuneus, left MCC and left medial frontal cortex, left middle temporal gyrus and left PCC, left precuneus and right precuneus, left middle orbital gyrus and left middle frontal gyrus, right PCC and left middle temporal gyrus, left precuneus and left frontal medial cortex) and between the right precentral gyrus and right superior frontal gyrus; also, with the neuropsychological factors visual cognition, language and executive.

4 | DISCUSSION

In this study we demonstrate the presence of a deficit associated to high speed discrimination in the elderly when compared to a young

TABLE 4 Conjunction analysis clusters of activation and seed-to-voxel connectivity

Contrast/region	BA	Cluster size	MNI coordinates			T value	Connected to		MNI Coordinates		
			x	y	z		YS>OS	OS>YS	x	y	z
YS∩OS (pos)											
Right precentral gyrus	6	729	46	6	28	7.36	Right superior frontal gyrus	—	16	4	66
Right inferior frontal gyrus	44		50	12	26	7.04	—	—			
Right inferior frontal gyrus 2	9		44	26	20	3.74	—	—			
Right supramarginal gyrus	40	693	42	−38	44	5	—	—			
Right inferior parietal lobule	7		38	−48	52	4.34	—	—			
Right superior parietal lobule	7		20	−60	54	3.94	—	—			
Left superior parietal lobule	7	600	−20	−58	54	5.46	—	—			
Left inferior parietal lobule	7		−30	−46	44	5.15	—	—			
Left inferior parietal lobule 2	1		−44	−34	44	3.57	—	—			
Right insula lobe	13	500	32	22	2	6.46	—	Left putamen	32	22	2
Left insula lobe	13	466	−32	20	2	6.92	—	—			
Right supplementary motor area	8	358	4	16	50	6.46	—	Right angular gyrus	42	−50	18
							—	Right temporal pole	44	0	−28
							—	Left thalamus	−16	−32	0
Left supplementary motor area	6		−8	14	46	4.2	—	Right middle temporal gyrus	54	−56	6
YS∩OS (neg)											
Left anterior cingulate	32	1473	−8	52	0	5.69	—	—			
Right middle orbital gyrus	10		6	48	−10	5.4	—	—			
Left middle orbital gyrus	10		−10	44	−10	5.31	Left middle frontal gyrus	—	−26	36	46
Left middle orbital gyrus 2	10		−8	48	−8	5.29	—	—			
Right middle orbital gyrus 2	11		4	42	−10	5.23	—	—			
Right superior medial gyrus	10		4	56	6	4.95	Right precuneus	—	6	−56	22
Left superior medial gyrus	10		−4	56	14	4.56	—	—			
Right anterior cingulate	32		4	26	−8	4.54	—	—			
Left olfactory cortex	25		−2	18	−8	3.94	—	—			
Left precuneus	23	1,455	−4	−56	26	6.67	Right precuneus	—	6	−44	26
							Right lateral occipital cortex	—	52	−66	34
							Left lateral occipital cortex	—	−46	−66	28
							Left frontal medial cortex	—	−4	54	−16
							Left middle temporal gyrus	—	−54	−10	−22
Left middle cingulate	23		−8	−44	34	5.9	Right frontal medial cortex	—	2	46	−16
							Left precuneus	—	−2	−60	8
							Left middle temporal	—	−54	−8	−24

(Continues)

TABLE 4 (Continued)

Contrast/region	BA	Cluster size	MNI coordinates			T value	Connected to		MNI Coordinates		
			x	y	z		YS>OS	OS>YS	x	y	z
gyrus											
Left precuneus 2	23		−8	−56	16	5.88	Left posterior cingulate	—	6	−44	26
							Left middle temporal gyrus	—	−60	−10	−24
Right posterior cingulate	23		6	−50	28	5.27	Right frontal medial cortex	—	2	44	−16
							Left precuneus	—	−6	−54	20
							Left middle temporal gyrus	—	−56	−18	−14
Right precuneus	23		10	−54	18	5.18	—	—			
Left angular gyrus	39	434	−38	−76	46	5.04	Left paracingulate gyrus	—	−12	40	4
Left angular gyrus 2	39		−42	−72	38	4.84	Left precuneus	—	−4	−60	8
Left angular gyrus 3	39		−48	−70	28	4.63	—	—			
Left middle temporal gyrus	21	309	−60	−14	−8	5.07	—	—			
Left middle temporal gyrus 2	21		−62	−10	−12	5.06	Left precuneus	—	−10	−68	20
							Left posterior cingulate	—	−8	−36	40
Left middle temporal gyrus 3	21		−56	−14	−18	4.54	Right posterior cingulate	—	12	−44	28
Left middle temporal gyrus 4	21		−58	−4	−18	4.31	—	Left frontal pole	−32	48	8

BA = Broadmann Area, YS = Young Subjects, OS = Older Subjects.

