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Sniffing out meaning: Chemosensory and semantic neural network changes in sommeliers

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Abstract

Wine tasting is a very complex process that integrates a combination of sensation, language, and memory. Taste and smell provide perceptual information that, together with the semantic narrative that converts flavor into words, seem to be processed differently between sommeliers and naïve wine consumers. We investigate whether sommeliers' wine experience shapes only chemosensory processing, as has been previously demonstrated, or if it also modulates the way in which the taste and olfactory circuits interact with the semantic network. Combining diffusion-weighted images and fMRI (activation and connectivity) we investigated whether brain response to tasting wine differs between sommeliers and nonexperts (1) in the sensory neural circuits representing flavor and/or (2) in the neural circuits for language and memory. We demonstrate that training in wine tasting shapes the microstructure of the left and right superior longitudinal fasciculus. Using mediation analysis, we showed that the experience modulates the relationship between fractional anisotropy and behavior: the higher the fractional anisotropy the higher the capacity to recognize wine complexity. In addition, we found functional differences between sommeliers and naïve consumers affecting the flavor sensory circuit, but also regions involved in semantic operations. The former reflects a capacity for differential sensory processing, while the latter reflects sommeliers' ability to attend to relevant sensory inputs and translate them into complex verbal descriptions. The enhanced synchronization between these apparently independent circuits suggests that sommeliers integrated these descriptions with previous semantic knowledge to optimize their capacity to distinguish between subtle differences in the qualitative character of the wine.

KEYWORDS

connectivity, flavor, fMRI, language network, sommelier, taste, wine

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1 | INTRODUCTION

“A very complex wine, as a result of blending Grenache, Cabernet Sauvignon, Carignan, and Syrah. Purple colored, with blue hues. Its aroma is concentrated and heady, covered with tobacco and ripe cherries. With moderate acidity and abundant earthy red fruits, it overlaps with coffee, licorice, and spices, all harmonized by the subtle and well-balanced tannins. Its presence in the mouth is long and with a final touch of peach.” (Description of 2012 Clos Mogador by a sommelier who participated in this study).

Wine tasting is a complex process that integrates sensory modalities of taste, smell, and oral somatosensation with language and memory. During this process, the expert taster uses typical vernacular to form a narrative that describes a wine's aroma, flavor, and structure—as we can appreciate from the above description. Aromas and flavors of wine provide rich information that can be experienced in different ways by wine experts (e.g., sommeliers) and nonexperts. Skilled sommeliers can extract information about the wine's origin, grape (varietal), producer, age, type of soil, acidity, tannins, and so forth, and also express the range of flavors and aromas which characterize a given wine (Croijmans et al., 2020; Paradis et al., 2019). The process of accurately describing and conveying information about wine is essential to the profession as many sommeliers directly interact with restaurant patrons and retailers to recommend wines. As such, sommeliers might differ from nonexperts in their linguistic or semantic capacities as they relate to wine (Spence & Wang, 2019; Wang & Spence, 2018). Here, we investigate whether sommeliers' wine experience shapes only the chemosensory circuit, as has been previously demonstrated, or if it also modulates the way in which the taste and olfactory circuits interact with the semantic network.

The functional and structural brain changes associated with experience have been documented in several domains including literacy (Carreiras et al., 2009), music (Herholz & Zatorre, 2012), and flavor (Banks et al., 2016; May, 2011). Analogously, previous research has highlighted that prior experience and the context in which the flavors are presented influence the response to flavors (de Araujo et al., 2013; Veldhuizen, 2017). Moreover, differences in functional brain activation between sommeliers and controls during wine tasting have also been reported (Castriota-Scanderbeg et al., 2005; Frost et al., 2015; Pazart et al., 2014). These activation patterns are particularly sensitive to specific wine characteristics, including alcohol content, and are observed in regions associated with chemosensory and emotional circuits (Frost et al., 2015; Plassmann et al., 2008). These findings suggest that sommeliers' experience in wine may shape the chemosensory circuitry both functionally and structurally, similar to how intensive training in other domains leads to cortical reorganization.

However, defining experience is challenging in wine-related research as the field of wine comprises many professions with varying levels of tenure and experience with tasting (winemakers, enology students, viticulturists, etc.). Experts are known to employ a

specialized vocabulary (Parr et al., 2011) to describe wine and such descriptions demonstrate greater consistency between experts compared to nonexperts (Croijmans & Majid, 2016). Crucially, sommeliers are assumed to have extensive wine tasting experience compared to other experts, which implies that studies using only sommeliers may differ from those of heterogeneous wine experts. Sommelier abilities have been observed to evolve over the course of their training. Novice sommelier students demonstrate a heightened ability to identify odors in an olfactory recognition test, but do not differ from controls in olfactory detection threshold or olfactory memory tests (Poupon et al., 2019). This is notable because flavors are identified by retronasal olfaction (Mozell et al., 1969). Another study that examined sommeliers with three different levels of experience found that all three groups outperformed novices in a wine recognition matching-to-sample task (Zucco et al., 2011). However, semantic experience, measured by the quantity and specificity of descriptors generated while smelling wine-relevant aromas, improved as a function of experience (Zucco et al., 2011).

The wine experience of sommeliers is based on the combination of discriminative abilities to perceive, process, and categorize subtle sensory differences in taste (e.g., sweetness, sourness) chemesthesis (e.g., astringency) and retronasal olfactory components of flavor (e.g., berry, earth) and of language and memory abilities to relate lexical labels to these perceptual distinctions (see Chen, 2020; Hughson & Boakes, 2001). Attaching labels to flavors in a way that makes these fine-grain perceptual distinctions possible is certainly a difficult feat. Whether recognition and identification of flavors in sommeliers are attributable to enhanced semantic knowledge and/or perceptual memory remains an open question (Ballester et al., 2008; Gawel, 1997; Parr et al., 2004). The precise mechanisms that coordinate activity between different neural ensembles, specifically the chemosensory and semantic circuits involved in the wine-tasting process, remain unclear (Carreiras et al., 2009; Herholz & Zatorre, 2012; Maguire et al., 2000). Activation of the language circuit is expected for sommeliers if their skills indeed heavily rely on their extensive flavor and aroma lexicon. However, changes in activation and/or changes in connectivity in the flavor circuit, especially in primary areas, are also expected if sommeliers rely on fine perceptual distinctions.

1.1 | Flavor perception

Flavor is a complex multisensory percept that results from the central integration of gustatory, oral somatosensory, and retronasal olfactory inputs (Small, 2012). These three discrete sensory modalities are derived from distinct receptors within the oral and nasal cavities, and project to the brain via separate cranial nerves. Taste refers to sensations such as sweet, sour, salty, savory, and bitter that are produced when molecules bind to discrete receptors along the tongue and soft palate. Oral somatosensory receptors blanket the oral cavity, such that mechanical and thermal stimulation give rise to sensations such as creaminess and coolness, while chemical stimulation

(chemesthesis) creates sensations such as astringency and spiciness (Green, 2018; Veldhuizen et al., 2020). Ethyl alcohol, which comprises ~9–15% of a typical wine, is associated with chemesthetic burning/tingling sensations as well as sweet and bitter tastes (Nolden & Hayes, 2015). Arguably, the most critical sensory afferents for flavor perception involve olfaction. Specifically, retronasal olfaction defines flavor identity and quality and occurs when volatiles traverse the oral cavity to bind to receptors in the olfactory epithelium (Mozell et al., 1969). This contrasts with orthonasal olfaction, where stimuli reach the olfactory epithelium directly through the nose (see Shepherd, 2006 for an overview of olfaction and flavor perception). Sensations of retronasal olfaction such as flavors of strawberry, coffee, or smoke, are often misattributed to the gustatory system because they are referred to the mouth. This illusion is driven by the “capture” of smell by taste perception (Lim & Johnson, 2010) and likely relies on neural computations in the somatomotor mouth cortical area (Small et al., 2005). Taste, smell, and somatosensory inputs interact at multiple levels of the neuroaxis. Flavor perception, however, is thought to depend upon a circuit encompassing the anterior cingulate cortex (ACC), anterior insula, and orbitofrontal cortex (OFC), where responses to combined taste and odor mixtures are greater than those to either component by itself (De Araujo et al., 2003; Small et al., 2004). This network also responds to spiciness (Kawakami et al., 2016), creaminess (Eldeghaidy et al., 2011), hunger (Führer et al., 2008; Siep et al., 2009), fullness (Veit et al., 2020), as well as expectations and attention (Veldhuizen et al., 2011).

The relationship between the flavor and lexico-semantics circuits has been previously examined (Barrós-Loscertales et al., 2012; Croijmans et al., 2021; González et al., 2006; Speed & Majid, 2020). A comprehensive review of cognitive and perceptual studies examining wine experience suggests that the effect of experience is primarily cognitive (Spence & Wang, 2019). Perceptually, most reports indicate that experts have comparable olfactory detection thresholds for wine-related aromas compared to controls. Additionally, experts appear to perform only modestly better (if at all) in taste/olfactory discrimination in triangle “odd-one-out” tests. However, experts were generally found to excel in matching wines to written descriptions, wine odor recognition, and categorizing wines by varietal (Spence & Wang, 2019). This review suggested that these findings reflect improved recognition memory and semantic memory abilities for wine stimuli in experts, compared to controls, paired with more structured and stable memory representations of wine sensory attributes. Finally, a more recent study that evaluated the contribution of language to memory of wine odors found superior odor recognition in wine experts than novices, but no effect of language (Croijmans et al., 2021). In Experiment 1, participants were presented with 24 odors from three categories (wine, wine-related, common scents) under two conditions: either overtly naming what they thought the odor was, or remaining silent (encoding phase). After a 10-min break, the original and 24 novel odors were presented in a recognition task. Results showed that experts outperformed novices at recognizing wine odors only, but that overt naming did not improve expert or novice recognition. A second experiment using a verbal interference

condition (keeping a digit span task in working memory while smelling) with written naming also found that experts outperformed novices at recognizing wine odors, but no main effect of interference was found. The lack of a general superior odor recognition in wine experts compared with novices is consistent with the view that experience is limited to a specific domain. The authors concluded that increased performance in experts is not linguistically grounded or dependent on the accuracy of naming (Croijmans et al., 2021).