FIGURE 4 Task > Control shared and differential activation patterns between groups. Color-coded activation (hot) and deactivation (winter) parametrical maps. Clusters were FWE-corrected at $p < .05$. YS = young subjects; OS = older subjects

FIGURE 5 Seed-to-voxel functional connectivity revealed higher connectivity between DMN areas in young adults. Seeds (black font) and their targets (red font) reveal that (a–j) young subjects (YS) mainly show increased connectivity between DMN areas, while (k–m) older subjects (OS) have higher connectivity between frontal, parietal and basal regions. Connectivity clusters were FDR-corrected at $p < .05$. SMA = supplementary motor area; MCC = middle cingulate cortex; MT = middle temporal cortex, PCC = posterior cingulate cortex, LOC = - lateral occipital cortex

adult control group, in spite of a wide frontoparietal and cerebellar hyperactivation pattern, in conjunction with reduced DMN deactivation and connectivity within its areas. Moreover, we found that performance in HSD in YS is closely associated to frontoparietal activation, within-DMN connectivity, attention and verbal cognition. Finally, our driving simulator test revealed that younger adults drive at a higher Speed and this factor is related to proper DMN dynamics and executive functioning. Both associations are lost in older individuals.

4.1 | Default mode network dynamics are restricted in the elderly during high speed discrimination

Using the task > control contrast our speed discrimination paradigm revealed a shared between-group set of activated/deactivated areas, as well as differential activation when examined separately by group. Shared group activations were found in the bilateral insulae and right DLPFC, areas usually found to in task-positive experiments (Cabeza & Nyberg, 2000); also the bilateral intraparietal sulcus (IPS) and the supplementary eye fields (SEF), structures that conform the dorsal attention network (Corbetta & Shulman, 2002). These areas are involved in goal directed (top-down) control, by supporting visuo-spatial attention and decision making through retention in short-term spatial memory which may participate in correct discrimination between moving stimuli. Shared deactivation was detected in DMN regions (ventral

precuneus, PCC, angular gyrus, middle temporal gyrus, medial frontal cortex) an effect usually present in task-positive paradigms (Raichle, 2015; Raichle et al., 2001).

Hyperactivation of the elderly group when compared with young adults is widespread, and included the SMA, ACC, left inferior frontal gyrus, dorsal precuneus, bilateral basal ganglia, fusiform gyrus and the cerebellum. These changes were characterized by a rise in activation in the aforementioned areas along with a diminished deactivation of the dorsal precuneus. All of these results are in consonance with the compensation hypothesis for the aging brain (Reuter-Lorenz & Campbell, 2008; Reuter-Lorenz & Park, 2014) which proposes that widespread hyperactivation from areas such as the cerebellum (Grady et al., 2010) or the frontoparietal cortex (Hakun & Johnson, 2017), along with DMN reduced deactivation, may act as a compensation measure, needed to reach youth-like levels of task performance until it reaches a maximum and starts to decline. Usually, these changes in activation are in close relationship with changes in behavioral performance, which were also corroborated in this study.

Besides examining similarities and differences in group activation, we also aimed to compare the functional connectivity patterns emerging from areas shared between both age groups. From the positive conjunction analysis, the young group showed a stronger connectivity than the elderly between the precentral gyrus and SMA; in the inverse contrast, the elderly had stronger connections than the young group between the SMA and the PPC and right temporal cortex; and the right

TABLE 5 Mean and standard deviation (SD) of lasso coefficients for variables (BOLD activation, connectivity and neuropsychological factors) included in the models for HSD accuracy and driving factors in YS

Variable	Mean (SD)
HSD accuracy ($\lambda = 0.091$)	
Attention	0.217 (0.528)
<i>Left precuneus - left middle temporal gyrus</i>	0.209 (0.128)
<i>Left middle temporal gyrus 3 - left PCC</i>	0.163 (0.075)
<i>Left precuneus - left lateral occipital cortex</i>	0.017 (0.026)
Left supplementary motor area	0.003 (0.001)
<i>Right posterior cingulate - left middle temporal gyrus</i>	−0.121 (0.171)
Verbal cognition	−0.159 (0.053)
Right insula lobe	−0.165 (0.264)
Right inferior parietal lobule	−0.224 (0.150)
<i>Left middle temporal gyrus 2 - left posterior cingulate</i>	−0.371 (0.511)
Speed ($\lambda = 0.013$)	
Left middle orbital gyrus 2 ^a	0.397 (0.021)
Right superior medial gyrus ^a	0.247 (0.045)
<i>Right superior medial gyrus - right precuneus</i>	0.234 (0.026)
<i>Left middle temporal gyrus 2 - left precuneus</i>	0.219 (0.041)
<i>Right precentral gyrus - right superior frontal gyrus</i>	0.165 (0.015)
<i>Left MCC - left frontal medial cortex</i>	0.128 (0.012)
Right precentral gyrus	0.078 (0.012)
<i>Left middle temporal gyrus 3 - left posterior cingulate</i>	0.047 (0.008)
Visual cognition	−0.007 (0.001)
Right posterior cingulate ^a	−0.014 (0.002)
<i>Left precuneus - right precuneus</i>	−0.034 (0.008)
Left angular gyrus ^a	−0.038 (0.006)
Language	−0.077 (0.015)
<i>Left middle orbital gyrus - left middle frontal gyrus</i>	−0.110 (0.025)
<i>Right posterior cingulate - left middle temporal gyrus</i>	−0.122 (0.002)
<i>Left precuneus - left frontal medial cortex</i>	−0.170 (0.017)
Left angular gyrus 2 ^a	−0.256 (0.026)
Executive	−0.262 (0.039)
Left middle temporal gyrus 2 ^a	−0.500 (0.114)

Note. λ = Mean optimal lambda value. Conjunction analysis variables are underlined; seed-to-voxel connectivity variables are italicized; neuropsychological factors are unformatted.