1.2 | Neural correlates of wine tasting

The number of studies investigating the neural correlates of wine tasting in skilled sommeliers is very limited (Banks et al., 2016; Castriota-Scanderbeg et al., 2005; Pazart et al., 2014; Sreenivasan et al., 2017). A *blind* wine-tasting task conducted by Castriota-Scanderbeg et al. (2005) showed greater activation for sommeliers over controls in the left insula and adjoining OFC, areas implicated in gustatory/olfactory integration. In addition, they also reported bilateral recruitment of the dorsolateral prefrontal cortex in sommeliers compared to naïve participants, coupled with a decrease in the activation of the left amygdala, hippocampus, and right OFC. Unfortunately, this study included only seven participants per group, which limits the generalizability of the conclusions drawn. In contrast, Pazart et al. (2014) using the same task showed similar brain activations between experts and control subjects in the insula, OFC, and amygdala. However, sommeliers showed more activation in the brain stem and left hippocampal and parahippocampal formations, as well as the temporal pole. Some of the discrepancies between the two studies may be attributable to differences in procedure. Crucially, while Castriota-Scanderbeg et al. (2005) used glucose as baseline, Pazart et al. (2014) used water. Furthermore, Pazart et al. (2014) used two wines, one white and one red, while Castriota-Scanderbeg et al. (2005) used three: a white, a red, and a dessert wine. Both studies also used a relatively low number of trials and participants, which could have reduced the sensitivity for differences in activation.

The other two studies investigating this unique population are Banks et al. (2016) and Sreenivasan et al. (2017), which both used the same cohort to characterize functional differences in odor recognition and odor discrimination between sommeliers and controls. On the one hand, Banks et al. (2016) reported that sommeliers exhibited significantly increased activation in the right insula, an area related to olfactory perception, but also regions such as the right middle temporal gyrus and the right inferior parietal gyrus, which have been previously associated with memory-related processes. They also investigated differences between sommeliers and naïve consumers in brain structure. They reported an increase in gray-matter volume in the right insula and bilateral entorhinal cortex of sommeliers. The cortical thickness of the right entorhinal cortex correlated with experience, measured as years as a sommelier. However, it is important to keep in mind that these effects are statistically uncorrected for multiple comparisons and should be interpreted with caution. Finally, Sreenivasan et al. (2017) showed greater connectivity in functional

TABLE 1 Description of the wines used.

Commercial name	Wine type	Vintage	Producer	D.O.	Varietal	Region	Alcohol level	Complexity
La Calma	White	2011	Can Ràfols dels Caus	Penedès	Chenin blanc	Spain	13	--
As Sortes	White	2011	Bodegas Rafael Palacios	Valdeorras	Godello	Spain	14	-
Alion	Red	2012	Bodegas y Viñedos Alión	Ribera del Duero	Tinta del país 100% (Tempranillo)	Spain	14.5	+
Clos Mogador	Red	2012	Clos Mogador, S.C.C.L.	Priorat	Garnacha, Cabernet Sauvignon, Syrah, and Cariñena	Spain	15	++

Note: Notice that although color is not the subject of this research, in the present study there is an overlap between color and complexity: the most complex wines were reds, while the least complex were whites. The complexity was quantified by a group of oenologists from the Basque Culinary Center in San Sebastian (Spain) that was not included in the experimental sample. Although all four wines used are very complex, values ranging from “--” for the least complex to “++” for the most complex were used to characterize them according to complexity.

connections involving the precuneus, caudate, putamen, and several frontal and temporal regions as compared to nonexpert controls, while the controls showed increased connectivity from the left hippocampus to the frontal regions. Most connectivity differences involved multisensory integration and higher-order cognitive processes rather than the primary olfactory regions.

1.3 | The current study

We investigate structural connectivity differences in white matter between sommeliers and controls, and brain activation and functional connectivity differences in the same cohort during a passive *blind* wine tasting task. Our aim was to examine whether rigorous wine-related training shapes brain architecture, thus modulating the processing of the sensory information embedded in wines. Unlike previous studies, we selected four wines with varying complexity to investigate the effect of wine complexity on brain responses between sommeliers and controls (see Table 1). Complexity is a wine tasting term that describes a wine's flavor and is an integral component of wine quality. Though experts tend to agree on judgments of wine complexity, pure objective criteria for complexity are not immediately evident. Typically, “complex” wines are described by professionals as structured and well-balanced, having primary and secondary layers of flavors that carry a range of aromas that coalesce with textural qualities resulting in the subjective perception of depth and subtlety. The term suggests that keen perceptual senses are needed to fully tease apart and label the full array of flavors and aromas within the glass. Because of their extensive tasting experience, sommeliers may be able to extract more sensory information than controls from a complex wine. Thus, sommeliers may demonstrate more drastic differences in neural activation over control participants as the complexity of the wines increases. In sum, in the current study, we investigate (1) whether experience and training in wine tasting are associated with structural connectivity changes in the white-matter microstructure; (2) whether years of experience/training mediate the relationship between white-matter

microstructure and the capacity to assess wine complexity; and (3) and whether experience and training in wine tasting are associated with functional changes (brain activation and/or functional connectivity) in the flavor sensory circuit, and/or language circuit.

2 | MATERIALS AND METHODS

2.1 | Participants

Following the procedure described in Durnez et al. (2016), we used retrospective fMRI data collected by our group (Frost et al., 2015) to estimate the necessary sample size for a statistical power higher than 80%. Based on this power analysis, 28 healthy adults participated as volunteers in the current study reaching a power of 0.90 for the FDR correction (Benjamini & Hochberg, 1995). To minimize the influence of socioeconomic, cultural, or lifestyle factors that differentially affect each population, the present study followed a paired design. Then, 14 pairs of sommeliers and inexperienced wine consumers were recruited to minimize group differences in age (controls: mean = 37.47 [11.15 std.] years; sommeliers: mean = 38.53 [11.31 std.] years), gender (11 males per group) and educational level (all had pursued education after high school). To avoid including people with alcohol use disorders in the sample, participants in both groups underwent a questionnaire on drinking habits, which was used as an exclusion criterion. In addition, wine consumption habits were assessed and only those subjects who consumed wine on a regular basis, but not more than once per week, were classified as inexperienced wine consumers and selected for the control group. All participants, sommeliers and naive consumers, were nonsmokers. The sommeliers were selected as wine experts by the Basque Culinary Centre (years of professional training: mean = 12.81, STD = 12.46, minimum = 3, maximum = 40).

Participants had no self-reported psychiatric or neurological disorders, and no impairments in smell, taste, or digestion. They gave their written informed consent in accordance with guidelines

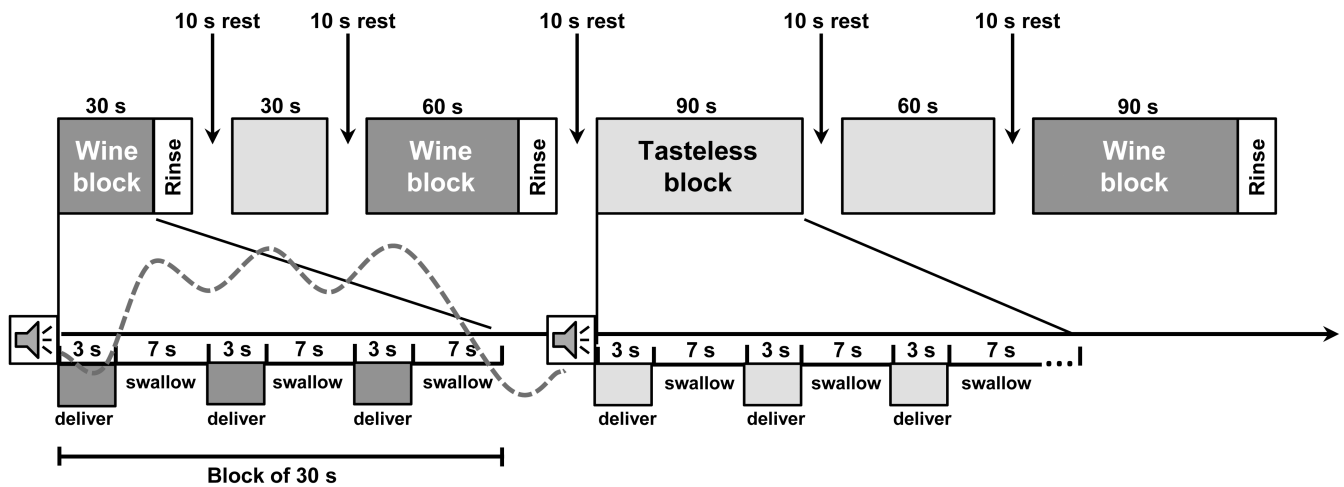


FIGURE 1 Each scan consists of a serial delivery of one of three different types of taste stimuli (a block). A block consists of a series of three, six, or nine presentations. An auditory cue was presented before each block to alert participants which type of stimuli (wine or solution) will be delivered. Each presentation starts with a 0.75 ml delivery of liquid over 3.00 s followed by a 7.00 s window to swallow. Each wine block was followed by a rinse (0.75 ml distilled water). Before the start of a new block, there was a rest period of 10 s. Blocks varied in length between 30 and 90 s, and the order of blocks was counterbalanced across subjects. The hemodynamic response function predicted for each block was schematically represented with the grey dotted line.

approved by the Ethics and Research Committees of the Basque Center on Cognition, Brain and Language (BCBL). Following BCBL data sharing policy, all data used in this study can be shared upon specific request to the authors and according to a formal data sharing agreement (https://www.bcbl.eu/DataSharing/HBM2023_Sommeliers).

2.2 | Stimuli and experimental design

Wine is a very complex entity with a wide range of flavors, aromas, alcohol content, tannins, and so forth. Nevertheless, assessment of wine can be highly influenced by expectations (Parr et al., 2003; Plassmann et al., 2008). Therefore, in the present study, we carried out a passive *blind* wine-tasting task, using magnetic resonance imaging to identify potential functional changes in response to white and red wines, so that participants were not informed about the wines they tasted within the scanner. Participants were required to taste and enjoy the wines during the resonance sessions.

Four different Spanish wines, two reds, and two whites, were selected by two experienced sommeliers who did not participate in the study. The wines varied in complexity enabling their classification as low (−−), moderately low (−), high (+), and very high (++) complexity (Table 1). Wine complexity is a multicomponent concept that does not necessarily reflect the chemical complexity of the wine. It is generally associated with the presence of many aromatic elements and it has been related to viticulture practices (e.g., grape varieties, irrigation, and oenological practices), grape skin maceration, micro-oxygenation, and microorganisms, among other factors (Wang & Spence, 2018). Complexity is perceived differently by experts and non-habitual consumers, but always as a result of multisensory

integration where the concept of balance remains a constant (Tempere et al., 2011; Tempère et al., 2018). Here, each participant was tested with the four wines, counterbalanced for the order of presentation. The tasteless solution consisted of 12.50 mM KCl and 1.25 mM NaHCO₃ in distilled water.

Solutions and wines were delivered through a gustometer system as 0.75 ml per trial, ~50 ml per session, and ~200 ml in total. The gustometer system consisted of 11 programmable BS-8000 syringe pumps (Braintree Scientific, Braintree, MA, USA) connected to a computer. This computer was synchronized with the scanner through a parallel port. Each pump controlled a 60 ml syringe connected to a 15-foot length of Tygon beverage tubing (Saint-Gobain Performance Plastics, Akron, OH, USA) that was passed through the waveguide to the magnet room. These tubes were attached to ports in a gustatory manifold that was anchored to the MRI head coil. When triggered, the pumps delivered the 0.75 ml bolus of liquid into the subjects' mouths. This system has been used and described in previous neuroimaging studies (Small et al., 2003; Small et al., 2008; Veldhuizen et al., 2011).

Each subject participated in four consecutive sessions consisting of four randomized repetitions of a block-design functional scan (Frost et al., 2015) (see Figure 1). Each session consisted of a serial delivery of two different wines (either, two white wines or two red wines) and a tasteless solution. An auditory cue was presented before each tasting period to alert participants about which type of stimuli (wine or tasteless solution) would be delivered. To optimize the design statistical efficiency, the duration of the taste period was randomized across blocks (18.00, 36.00, and 45.00 s, in the proportion of 3:3:3). At the end of each wine block, the tasteless solution was delivered in order to rinse the mouth and prepare participants for the next block. After that, a

baseline rest period was presented for 10 s. A total of eight blocks per wine were included in each session.

To avoid fatigue effects due to the duration and complexity of the task within the scanner, white and red wines were tested in different sessions. After each functional scanner session, participants completed a *blind* wine discrimination task. They received a set of 16 wine glasses organized in eight pairs containing two different wines, the same ones as used in the scanner (either, eight pairs of white wines or eight pairs of red wines). They were asked to taste the series of samples and classify the wines within each pair according to complexity. Participants were asked not to swallow the wines. Following the pattern used in the MRI session, white and red wines were tested separately.

2.3 | Image acquisition

Scanning was carried out on a Siemens MAGNETOM Trio, A Tim System 3-T scanner, using a standard 32-channel phased-array surface coil (Siemens, Erlangen, Germany). Functional event-related scans consisted of 262 echoplanar images acquired using a T2*-weighted gradient-echo pulse sequence with the following parameters: field of view (FOV; read) = 192 mm; FOV (phase) = 100%; base resolution = 76 pixels; phase resolution = 100%; echo time (ET) = 30 ms; repetition time (RT) = 3 s; time gap = no; flip angle = 90°; slices number = 46; slice thickness = 2.50 mm; in-plane resolution = 2.50 × 2.50 mm; orientation = axial; distance factor = 25%. In addition, an MPRAGE T1-weighted structural image (1 × 1 × 1 mm resolution) was acquired with the following parameters: TE = 2.97 ms, TR = 2530 ms, flip angle = 7° and FOV = 256 × 256 × 160 mm³. This yielded 176 contiguous 1 mm thick slices. Diffusion-weighted images (DWIs) were recorded by using a single-shot spin-echo diffusion-weighted echoplanar pulse sequence from 65 directions, 64 at *b*-value = 1500 s/mm², and one unweighted b₀ image. DWI-MRI were obtained along 58 contiguous slices with an isotropic voxel resolution with the following parameters: RT = 9300, ET = 99 ms, FOV = 1840 × 1840 mm², flip angle = 90°, voxel resolution = 1.80 mm³.

2.4 | DWI-MRI analysis

DWI images were processed by using FMRIB's Diffusion Toolbox included in the FSL Software Library. Eddy currents correction was applied to correct for the gradient coil distortions and participant head motions using affine registration to the b₀ image. After correction, individual diffusion parameters were estimated in each voxel. Mask brain definition was performed on the non-DWI using FSL-BET (Behrens et al., 2003). DTI fit was used to estimate each voxel's fractional anisotropy (FA) values per participant (Behrens et al., 2003). This measure describes the directional selectivity of the diffusion of water molecules (Pierpaoli & Basser, 1996). FA values close to 1.0 (maximum) are observed along highly myelinated white matter tracts, whereas areas where

the water molecule motion is random and isotropic exhibit FA values close to zero. FA values depend on axonal properties such as myelination levels, the degree of crossing fibers, axonal density, and mean axonal diameter (Beaulieu, 2002). Tract-based Spatial Statistics was used to solve the alignment and correspondence problem typically affecting voxel-based morphometry analysis (Smith et al., 2006). Following the procedure described by Smith et al. (2006), this issue is sorted by estimating a group mean FA skeleton, which represents the centers of all fiber bundles. Individual aligned FA data were then projected onto this skeleton and the resulting data were included in further statistical analysis. GLM analyses using paired samples were performed using individual FA skeletonized maps as dependent variables, including group (sommeliers and naïve consumers) as a between-subjects factor. The gender and the age of each participant were included as a nuisance covariate.

Following the identification of structural group differences, we performed a mediation analysis (Hayes, 2009; Tingley et al., 2013) to evaluate the following question: Does the relationship between structural changes and behavior find full mediation through the duration of experience, as represented by years of training? This statistical method excels in capturing the intricate web of relationships at play, aligning with the complexity inherent in such phenomena. This analysis was performed using ULLRToolbox (<https://sites.google.com/site/ullrtoolbox/>) based on R. Due to inadequate sample sizes within the sommelier group for an in-depth analysis exploring the direct relationship between years of experience and SLF structural features, all 48 participants were included in the analysis. We considered SLF FA values as dependent variable (treatment), years of experience/training as mediator, and participant's performance on the passive blind wine tasting task as outcome. The naïve consumers have zero years of experience, and instead of zero, we employed “eps” which is the smallest computationally definable number, to calculate the relevant statistics. This analysis comprise the estimation of two different statistical models (see Figure S1 and Figure 2c):

- a. Model 1—response model—aims to estimate the potential direct relationships between years of experience and behavior, as well as between the physiological variable (i.e., FA) and behavior.
- b. Model 2—mediator model—hypothesizes that the association between SLF FA values and behavior is necessarily mediated by years of experience. This model does not account for the possibility that an individual with FA similar to the control group, but lacking formal training, might exhibit behavioral traits akin to those of the expert group.

For each of these models, we calculated the average mediation effect (ACME). This effect quantifies the influence exerted by the mediator variable, in this scenario, years of experience, on the relationship between the independent variable (or treatment) and the dependent variable (or outcome). Additionally, we determined the average direct effect of the