^aRegions from the negative conjunction analysis.

insula with the contralateral insula and putamen. From negative conjunction analyses, we found a loss of connectivity between several DMN areas in the elderly (precuneus, PPC, posterior and anterior

cingulate) when compared to the young group. This DMN connectivity dysfunction has been found in other cognitive tasks such as spatial judgment tasks (Park et al., 2010), object tracking (Dørum et al., 2016), semantic classification (Andrews-Hanna et al., 2007), working (Grady et al., 2010; Sambataro et al., 2010) and episodic memory (Persson et al., 2014). It appears that the DMN loses efficiency as a network, since it is not able to deactivate appropriately and connections between components are weakened when compared to young-like DMN functioning.

4.2 | High speed discrimination accuracy is impaired in the elderly

In our high speed discrimination task, subjects had to compare two stimuli moving at high speeds and choose the fastest one. To our knowledge, this is the first study to explore speed discrimination with only high speed moving stimuli (>100°/s) and then compare performance between young and older adults. As expected, more errors were committed when the difference between stimuli was minimal, with a pronounced contrast between younger and older participants, hence confirming previous findings (Norman et al., 2003; Raghuram et al., 2005) and demonstrating its effect when discriminating at higher speeds. Mean RT was similar between groups which could be explained by the fact that subjects were not requested to answer as fast as they could, in order to try and to achieve maximum accuracy.

Moreover, the elderly group made more errors when the speed difference was negative, meaning that they incorrectly chose the first stimulus as the fastest when it was the second, especially when the speed difference between stimuli was reduced. This finding is seconded by OS having a higher RT in all stimuli with a negative speed difference, despite not having a significant difference when those negative speeds are compared against each other. When the opposite was true (first faster than the second) they performed similarly to the young group. This finding could be related to the fact that at the beginning of each trial, the elderly were not as attentive as the young, and therefore a fast first stimulus might have come as “unexpected”, leading to confusion and therefore taking a longer time to decide whether that stimulus was indeed the fastest. This attentional deficit was corroborated by the older group scores in the visual, sustained and divided attention tests.

Also, we found sex-related differences in our elderly group, where accuracy in females was lower. This effect has been found in previous speed discrimination studies but with slower stimuli (Norman et al., 2003; Raghuram et al., 2005), as well as in other direction discrimination studies (Atchley & Kramer, 1998; Gilmore, Wenk, Naylor, & Stuve, 1992); these differences have generally been attributed to men having better visuo-spatial abilities, especially when dealing with moving stimuli, although differences might be minimal and depend on the task at hand (Ardila, Rosselli, Matute, & Inozemtseva, 2011). In line with this, our results must be taken cautiously due to the unequal number of males and females in the elderly group.

4.3 | Task performance is associated to frontoparietal modulation, within-DMN connectivity and attention

The regression analysis method consistently showed that, only in YS, accuracy is strongly associated with activation in frontoparietal areas (right insula and inferior parietal lobule) and connectivity between DMN locations (PCC, precuneus, middle temporal gyrus). This relationship between frontoparietal activation and performance in other cognitive tasks, mostly working memory, has been described (Kaup, Drummond, & Eyler, 2014; Leung, Oh, Ferri, & Yi, 2007; Nagel et al., 2009) as well as the modulating role of the DMN connectivity in cognition (Elton & Gao, 2015; Krieger-Redwood et al., 2016) and how it is influenced by task difficulty (Liang, Zou, He, & Yang, 2016; Turner & Spreng, 2015; Vatansever, Menon, Manktelow, Sahakian, & Stamatakis, 2015). Alternatively, it has been widely documented how connectivity within the DMN is decreased in the elderly (Geerligs, Maurits, Renken, & Lorist, 2014; Grady et al., 2010; Sambataro et al., 2010). Moreover, studies examining working memory and spatial judgment tasks in aging found that performance depends on adequate DMN deactivation (Kennedy, Boylan, Rieck, Foster, & Rodrigue, 2017; Prakash, Heo, Voss, Patterson, & Kramer, 2012) and connectivity (Sambataro et al., 2010), proposing that proper DMN dynamics may be a sign of maintained cognitive ability in aging (Rieck, Rodrigue, Boylan, & Kennedy, 2017; Samu et al., 2017). Therefore, the lack of a valid AC model in OS, may be justified by the differences found in DMN dynamics—lower deactivation and connectivity—, suggesting that accuracy in HSD may rely on other areas, such as the frontoparietal cortices, usually found to be over-activated during task execution (Hakun & Johnson, 2017).