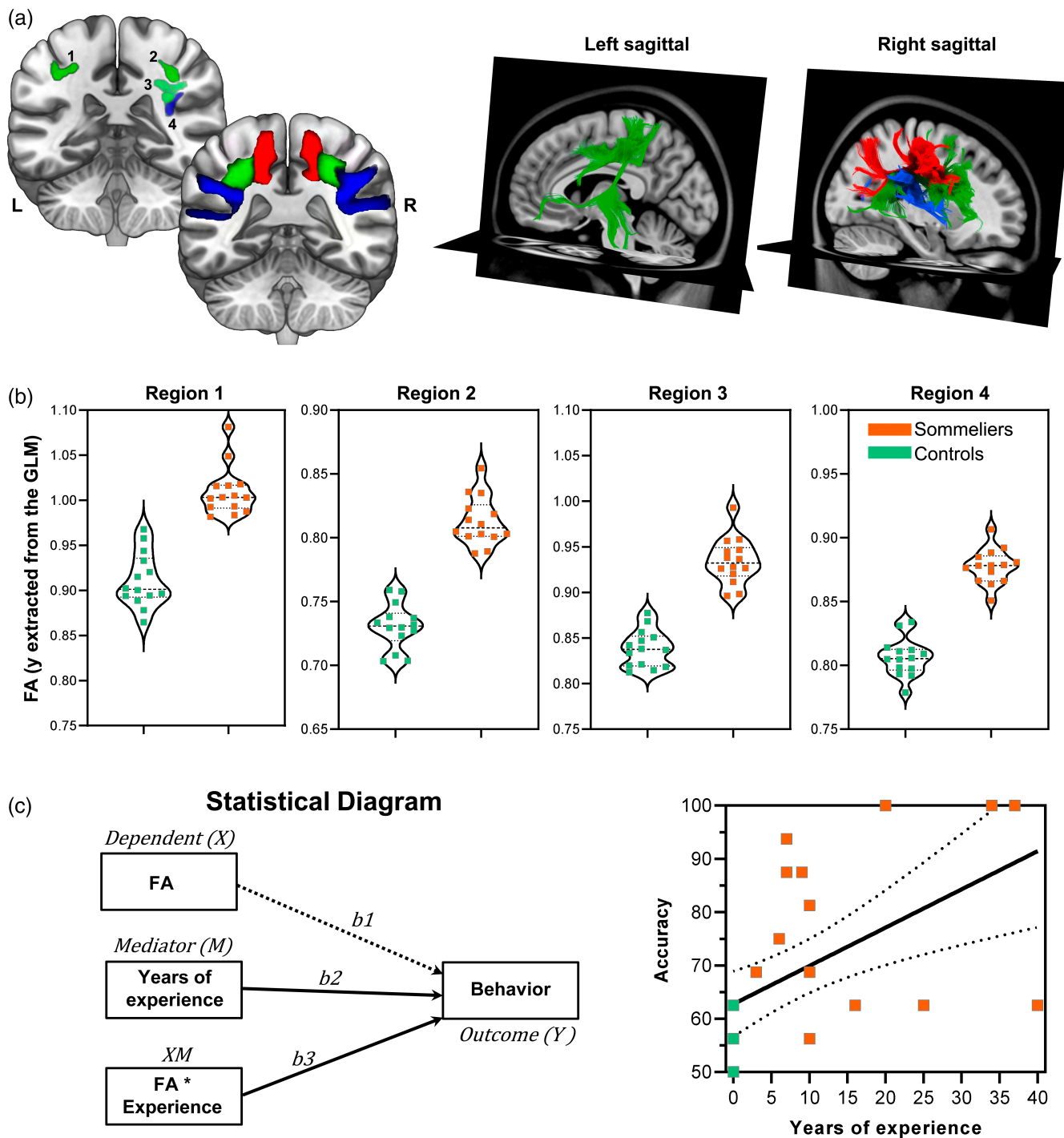


FIGURE 2 (a) Increase of fractional anisotropy (FA) in sommeliers as compared to naïve consumers in the superior longitudinal fasciculus (I, II, and III). (b) Macrostructural white matter (WM) connectivity in the atlas for SLF I, II, and III. (c) Violin plots for the four WM regions showing differences between sommeliers and controls. (d) Mediation analyses showing the effect of years of experience in the relationship between FA and the ability to discriminate wine complexity. The four clusters exhibiting significant differences between sommeliers and naïve consumers were used: three clusters within the right superior longitudinal fasciculus (I, II, and III) and one cluster within the left superior longitudinal fasciculus I. To assist us in interpreting the mediation result, we have represented the relationship between years of experience and performance in the discrimination task, and the differences in FA between the groups.

independent variable on the dependent variable (ADE). To enhance the statistical robustness of these estimations, we represented both the ACME and ADE as population averages.

These averages were derived from 1000 bootstrap random samples extracted from the dataset, thereby bolstering the accuracy and reliability of our results.

2.5 | GLM-based functional data analysis

Functional data were analyzed using SPM and related toolboxes (<http://www.fil.ion.ucl.ac.uk/spm>). Raw functional scans were time-slice corrected taking the middle slice as reference, spatially realigned, unwrapped, coregistered with the anatomical T1 (Collignon et al., 1995), and normalized to the MNI space using the unified normalization segmentation procedure. Global effects were then removed using a voxel-level linear model of the global signal proposed by Macey et al. (2004). Detrending fMRI time series were then smoothed using an isotropic 8 mm Gaussian kernel. The resulting time series from each voxel were high-pass filtered (128 s cut-off period).

Statistical parametric maps were generated by modeling the univariate general linear model, using, for each stimulus type (i.e., white wine with low complexity [wW^-]; white wine with high complexity [wW^-]; red wine with low complexity [rW^+]; red wine with high complexity [rW^{++}]), a regressor obtained by convolving the canonical hemodynamic response function with delta functions at block onsets with a duration corresponding to the length of each block. Tasteless trials were included as a regressor with a fixed duration of zero, and the six motion-correction parameters were included as nuisance regressors. Parameters of the GLM were estimated with a robust weighted-least-squares regression that also corrected for temporal autocorrelation in the data (<http://www.bangor.ac.uk/~pss412/imaging/robustWLS.html>) (Diedrichsen & Shadmehr, 2005). Pair-wise contrasts were performed comparing activity to each of the four critical conditions relative to the tasteless condition. Resulting contrast images were then used for the second-level 2×4 flexible factorial design with Group (sommeliers vs. naïve consumers) and Type of Wines (i.e., wW^- , wW^- , rW^+ , rW^{++}) as between-subject and within-subject factors, respectively.

Here, we use the family-wise error rate correction (FWER) combining both voxelwise and clusterwise levels of inference (degrees of freedom = [1,78]). This method combines the total number of comparisons with the spatial distribution of the data based on random field theory (see Nichols & Hayasaka, 2003 for further details). Clusters were defined as sets of contiguous voxels whose intensity exceeds a preselected cluster-defining threshold, then the null hypothesis was tested by examining whether the spatial extent of these clusters was larger than would be expected by chance. The local maximum peaks reported in the tables had T values greater than 4.9 which corresponds to a probability value lower than 0.05 using the FWER correction. All local maxima are reported as MNI coordinates (Evans et al., 1993).

2.6 | Functional connectivity analysis

We explored whether the regions resulting as significant from the functional analysis show differential coupling with other brain

regions depending on the group (sommeliers vs. naïve consumers). Here, generalized psychophysiological interactions (gPPI, <http://www.nitrc.org/projects/gppi>) (McLaren et al., 2012) were used to estimate individual whole-brain connectivity. This approach allowed us to individually explore whether the response pattern of a seed region would predict the response pattern in another region dependent on the context, without making any assumptions regarding the relationships between experimental conditions (Friston, 2011). The design matrix used to estimate possible psychophysiological interactions spanned the whole experimental space described above. For each experimental condition, a regressor obtained by convolving the canonical hemodynamic response function with delta functions at stimulus onsets was included as a dependent variable. Similarly, for each experimental condition, the gPPI terms that resulted from the convolution of the canonical HRF with the multiplication of the deconvolved neural response of the seed ROI and the task-related time course per condition were also included as explanatory variables. These models also comprised the deconvolved brain response for the corresponding seed ROI and also the six motion-correction parameters as regressors. After the estimation of each general linear model (per seed ROI, per participant), pair-wise contrasts comparing activity to each of the four critical conditions relative to the *Tasteless* condition were performed.

Here, a multiregional approach was performed (O'Reilly et al., 2012; Zalesky et al., 2012) including 30 spherical seed regions that were built in MNI space. Each ROI was defined for each participant as the first eigenvariate of the time series of all active voxels within 6 mm radius spheres centered on the maximum peak of activation resulting from the group-level F -test contrast wines versus tasteless ($p < 0.05$ FWER corrected at the peak level). After the estimation of each general linear model (per seed ROI, per participant), 30×30 connectivity matrices were created by averaging the β values of the voxels within each ROI, corresponding to the psychophysiological interaction effects for each condition. To identify reliable connections between pairs of regions at the group level, we included the individual connectivity matrices in a second-level analysis, using the Network-Based Statistic (NBS) toolbox (Zalesky et al., 2010) following a repeated measures ANOVA design. To make population inferences, the NBS creates a new set of data thresholding (T score > 3.435) for each pair-wise association included in the individual connectivity matrices. The network of connections emerging from this procedure (i.e., exceeding the threshold) was fed into a nonparametric permutation test (10,000 random permutations) across participants used to establish the significance of the number of connections of the network assigning a p -value controlled for multiple comparisons (FWER, $p < .05$). In addition, for those ROIs resulting from the interaction effect, individual gPPI contrast images were entered into a second-level 2×4 ANOVA with group (sommeliers vs. naïve consumers) and Type of Wines (i.e., wW^- , wW^- , rW^+ , rW^{++}) as between-subject and within-subject factors, respectively. Only those clusters with a p -

value corrected for multiple comparisons (FWER, $p < .05$) were considered significant.

3 | RESULTS

3.1 | Behavioral result of the passive blind wine tasting task

Sommeliers showed better abilities to discriminate wine complexity as compared to naïve consumers (sommeliers: mean accuracy = 79.02%; SD = 15.81, naïve consumers: mean accuracy = 58.48%; SD = 3.96). Wilcoxon matched-pairs signed rank test statistically confirmed this difference (sum of signed ranks [W] = 88.00; p -value = .0007; median of differences = 21.88).

3.2 | Microstructural differences between sommeliers and naïve consumers

To investigate possible white matter microstructural differences between sommeliers and naïve consumers we included the individual FA maps on a GLM analysis. We observed three clusters within the right superior longitudinal fasciculus (I, II, and III) and one cluster within the left superior longitudinal fasciculus I exhibiting an increase of FA in sommeliers as compared to naïve consumers (Figure 2a–c).

A mediation analysis was performed to test the role of years of experience in the relationship between SLF FA resulting from the above analysis and the ability to discriminate wine complexity. The results are depicted in Figure 2d, the response model (Model 1) is represented by the triangle on the left, where the years of experience and the white matter microstructure act as predictors of behavioral performance. The mediator model (Model 2) is represented on the right, where the effect of the treatment (white matter microstructure) over the outcome (participant's performance) is transmitted through a mediator (years of experience). This analysis revealed a significant direct effect of FA on years of experience ($ai: \beta = 8.60, t = 5.12, p < .0001$), and a significant direct effect of the mediator “years of experience” on the behavioral performance during the passive *blind* wine tasting task ($bi: \beta = 0.91, t = 2.29, p < .05$). The direct relationship between white matter microstructure and participant's performance was not significant. Interestingly, a significant effect of FA on behavioral performance through years of experience was found (ACME: $\beta = 7.77$ (CI: 0.76 – 16.22), $p = .016$). The direct effect of FA on behavioral scores, once the indirect effect through years of experience had been subtracted, was not significant ($ci: \beta = -8.72, t = -1.82, p > .05$).

3.3 | Brain response to wines

To characterize the functional neuroanatomical network associated with flavor processing we computed a whole-brain contrast

comparing wines against the control tasteless solution across all participants. Table 2 and Figure 3 show the areas resulting from this contrast (wines vs. tasteless), involving a bilateral set of regions typically associated with taste and flavor processing: anterior and posterior insula, Rolandic operculum, basal ganglia (including the caudate), putamen, thalamus, OFC, and cerebellum. Other regions such as the postcentral gyrus, the supplementary motor area, the inferior parietal, supramarginal, and angular gyri, as well as the anterior/middle cingulate cortex and the superior/middle temporal gyrus, exhibited changes in their brain activation patterns as a function of the stimulus type (i.e., wines or tasteless solution; see Frost et al., 2015 for a similar activation with different wines and different participants). Though these regions are not specifically related to taste processing, some are associated with language processing.

3.4 | Functional brain differences between sommeliers and naïve consumers modulated by the type of wine

To determine whether the activation profile of any of these areas varies as a function of the participant's experience and type of wine we extracted the main effect of group (i.e., sommeliers vs. naïve consumers) from the 2×4 ANOVA (see Table 3 and Figure 4), but more importantly the interaction between the two factors (see Table 3 and Figure 4). The interaction between group (i.e., sommeliers and naïve consumers) and Type of Wine (i.e., wW–, wW+, rW–, rW++) revealed many areas where activation was modulated by experience and wine type including the right middle and superior temporal gyrus, Rolandic operculum, fusiform gyrus, hippocampus, amygdala, and pallidum, as well as bilateral middle and superior frontal gyri. More specifically, as depicted in Figure 5, differences emerge between the groups when examining the wine's complexity; the red wine with very high complexity produces greater differences in brain responses than the white wine with low complexity in sommeliers but not in naïve consumers.

3.5 | Functional connectivity differences between sommeliers and naïve consumers

To characterize the synchrony and interplay between the 30 nodes resulting from the group-level F -test contrast wines versus tasteless, condition-dependent functional connectivity analyses were performed at both global and local network scales. First, we used the NBS (Zalesky et al., 2010) to compare the global network configuration across groups. Significant direct functional interactions were found in 40 out of 420 possible connections (see Figure 6). This analysis reveals increased connectivity in Sommeliers compared to controls affecting critical areas associated with the sensory neural circuits representing flavor and the neural circuits for language and memory.

TABLE 2 Statistical results of the contrast wines versus tasteless.

All wines versus tasteless							
	Hemisp.	Coord (mm)			Cluster level		Peak level
		x	y	z	p (FWE-corr)	Size (voxels)	F
Postcentral	R	56	-4	24	.000	6516	83.18
Rolandic_Oper		56	14	0	.000	6516	78.59
Supp_Motor_Area		6	0	64	.000	750	20.87
Parietal_Inf		52	-38	56	.000	170	13.54
Supramarginal		60	-28	24	.000	170	10.39
Angular		49	-57	27	.000	170	8.73
Cingulum_Mid		6	10	46	.000	750	12.56
Cingulum_Ant		16	46	6	.000	8672	25.46
Precuneus		10	-54	20	.000	8080	23.44
Temporal_Pole_Mid		34	18	-38	.000	2448	21.30
Temporal_Mid_ant		58	-10	-16	.000	2448	18.60
Temporal_Mid_post		56	-32	-12	.000	88	10.40
Fusiform		28	-36	-16	.000	2448	26.66
Thalamus		12	-16	6	.000	171	11.17
Cerebelum_6		18	-62	-20	.000	4962	42.45
Frontal_Sup_Medial	L	-14	52	2	.000	8672	27.77
Postcentral		-58	-6	24	.000	5418	61.13
Supramarginal		-61	-27	24	.000	1719	9.15
Parietal_Inf		-55	-40	40	.000	1719	9.42
Angular		-43	-71	32	.000	1719	11.77
Temporal_Mid_post		-44	-68	20	.000	1719	14.91
Temporal_Mid_ant		-62	-4	-20	.000	718	14.12
Temporal_Mid_medial		-50	-14	-16	.000	718	12.87
Temporal_Pole_Mid		-50	14	-30	.000	718	14.05
Fusiform		-28	-42	-10	.000	492	17.93
ParaHippocampal		-28	-26	-18	.000	492	11.98
Occipital_Sup		-24	-80	38	.000	1719	26.61
Occipital_Mid		-38	-78	34	.000	1719	23.27
Thalamus		-12	-20	0	.000	171	13.05
Cerebelum_6		-22	-66	-20	.000	4962	73.05

Figure 4 contains a detailed characterization of the connectivity profile of each node.

Additionally, we explored whole-brain connectivity profiles of the right middle temporal gyrus and the right superior frontal gyrus—the two clusters that exhibited significant interaction effects (i.e., group by type of wine). We investigated the functional connectivity of these clusters focusing on the differences between sommeliers and naïve consumers. This approach demonstrated that the connectivity pattern of the right superior frontal gyrus was similar across the two groups. However, whole-brain connectivity using the right middle temporal gyrus as seed identified a network showing significantly ($p < .05$, FWER corrected) increased connectivity in sommeliers compared to controls (Network 1) and a network showing the opposite pattern—that is, decreased connectivity in sommeliers compared to controls

(Network 2). These networks comprised 22 links, involving different brain regions in both hemispheres (Figure 7). Network 1 comprises 15 regions distributed in both hemispheres: right fusiform, right hippocampus, right amygdala, right orbitofrontal area, right insula, right and left posterior middle temporal gyrus, right and left middle occipital, left precuneus, and left pons. Whereas Network 2 is restricted to frontal regions and includes the right middle frontal gyrus, right and left ACC, superior frontal gyrus, and the supplementary motor area.

4 | DISCUSSION

Sommeliers are a unique population of individuals with extensive experience in learning and identifying specific features of wine based

All Wines vs Tasteless distinguishing between groups

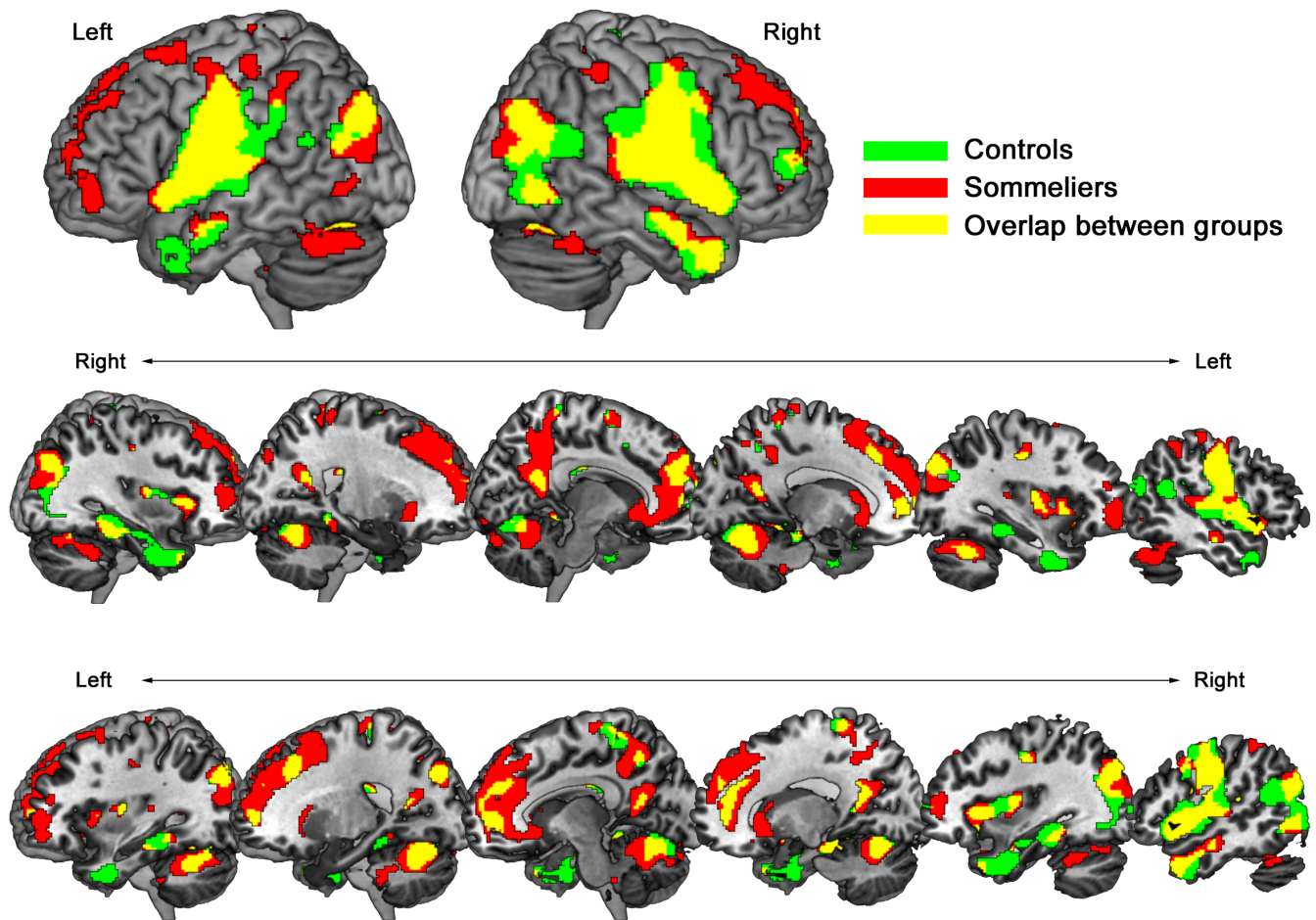


FIGURE 3 Brain activation for wine versus tasteless for naïve consumers (in green), sommeliers (in red), and the overlap between the two groups.

on subtle flavor cues. Here, we show functional (activation and connectivity) as well as structural differences between sommeliers and untrained controls (naïve consumers) in flavor and language circuits. As predicted, we observed that wine complexity amplified differential brain responses between sommeliers and naïve consumers. The structural contrasts showed that sommeliers, compared to controls, demonstrated microstructural changes affecting white matter tracts. We observed three clusters within the right superior longitudinal fasciculus (I, II, and III) and one cluster within the left superior longitudinal fasciculus I exhibiting an increase of FA in sommeliers as compared to naïve consumers. Mediation analyses have revealed significant associations involving SLF microstructure, years of experience, and behavioral outcomes. Notably, an interesting pattern emerges wherein the link between SLF FA and the capacity to discern wine complexity is fully mediated by years of experience.