Furthermore, this model revealed a strong association between both the Attention and Verbal Cognition factors and HSD performance in younger subjects, where better scores in both factors was associated to higher Accuracy. Within-DMN connectivity is strengthened by attention (Kwon, Watanabe, Fischer, & Bartels, 2017), which reinforces the idea that adequate attentional functioning and DMN modulation were required for proper HSD performance, both of them altered in our aging population.

4.4 | Driving speed is related with DMN dynamics and executive functioning

Driving simulator results revealed that OS drove at slower speeds, steering was increased and more variable, hard braked for more time and committed more road infractions, behaviors commonly found in older drivers (Park et al., 2011; Thompson et al., 2012). Driving in a scenario such as the one used in this study—and driving in general—, is an example of multitasking where being aware of your surroundings, dealing with actual traffic, following road rules and remembering voice commands, place an increased amount of cognitive load which compete for neural resources, particularly those located in the prefrontal cortex (Schweizer et al., 2013). When cognitive load is added while driving (using a task that demanded sustained attention, working

memory and processing speed) elderly drivers tended to drive at a slower speed and increase steering frequency, findings similar to those found in our aging group (Thompson et al., 2012). Driving is a task that relies on attentional and executive functions (Adrian, Postal, Moesinger, Rasclé, & Charles, 2011; León-Domínguez, Solís-Marcos, Barrio-Álvarez, Barroso y Martín, & León-Carrión, 2017) even in simulated driving (Mäntylä, Karlsson, & Marklund, 2009), both of which decline with age, as corroborated in this study, and are associated to poor driving performance (Emerson et al., 2012; Papandonatos, Ott, Davis, Barco, & Carr, 2015; Vaucher et al., 2014; Whelihan, DiCarlo, & Paul, 2005), including car crashes (Ball et al., 2006; Stutts, Stewart, & Martell, 1998).

In an attempt to explore and classify driving performance, an exploratory factor analysis was performed, which resulted in five main factors that could be grouped in five driving-related dimensions: speed, hard braking, and braking, all of these directly related to speed and time; dexterity, which measured the degree of sudden driving wheel turns; and collision risk, which included high acceleration and car collisions. Such measures might represent good indicators of driving performance and profiling, as well as a tool to evaluate responses to challenging driving events (Bélanger, Gagnon, & Yamin, 2010). Significant differences in driving factors between groups were only found in Speed, where the elderly were found to drive slower overall. These results confirm previous findings on simulated driving where older adults drive at slower (Cantin et al., 2009; Lee, Drake, & Cameron, 2002; Shanmugaratnam, Kass, & Arruda, 2010) and more variable speeds (Urwiler et al., 2015), which tend to be even slower than in on-road assessments (Lee et al., 2003).

We employed lasso regression's method for feature selection with the objective of exploring how driving behavior, as determined by the five factors extracted from our simulator, is associated to individual neuropsychological status and neural correlates of a driving related task such as HSD. We were only able to find an association in YS between the Speed factor and activation and connectivity between regions of the DMN, as well as with the right precentral gyrus modulation and the neuropsychological factors Executive, and to a lesser degree visual cognition and language. From these, stronger positive associations (decreased deactivation at higher speed) were found with activation in the left middle orbital gyrus and superior medial gyrus, regions from the anterior DMN; stronger negative associations (increased deactivation at higher speed) were found with the left angular gyrus and middle temporal gyrus, areas from the posterior DMN. On the other hand, within-DMN connections were both positive and negatively associated with Speed. Also, the Executive factor played a strong role in this model, where better scores were associated with higher Speed values. Therefore, the fact that no effect was found in the Speed factor for OS and that DMN involvement and executive functions are deficient in the elderly suggests that either a) speed while driving is mediated through a different mechanism than in younger adults or that b) slower driving can be indeed related to limitations in DMN modulation and executive functions.

4.5 | Limitations and future directions

As with other driving simulator studies, our simulator might have introduced bias since it does not fully represent the act and experience of driving, therefore altering how our participants approach and execute the driving evaluation. Also, this particular task may have proven difficult to some drivers, since it required navigation in a complex environment while following instructions; despite these throwbacks, we opted for this naturalistic approach since it allowed us to collect reliable telemetric data, since drivers had to follow the same route and face similar obstacles. Additionally, our subjects had only a relatively short time to get familiarized with the simulator, which could have hindered their performance, especially in the elderly. Moreover, several of our subjects presented simulator sickness, a feature intrinsic to virtual simulators due to perceptual (visual, vestibular, proprioceptive) mismatch.

Based on the results obtained in this study, future work can be applied on exploring how performance in HSD and its neural correlates change with practice older adults. Another important question lies on the impact of multiple training sessions on driving behavior -especially driving speed- and whether it relates to changes in high speed discrimination or not. Finally, it remains of interest how neurocognitive status in the elderly, in particular the attentional and executive domains, is predictive of driving behavior.