As far as the SLF are concerned, this track connects the superior parietal lobe (SLF-I), the angular gyrus (SLF-II), and the supramarginal gyrus (SLF-III), to ipsilateral frontal and opercular areas (Dick &

Tremblay, 2012; Kamali et al., 2014; Makris et al., 2005; Martino et al., 2013). In particular, SLF-I links the superior parietal and superior frontal regions extending to the dorsal premotor and dorsolateral prefrontal areas. The SLF-II travels above the insula connecting the angular gyrus to caudal dorsolateral prefrontal regions. Finally, The SLF-III connects the supramarginal gyrus to ventral prefrontal regions. This large bundle of white matter fibers is involved in core processes such as attention, executive processes, memory, emotions, and language, all of which operate during wine tasting. Indeed, it has been reported that FA and axial diffusivity values of the bilateral superior longitudinal fasciculus positively correlate with executive functions, while FA values of the left superior longitudinal fasciculus correlate with attention and language (Urger et al., 2015). Specifically, FA in the left longitudinal fasciculus correlates positively with the speed of processing in visual word recognition (Gold et al., 2007) while FA damage correlates with language dysfunction in syntactic comprehension and production (Wilson et al., 2011). In addition, associations of FA changes and processes related to taste/odor/flavor have been also reported, and

TABLE 3 Flexible factorial analysis using group and type of wine as between-subject and within-subject factors, respectively.

Main effect of group							
	Hemisp.	Coord (mm)			Cluster level		Peak level
		x	y	z	p-Values (FWE-corr)	Size (voxels)	T
Frontal_Mid	R	38	50	12	.063	276	-7.37
Frontal_Sup		22	22	44	.003	598	-5.89
Cingulum_Ant		10	48	8	.000	1216	-5.41
Temporal_Sup		62	-2	-2	.194	174	-6.20
Precuneus		6	-46	42	.000	1231	-5.75
Thalamus		12	-14	16	.187	177	-4.87
Frontal_Sup	L	-24	14	66	.008	490	-6.81
Frontal_Mid		-26	4	52	.009	490	-3.98
Frontal_Med_Orb		-12	40	-10	.000	1216	-5.17
Frontal_Sup		-18	42	32	.001	789	-4.99
Frontal_Mid		-24	48	10	.002	789	-4.93
Precuneus		-2	-46	44	.000	1231	-5.88
Postcentral	R	58	-2	26	.011	453	+6.50
Cerebellum_Crus2		8	-82	-28	.395	112	+5.28
Postcentral	L	-60	-8	34	.068	269	+5.60
Precentral		-46	-4	58	.724	55	+5.47
Temporal_Mid		-46	-47	20	.133	207	+5.61
Cerebellum_6		-20	-64	-20	.000	3286	+7.92
Main effect of type of wine							
Temporal_Sup	R	62	0	2	.709	226	-4.76
Temporal_Pole_Sup		56	16	-6	.709	226	-4.51
Frontal_Sup	L	-14	12	58	.000	2116	+4.80
Frontal_Sup_Medial		0	30	58	.000	2116	+4.69
Precentral		-46	8	44	.000	2116	+4.74
Interaction effect							
Temporal_Mid	R	58	-16	-12	.000	2401	-6.00
Temporal_Sup		52	-4	-6	.000	2401	-4.39
Rolandic_Oper		48	-21	12	.000	2401	-3.29
Fusiform		26	-34	-20	.000	2401	-4.30
ParaHippocampal		24	-8	-24	.000	2401	-3.27
Hippocampus		28	-18	-16	.000	2401	-3.39
Amygdala		31	-4	-10	.000	2401	-3.14
Pallidum		27	-2	-5	.000	2401	-3.25
Frontal_Mid	R	38	56	8	.014	988	+4.57
Frontal_Sup	L	-40	48	14	.002	1420	+5.38

Note: Values highlighted in bold are because, in addition to reaching significance with the established cluster-based criterion, they also reach it taking into account the peak of activation.

quantitative meta-analysis of DTI studies identified decreased FA in the left SLF-II in patients with anorexia nervosa as compared to healthy controls (Barona et al., 2019; Gaudio et al., 2019). It has also been found that FA in the SLF correlates with olfactory performance (Segura et al., 2013). In sum, the white matter changes observed in the SLF in sommeliers point to its pivotal engagement in cognitive

functions involved in sommeliers' experience. Future research should investigate further the relations of the SLF with language and chemo-sensory processing.

Differences in white matter tracts between sommeliers and naïve controls could be caused by training and/or a biological predisposition. In other words, the changes in white matter brain reorganization

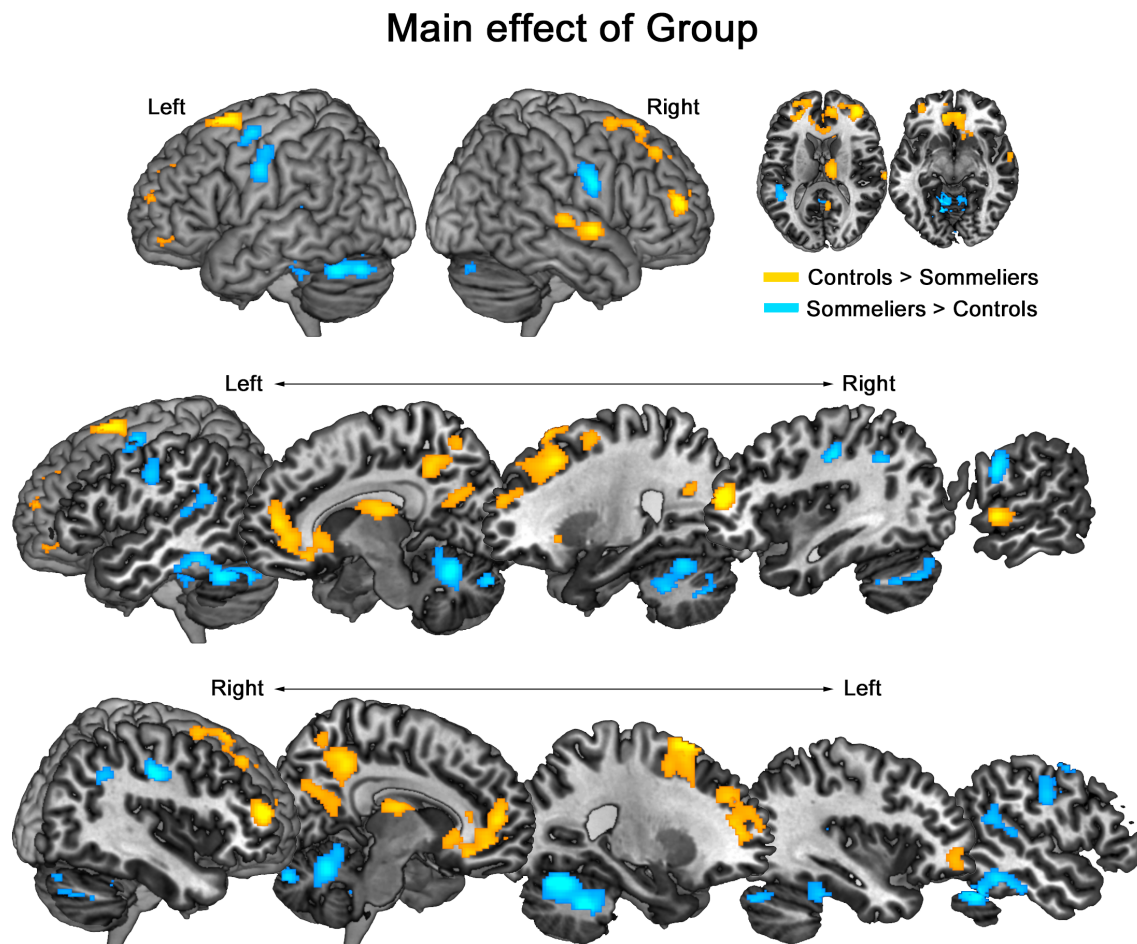


FIGURE 4 Main effect of group. Controls > sommeliers in yellow. Sommeliers > controls in blue.

observed for sommeliers as compared to naïve controls could be a response to learning or caused by a specific brain bias to chemosensory processing. Here, we try to assess this hypothesis by examining whether the relation between white matter pathways and behavior was mediated by years of experience. Our mediation analysis shows that the relation between FA and the ability to discriminate wine complexity is indeed mediated by years of practice. Thus, while we cannot fully discard that some biological predisposition to become a sommelier is at work, the present data show that years of experience (i.e., training) play an important role. While it holds promise to explore alternative models that could shed light on the interplay among these variables, such endeavors necessitate a larger sample size. Delving into a deeper comprehension of the intricate connection between tract microstructure and years of experience proves to be a captivating avenue. The question arises whether microstructural transformations unfold in tandem with subject specialization and/or if this very architecture forms the bedrock of successful learning. Unveiling these intricacies would entail longitudinal designs that trace the structural shifts intertwined with the trajectory of taste training.

On the other hand, our results also demonstrate that flavor perception depends upon the integration of gustatory, olfactory, and oral somatosensory inputs that are integrated into flavor perceptions by a

network spanning the anterior and ventral insula, anterior cingulate, and OFC. This perfectly matches with what has been found by other authors (De Araujo et al., 2003; Small et al., 2004). The piriform primary olfactory cortex is the major output for the olfactory bulbs and has dense connections with both limbic and paralimbic regions. However, it lacks strong connections with cortical areas that may link an odor with lexicosemantic content. This arrangement may account for the rich emotional and experiential aspects of olfaction, as well as the difficulty that many have with naming specific aromas (Olofsson & Gottfried, 2015). Retronasal, as opposed to orthonasal, olfaction enables the identification of flavors (Mozell et al., 1969) and therefore is often considered dominant in flavor perception.

Both the hemodynamic response analysis by condition and the functional connectivity results support the complexity of this process in cognitive and neural terms. Regardless of experience, both groups recruited a widely distributed network that included limbic structures such as the amygdala, ACC, and OFC. Functional connectivity analysis showed an interaction between these regions and language-related areas. Consistently, there is evidence demonstrating that olfactory labels—typically attributed to objects—have qualities and connotations that can bias olfactory perception (De Araujo et al., 2005). Thus, by changing the object an odor is attributed to, the perception of that

Interaction between Group and Type of Wine

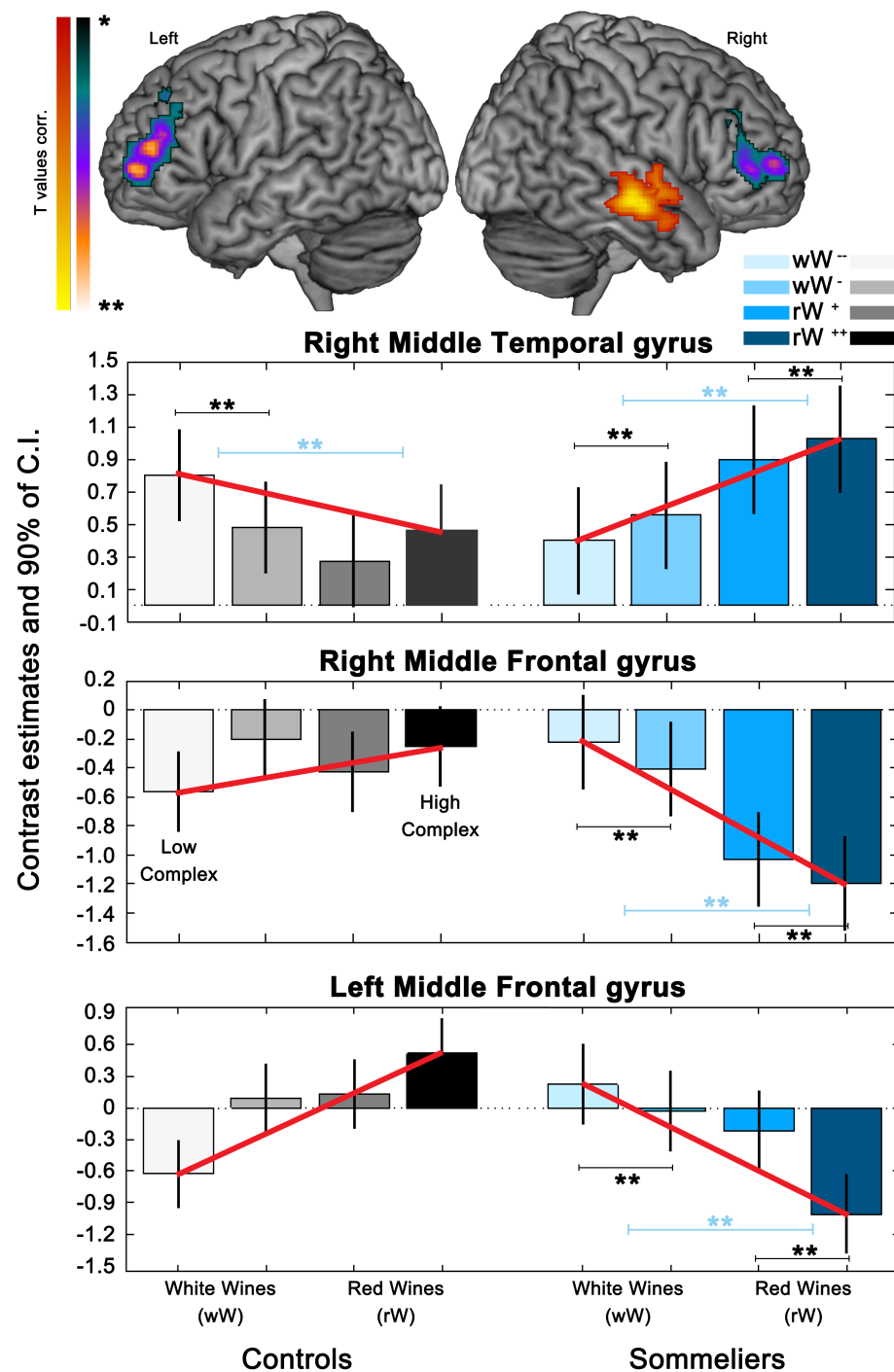


FIGURE 5 Upper: brain activation for the interaction between group and type of wine. Lower: Brain activity in the right middle temporal gyrus and the right middle frontal gyrus is related to wine complexity in sommeliers (blue bars) but not in naïve consumers (gray bars).

odor can be changed as well. For example, the same odor differentially activates OFC and ACC when labeled “cheese” compared to “body odor” (De Araujo et al., 2005). Likewise, the same low-calorie beverages produce activation of the midbrain and hypothalamic regions similar to milkshake stimulus when labeled as “treat”, but not when labeled as “healthy” (Veldhuizen et al., 2013). When an odor is paired with verbal context such as a “source” category (e.g., flower, fruit) or “use” category (e.g., soap, lotion), differential activation of the OFC is evident (Bensafi et al., 2014). Additional activation of the cingulate

cortex and insula occurs when “use” category verbal context is paired with an odor, thus suggesting differential top-down modulation of olfactory representations by specific verbal cues. In the case at hand, wine perception seems to depend on the synchronization between the networks that support flavor perception, language, and emotions/rewards.

Integration of olfactory and lexicosemantic information that allows for odor recognition relies primarily on the temporal pole and inferior frontal gyrus (which contains Broca’s area) (Olofsson

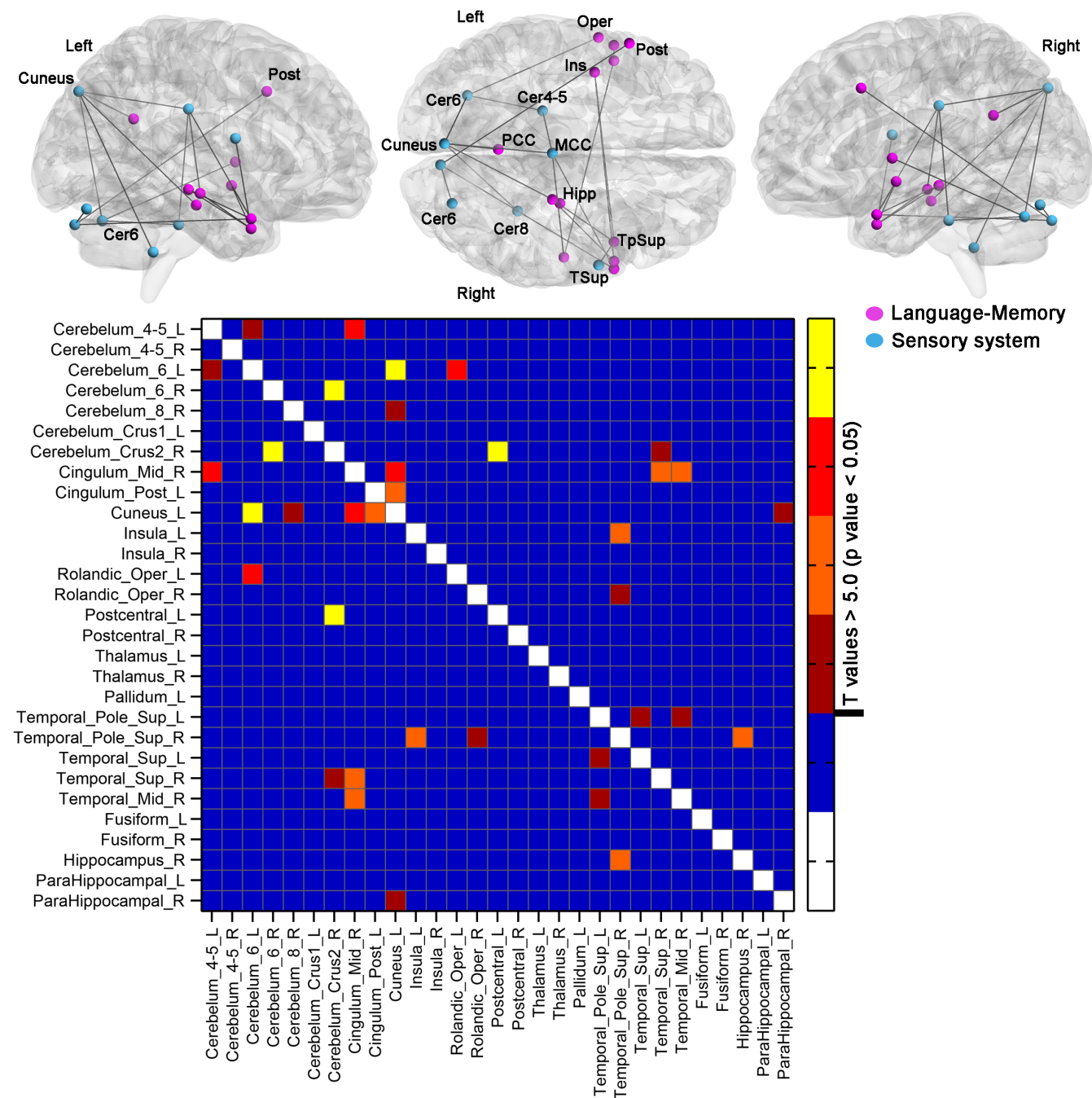


FIGURE 6 Changes in brain network configuration between sommeliers and controls using as seeds 30 ROIs resulting from the group-level *F*-test contrast wines versus tasteless. In the upper part, all the significant interactions are superimposed in a 3D reconstruction of a brain surface template (Xia et al., 2013). The matrix of functional interactions between the 30 regions of interest is represented in the lower part. The color change from dark red to yellow indicates an increase in the *t* value of the significant connections. Blue cells represent no connection.

et al., 2013). With the methodological approach used in the current study, we were able to capture this interaction. Specifically, our functional analyses showed that wine tasting compared to tasting the control tasteless and odorless solution recruited numerous areas both in sommeliers and nonexperts, including the flavor circuit, areas related to language and memory, and regions that mediate attentional/control processes. These findings are consistent with prior research

(Castriota-Scanderbeg et al., 2005; Frost et al., 2015; Pazart et al., 2014; Small et al., 2004). For instance, patients with primary progressive aphasia demonstrate deficits in odor familiarity that correlate with their degree of temporal pole cortical thinning, as well as deficits in odor naming that correlate with their degree of inferior frontal gyrus thinning (Olofsson et al., 2013). Importantly, when presented with visual or verbal cues, the same patients' odor-matching

Differences in functional connectivity between sommeliers and controls using as seeds the 3 ROIs resulting from the interaction effect