5 | CONCLUSIONS

In summary, our study delivers evidence on how high speed discrimination is impaired in an otherwise healthy older adult population and how this alteration is associated with a widespread hyperactivation pattern that included an increase in activity in frontoparietal areas, the basal ganglia and the cerebellum, along with reduced deactivation in the DMN and a loss of connectivity within DMN areas. Better performance in the young group was associated to activation in frontoparietal areas, connectivity within-DMN regions and with the attention and verbal cognition neuropsychological factors; in the elderly this effect is lost. Finally, our driving simulator task showed faster driving in the young, which was mainly modulated by activation and connectivity within-DMN regions, as well as better executive factor scores. In conclusion, the age-related changes in DMN dynamics found in this study intervene in high speed discrimination performance in healthy aging, a condition that is reflected in simulated driving speeding behavior.

ACKNOWLEDGMENTS

This work was funded by the Foundation Caja Navarra grant (Ref: FBCN 15/70757) for biomedical research. LE was financially supported by a grant from the University of Navarra Friends Association.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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REFERENCES

- Adrian, J., Postal, V., Moessinger, M., Rasclé, N., & Charles, A. (2011). Personality traits and executive functions related to on-road driving performance among older drivers. *Accident Analysis and Prevention*, 43(5), 1652–1659. <https://doi.org/10.1016/j.aap.2011.03.023>
- Andrews-Hanna, J. R., Snyder, A. Z., Vincent, J. L., Lustig, C., Head, D., Raichle, M. E., & Buckner, R. L. (2007). Disruption of large-scale brain systems in advanced aging. *Neuron*, 56(5), 924–935. <https://doi.org/10.1016/j.neuron.2007.10.038>
- Andrews, E. C., & Westerman, S. J. (2012). Age differences in simulated driving performance: Compensatory processes. *Accident Analysis and Prevention*, 45, 660–668. <https://doi.org/10.1016/j.aap.2011.09.047>
- Ardila, A., Rosselli, M., Matute, E., & Inozemtseva, O. (2011). Gender differences in cognitive development. *Developmental Psychology*, 47(4), 984–990. <https://doi.org/10.1037/a0023819>
- Atchley, P., & Kramer, A. F. (1998). Spatial cuing in a stereoscopic display: attention remains "depth-aware" with age. *The Journals of Gerontology. Series B, Psychological Sciences and Social Sciences*, 53B(5), P318–P323.
- Ball, K. K., Roenker, D. L., Wadley, V. G., Edwards, J. D., Roth, D. L., McGwin, G., ... Dube, T. (2006). Can high-risk older drivers be identified through performance-based measures in a department of motor vehicles setting?. *Journal of the American Geriatrics Society*, 54(1), 77–84. <https://doi.org/10.1111/j.1532-5415.2005.00568.x>
- Bélanger, A., Gagnon, S., & Stinchcombe, A. (2015). Crash avoidance in response to challenging driving events: The roles of age, serialization, and driving simulator platform. *Accident Analysis and Prevention*, 82, 199–212. <https://doi.org/10.1016/j.aap.2015.04.030>
- Bélanger, A., Gagnon, S., & Yamin, S. (2010). Capturing the serial nature of older drivers' responses towards challenging events: A simulator study. *Accident Analysis and Prevention*, 42(3), 809–817. <https://doi.org/10.1016/j.aap.2009.07.010>
- Brown, B., & Bowman, K. J. (1987). Sensitivity to changes in size and velocity in young and elderly observers. *Perception*, 16(1), 41–47.
- Cabeza, R., & Nyberg, L. (2000). Imaging Cognition II: An Empirical Review of 275 PET and fMRI Studies. *Journal of Cognitive Neuroscience*, 12(1), 1–47. <https://doi.org/10.1162/08989290051137585>
- Campagne, A., Pebayle, T., & Muzet, A. (2004). Correlation between driving errors and vigilance level: Influence of the driver's age. *Physiology and Behavior*, 80(4), 515–524. <https://doi.org/10.1016/j.physbeh.2003.10.004>
- Cantin, V., Lavallière, M., Simoneau, M., & Teasdale, N. (2009). Mental workload when driving in a simulator: Effects of age and driving complexity. *Accident Analysis and Prevention*, 41(4), 763–771. <https://doi.org/10.1016/j.aap.2009.03.019>
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201–229. <https://doi.org/10.1038/nrn755>
- Cuenen, A., Jongen, E. M. M., Brijs, T., Brijs, K., Lutin, M., Van Vlierden, K., & Wets, G. (2015). Does attention capacity moderate the effect of driver distraction in older drivers?. *Accident Analysis and Prevention*, 77, 12–20. <https://doi.org/10.1016/j.aap.2015.01.011>

- de Bruyn, B., & Orban, G. A. (1988). Human velocity and direction discrimination measured with random dot patterns. *Vision Research*, 28 (12), 1323–1335. [https://doi.org/10.1016/0042-6989\(88\)90064-8](https://doi.org/10.1016/0042-6989(88)90064-8)
- Dørum, E. S., Alnaes, D., Kaufmann, T., Richard, G., Lund, M. J., Tønnesen, S., ... Westlye, L. T. (2016). Age-related differences in brain network activation and co-activation during multiple object tracking. *Brain and Behavior*, 6(11), e00533. <https://doi.org/10.1002/brb3.533>
- Elton, A., & Gao, W. (2015). Task-positive functional connectivity of the default mode network transcends task domain. *Journal of Cognitive Neuroscience*, 27(12), 2369–2381. https://doi.org/10.1162/jocn_a_00859
- Emerson, J. L., Johnson, A. M., Dawson, J. D., Uc, E. Y., Anderson, S. W., & Rizzo, M. (2012). Predictors of driving outcomes in advancing age. *Psychology and Aging*, 27(3), 550–559. <https://doi.org/10.1037/a0026359>
- Geerligs, L., Maurits, N. M., Renken, R. J., & Lorist, M. M. (2014). Reduced specificity of functional connectivity in the aging brain during task performance. *Human Brain Mapping*, 35(1), 319–330. <https://doi.org/10.1002/hbm.22175>
- Gilmore, G. C., Wenk, H. E., Naylor, L. A., & Stuve, T. A. (1992). Motion perception and aging. *Psychology and Aging*, 7(4), 654–660. <https://doi.org/10.1037/0882-7974.7.4.654>
- Grady, C. L., Protzner, A. B., Kovacevic, N., Strother, S. C., Afshin-Pour, B., Wojtowicz, M., ... McIntosh, A. R. (2010). A multivariate analysis of age-related differences in default mode and task-positive networks across multiple cognitive domains. *Cerebral Cortex*, 20(6), 1432–1447. <https://doi.org/10.1093/cercor/bhp207>
- Hakun, J. G., & Johnson, N. F. (2017). Dynamic range of frontoparietal functional modulation is associated with working memory capacity limitations in older adults. *Brain and Cognition*, 118(August), 128–136. <https://doi.org/10.1016/j.bandc.2017.08.007>
- Hills, B. L. (1980). Vision, visibility, and perception in driving. *Perception*, 9(2), 183–216. <https://doi.org/10.1068/p090183>
- Hoffman, L., McDowd, J. M., Atchley, P., & Dubinsky, R. (2005). The role of visual attention in predicting driving impairment in older adults. *Psychology and Aging*, 20(4), 610–622. <https://doi.org/10.1037/0882-7974.20.4.610>
- Kau, S., Strumpf, H., Merkel, C., Stoppel, C. M., Heinze, H. J., Hopf, J. M., & Schoenfeld, M. A. (2013). Distinct neural correlates of attending speed vs. coherence of motion. *NeuroImage*, 64, 299–327. (1), <https://doi.org/10.1016/j.neuroimage.2012.08.080>
- Kaup, A. R., Drummond, S. P. A., & Eyler, L. T. (2014). Brain Functional Correlates of Working Memory: Reduced Load-Modulated Activation and Deactivation in Aging without Hyperactivation or Functional Reorganization. *Journal of the International Neuropsychological Society*, 20(09), 945–950. <https://doi.org/10.1017/S1355617714000824>
- Kennedy, K. M., Boylan, M. A., Rieck, J. R., Foster, C. M., & Rodrigue, K. M. (2017). Dynamic range in BOLD modulation: lifespan aging trajectories and association with performance. *Neurobiology of Aging*, 60, 153–163. <https://doi.org/10.1016/j.neurobiolaging.2017.08.027>
- Krieger-Redwood, K., Jefferies, E., Karapanagiotidis, T., Seymour, R., Nunes, A., Ang, J. W. A., ... Smallwood, J. (2016). Down but not out in posterior cingulate cortex: Deactivation yet functional coupling with prefrontal cortex during demanding semantic cognition. *NeuroImage*, 141, 366–377. <https://doi.org/10.1016/j.neuroimage.2016.07.060>
- Kwon, S., Watanabe, M., Fischer, E., & Bartels, A. (2017). Attention reorganizes connectivity across networks in a frequency specific manner. *NeuroImage*, 144, (March 2016), 217–226. <https://doi.org/10.1016/j.neuroimage.2016.10.014>
- Lappin, J. S., Bell, H. H., Harm, O. J., & Kottas, B. (1975). On the relation between time and space in the visual discrimination of velocity. *Journal of Experimental Psychology. Human Perception and Performance*, 1 (4), 383–394.
- Lee, H. C., Cameron, D., & Lee, A. H. (2003). Assessing the driving performance of older adult drivers: On-road versus simulated driving. *Accident Analysis and Prevention*, 35(5), 797–803. [https://doi.org/10.1016/S0001-4575\(02\)00083-0](https://doi.org/10.1016/S0001-4575(02)00083-0)
- Lee, H. C., Drake, V., & Cameron, D. (2002). Feature Article Identification of appropriate assessment criteria to measure older adults' driving performance in simulated driving. *Australian Occupational Therapy Journal*, 49(3), 138–145. (November 2001),
- 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>
- Leung, H. C., Oh, H., Ferri, J., & Yi, Y. (2007). Load response functions in the human spatial working memory circuit during location memory updating. *NeuroImage*, 35(1), 368–377. <https://doi.org/10.1016/j.neuroimage.2006.12.012>
- Liang, X., Zou, Q., He, Y., & Yang, Y. (2016). Topologically reorganized connectivity architecture of default-mode, executive-control, and salience networks across working memory task loads. *Cerebral Cortex*, 26 (4), 1501–1511. <https://doi.org/10.1093/cercor/bhu316>
- 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>
- McKee, S. P. (1981). A local mechanism for differential velocity detection. *Vision Research*, 21(4), 491–500. [https://doi.org/10.1016/0042-6989\(81\)90095-X](https://doi.org/10.1016/0042-6989(81)90095-X)
- Nagel, I. E., Preuschhof, C., Li, S.-C., Nyberg, L., Bäckman, L., Lindenberger, U., & Heekeren, H. R. (2009). Performance level modulates adult age differences in brain activation during spatial working memory. *Proceedings of the National Academy of Sciences*, 106(52), 22552–22557. <https://doi.org/10.1073/pnas.0908238106>
- Norman, J. F., Ross, H. E., Hawkes, L. M., & Long, J. R. (2003). Aging and the perception of speed. *Perception*, 32(1), 85–96. <https://doi.org/10.1068/p3478>
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113. [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4)
- Orban, G. A., de Wolf, J., & Maes, H. (1984). Factors influencing velocity coding in the human visual system. *Vision Research*, 24(1), 33–39. [https://doi.org/10.1016/0042-6989\(84\)90141-X](https://doi.org/10.1016/0042-6989(84)90141-X)
- Orban, G. A., Dupont, P., De Bruyn, B., Vandenberghe, R., Rosier, A., & Mortelmans, L. (1998). Human brain activity related to speed discrimination tasks. *Experimental Brain Research*, 122(1), 9–22. <https://doi.org/10.1007/s002210050486>
- Papandonatos, G. D., Ott, B. R., Davis, J. D., Barco, P. P., & Carr, D. B. (2015). Clinical utility of the trail-making test as a predictor of driving performance in older adults. *Journal of the American Geriatrics Society*, 63(11), 2358–2364. <https://doi.org/10.1111/jgs.13776>
- Park, D. C., Polk, T. A., Hebrank, A. C., & Jenkins, L. J. (2010). Age differences in default mode activity on easy and difficult spatial judgment tasks. *Frontiers in Human Neuroscience*, 3(January), 75. <https://doi.org/10.3389/fnhum.2009.0075.2009>
- Park, S.-W., Choi, E. S., Lim, M. H., Kim, E. J., Hwang, S. I., Choi, K.-I., ... Jung, H.-E. (2011). Association between unsafe driving performance and cognitive-perceptual dysfunction in older drivers. *PM and R*, 3(3), 198–203. <https://doi.org/10.1016/j.pmrj.2010.12.008>

- Peirce, J. W. (2008). Generating stimuli for neuroscience using PsychoPy. *Frontiers in Neuroinformatics*, 2(January), 1–8. <https://doi.org/10.3389/neuro.11.010.2008>
- Persson, J., Pudas, S., Nilsson, L.-G., & Nyberg, L. (2014). Longitudinal assessment of default-mode brain function in aging. *Neurobiology of Aging*, 35(9), 2107–2117. <https://doi.org/10.1016/j.neurobiolaging.2014.03.012>
- Prakash, R. S., Heo, S., Voss, M. W., Patterson, B., & Kramer, A. F. (2012). Age-related differences in cortical recruitment and suppression: Implications for cognitive performance. *Behavioural Brain Research*, 230(1), 192–200. <https://doi.org/10.1016/j.bbr.2012.01.058>
- Raghuram, A., Lakshminarayanan, V., & Khanna, R. (2005). Psychophysical estimation of speed discrimination. II. Aging effects. *Journal of the Optical Society of America A*, 22(10), 2269–2280. <https://doi.org/10.1364/JOSAA.22.002269>
- Raichle, M. E. (2015). The brain's default mode network. *Annual Review of Neuroscience*, 38(1), 433–447. <https://doi.org/10.1146/annurev-neuro-071013-014030>
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, 98(2), 676–682. <https://doi.org/10.1073/pnas.98.2.676>
- Reuter-Lorenz, P. A., & Cappell, K. A. (2008). Neurocognitive ageing and the Compensation Hypothesis. *Current Directions in Psychological Science*, 17(3), 177–182.
- Reuter-Lorenz, P. A., & Park, D. C. (2014). How Does it STAC Up? Revisiting the scaffolding theory of aging and cognition. *Neuropsychology Review*, <https://doi.org/10.1007/s11065-014-9270-9>
- Rieck, J. R., Rodrigue, K. M., Boylan, M. A., & Kennedy, K. M. (2017). Age-related reduction of BOLD modulation to cognitive difficulty predicts poorer task accuracy and poorer fluid reasoning ability. *NeuroImage*, 147, (July 2016), 262–271. <https://doi.org/10.1016/j.neuroimage.2016.12.022>
- Sambataro, F., Murty, V. P., Callicott, J. H., Tan, H. Y., Das, S., Weinberger, D. R., & Mattay, V. S. (2010). Age-related alterations in default mode network: Impact on working memory performance. *Neurobiology of Aging*, 31(5), 839–852. <https://doi.org/10.1016/j.neurobiolaging.2008.05.022>
- Samu, D., Campbell, K. L., Tsvetanov, K. A., Shafto, M. A., Brayne, C., Bullmore, E. T., ... Tyler, L. K. (2017). Preserved cognitive functions with age are determined by domain-dependent shifts in network responsivity. *Nature Communications*, 8(May), 14743. <https://doi.org/10.1038/ncomms14743>
- Schweizer, T. A., Kan, K., Hung, Y., Tam, F., Naglie, G., & Graham, S. J. (2013). Brain activity during driving with distraction: An immersive fMRI study. *Frontiers in Human Neuroscience*, 7(February), 1–11. <https://doi.org/10.3389/fnhum.2013.00053>
- Scialfa, C. T., Guzy, L. T., Leibowitz, H. W., Garvey, P. M., & Tyrrell, R. A. (1991). Age differences in estimating vehicle velocity. *Psychology and Aging*, 6(1), 60–66. <https://doi.org/10.1037/0882-7974.6.1.60>
- Shanmugaratnam, S., Kass, S. J., & Arruda, J. E. (2010). Age differences in cognitive and psychomotor abilities and simulated driving. *Accident Analysis and Prevention*, 42(3), 802–808. <https://doi.org/10.1016/j.aap.2009.10.002>
- Siman-Tov, T., Bosak, N., Sprecher, E., Paz, R., Eran, A., Aharon-Peretz, J., & Kahn, I. (2017). Early age-related functional connectivity decline in high-order cognitive networks. *Frontiers in Aging Neuroscience*, 8(JAN), 1–17. <https://doi.org/10.3389/fnagi.2016.00330>
- Snowden, R. J., & Kavanagh, E. (2006). Motion perception in the ageing visual system: Minimum motion, motion coherence, and speed discrimination thresholds. *Perception*, 35(1), 9–24. <https://doi.org/10.1068/p5399>
- Stinchcombe, A., Gagnon, S., Zhang, J., Montembeault, P., & Bedard, M. (2011). Fluctuating Attentional Demand in a Simulated Driving Assessment: The Roles of Age and Driving Complexity. *Traffic Injury Prevention*, 12(6), 576–587. <https://doi.org/10.1080/15389588.2011.607479>
- Stutts, J. C., Stewart, J. R., & Martell, C. (1998). Cognitive test performance and crash risk in an older driver population. *Accident Analysis & Prevention*, 30(3), 337–346. [https://doi.org/10.1016/S0001-4575\(97\)00108-5](https://doi.org/10.1016/S0001-4575(97)00108-5)
- Sunaert, S., Van Hecke, P., Marchal, G., & Orban, G. A. (2000). Attention to Speed of Motion, Speed Discrimination, and Task Difficulty: An fMRI Study. *NeuroImage*, 11(6), 612–623. <https://doi.org/10.1006/nimg.2000.0587>
- Thompson, K. R., Johnson, A. M., Emerson, J. L., Dawson, J. D., Boer, E. R., & Rizzo, M. (2012). Distracted driving in elderly and middle-aged drivers. *Accident Analysis and Prevention*, 45, 711–717. <https://doi.org/10.1016/j.aap.2011.09.040>
- Turner, G. R., & Spreng, R. N. (2015). Prefrontal Engagement and Reduced Default Network Suppression Co-occur and Are Dynamically Coupled in Older Adults: The Default-Executive Coupling Hypothesis of Aging. *Journal of Cognitive Neuroscience*, 27(12), 2462–2476. https://doi.org/10.1162/jocn_a_00869
- Urwyler, P., Gruber, N., Müri, R. M., Jäger, M., Bieri, R., Nyffeler, T., ... Nef, T. (2015). Age-dependent visual exploration during simulated day- and night driving on a motorway: a cross-sectional study. *BMC Geriatrics*, 15(1), 18. <https://doi.org/10.1186/s12877-015-0015-2>
- Vatanserver, D., Menon, D. K., Manktelow, A. E., Sahakian, B. J., & Stamatidis, E. A. (2015). Default mode dynamics for global functional integration. *Journal of Neuroscience*, 35(46), 15254–15262. <https://doi.org/10.1523/JNEUROSCI.2135-15.2015>
- Vaucher, P., Herzig, D., Cardoso, I., Herzog, M. H., Mangin, P., & Favrat, B. (2014). The trail making test as a screening instrument for driving performance in older drivers; a translational research. *BMC Geriatrics*, 14(1), 123. <https://doi.org/10.1186/1471-2318-14-123>
- Whelihan, W. M., DiCarlo, M. A., & Paul, R. H. (2005). The relationship of neuropsychological functioning to driving competence in older persons with early cognitive decline. *Archives of Clinical Neuropsychology*, 20(2), 217–228. <https://doi.org/10.1016/j.acn.2004.07.002>

SUPPORTING INFORMATION

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How to cite this article: Eudave L, Martínez M, Luis EO, Pastor MA. Default-mode network dynamics are restricted during high speed discrimination in healthy aging: Associations with neurocognitive status and simulated driving behavior. *Hum Brain Mapp*. 2018;39:4196–4212. <https://doi.org/10.1002/hbm.24240>