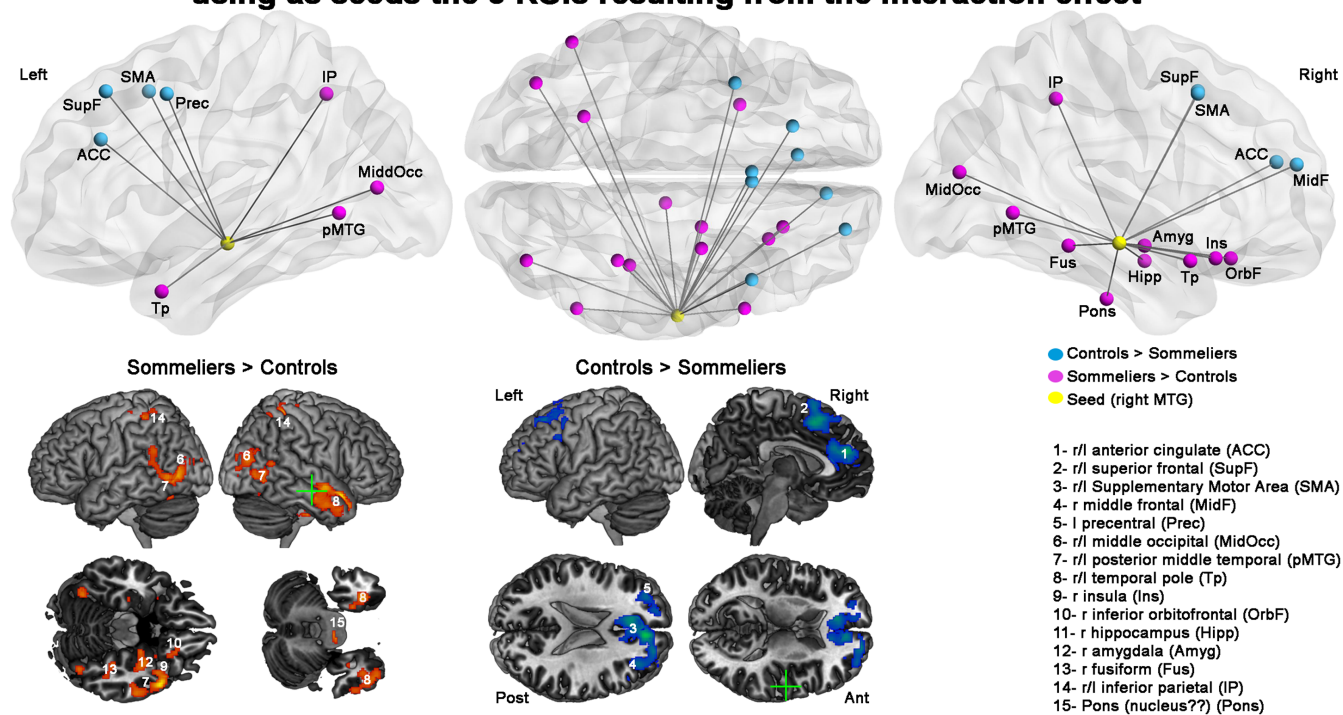


FIGURE 7 Changes in brain network configuration between sommeliers and controls using as seeds the middle temporal cluster resulting from the interaction between group and type of wine.

performance was similar to control participants, suggesting that these temporo-frontal regions are necessary for retrieval of odor names, but less so for recognition in the presence of available cues. Following odor recognition, actual verbalization of an odor is thought to primarily involve the inferior frontal gyrus. Support comes from evidence showing that easily named odors produced sustained activation of the inferior frontal gyrus, whereas difficultly named odors led to sustained piriform cortex activation (Zelano et al., 2009). The authors suggested the latter activation represented a buffering function of the primary olfactory cortex, whereby unidentifiable odor information is temporarily maintained for further appraisal.

In terms of differential activation between the two groups, direct contrast revealed that sommeliers showed greater activation in central, temporal, and posterior areas related to memory and language processes. However, the reverse contrast showed more activation for naïve participants in frontal areas (e.g., OFC, middle, and superior frontal gyrus, ACC). To determine if the type of wine influenced brain response differently in experts vs. nonexperts, we examined the interaction between *Group* and *Wine Type*. This revealed that sommeliers had greater activation of temporal and limbic structures and decreased activation of frontal structures when tasting more complex wines. Although many common areas were activated when comparing wines versus tasteless solutions in the two groups, the presence of significant differential responses suggests that sommeliers process the wine differently from naïve participants. Moreover, this effect

became more apparent as the complexity of the wine increased. Figure 3 captures the effect of wine complexity on the activation profiles of sommeliers in the right middle temporal gyrus and the right middle frontal gyrus. This finding was not observed in naïve participants. Additionally, we report differences in connectivity between sommeliers and controls. While the connectivity pattern of the right superior frontal gyrus seed was similar across the two groups, connectivity varied when using the right middle temporal gyrus as a seed. Here, two networks were identified, one network showing increased connectivity in sommeliers compared to controls, and another showing the opposite pattern. The first network included a range of regions belonging to the taste and language circuits while the second network was restricted to frontal regions.

Overall, these findings demonstrated the intricate interplay among the networks underpinning language, emotion/rewards, and taste perception in both cohorts. Nevertheless, nuanced distinctions between groups emerged concerning the engagement of the distinct nodes within these networks. A notable bias in the neural response of sommeliers was apparent within semantic regions, while naïve consumers exhibited a pronounced bias within regions implicated in emotional/reward systems. This juxtaposition of findings resonates with previous behavioral findings, underscoring that individuals lacking habitual exposure to wines tend to employ more evaluative and emotion-related descriptors (e.g., nice, hard) compared to their expert counterparts who tend to use more source-based terms (e.g., vanilla,

chocolate, alcohol) (Croijmans & Majid, 2016). In light of these findings, future investigations should consider potential variations in the synchronization of these networks, a phenomenon that may be influenced by environmental factors such as wine-related experiences, as well as developmental factors, including the distinctive structural configurations of brain networks inherent to each individual.

The integration of taste (i.e., the chemical stimulation of taste receptors in the mouth) with oro-sensory and retronasal olfactory signals in the brain results in the percept of flavor (Prescott, 2015; Small, 2006; Small, 2012; Small et al., 2004). The sensory inputs that contribute to flavor are thought to be integrated in the insula (Iannilli et al., 2014) before traveling to brain regions such as the brainstem, thalamus, amygdala, OFC, and ACC. The present results agree with the involvement of these areas during wine tasting in both groups but also show that the two groups process information differently. Sommeliers gain their ability to integrate information from gustatory and olfactory senses through experience and/or by training associative memory—in this case, attributing distinct labels to characterize the gustatory qualities of a particular wine. Therefore, it is likely that sommeliers utilize language and memory processes that activate the language brain circuit including temporal areas. The anterior temporal lobe, particularly the hippocampal and parahippocampal regions, underpins semantic memory. Some degree of associative memory displayed by sommeliers may be present in nonexperts. However, it is possible that the process of accessing a lexicon to describe sense percepts is likely much less automatized and thus requires greater frontal activation. Finding differences between sommeliers and naïve consumers in regions that have typically been associated with linguistic operations suggests that the language network responds whenever the system needs to access the conceptual representation of a stimulus, regardless of whether the task involves such access or not. For instance, a recent study has shown that fundamental language operations, such as lexical access, can be observed in a nonverbal size judgment task (Branzi et al., 2023). Similarly, (Sueoka et al., 2022), using a naturalistic cognition paradigm, have demonstrated that all regions of the language network significantly respond to nonverbal stimuli. These authors showed significant intersubject correlations between the BOLD response associated with nonlinguistic information and semantically rich nonverbal stimuli (see also Ivanova et al., 2019; Ivanova et al., 2021).

In the current study, functional (activation and connectivity) differences between groups may reflect cognitive mechanisms underpinning sommeliers' experience in wine tasting. An alternative interpretation concerns experiential (perceptual) differences between sommeliers and nonexperts. The observed neural differences between groups could represent significant differences in how each group perceived the wines they tasted (Masaoka et al., 2010). In the same vein, the correlation between regional activity and wine complexity in sommeliers may reflect the fact that more complex wines produce richer perceptual experiences in experts. Prior evidence suggests that the perceptual representations of wine experts and novices are similar (Chollet & Valentin, 2000), and that any differences in perception are less

pronounced than differences in cognition (flavor labeling, schematization, and typicality judgments [Hughson & Boakes, 2001]). That is, greater experience is associated with the ability to describe a perceptual representation rather than a change in the representation itself. This difference in descriptive ability can be observed in the tendency for wine novices to use concrete descriptors over abstract ones when attempting to differentiate wines (Gawel, 1997). It is also possible that experience may alter perceptual experiences. Extensive prior experience with a wine varietal or regional style can produce a representative sensory concept of a specific wine type that is shared among experts (Ballester et al., 2008). During tastings, this information may be used to increase salience for prototypical characteristics to increase the chance of detecting components indicative of a certain wine type (Gawel, 1997). However, it is unclear whether this would constitute a change in a perceptual representation itself rather than a heightened awareness of an aspect of the original representation.

Finally, there are three caveats with the current study: (a) *Potential effect of alcohol exposure*. Individuals with alcohol use disorder showed reduced gray matter volume in corticostriatal-limbic circuits (van Holst et al., 2012; Yang et al., 2016), as well as reduced white matter integrity, particularly in the superior longitudinal fasciculus (Elofson et al., 2013; Zahr & Pfefferbaum, 2017). Notably, 75% (12/16) of our sommeliers reported consuming wine every day. This may imply some effect of alcohol exposure in our study, though this effect is likely minimal given that the effects of alcohol and wine experience on white matter follow opposite directions. (b) *Degree of experience*. Past experiments on sommeliers have used sommeliers with varying degrees of experience. However, (Banks et al., 2016; Sreenivasan et al., 2017) only recruited master sommeliers—wine experts who passed rigorous exams assessing knowledge and tasting ability. Similarly, (Pazart et al., 2014) recruited sommeliers who received national or international awards. (Castriota-Scanderbeg et al., 2005) recruited from a list provided by the Italian Wine Association, suggesting that their participants had not received the same degree of recognition. As olfactory discrimination, semantic association, and representations of wine complexity differ as a result of experience (Parr et al., 2011; Zucco et al., 2011), assessments of a sommelier's ability by a widely recognized organization (e.g., Court of Master Sommeliers, Institute of Masters of Wine) are important considerations for such experiments. Our sommeliers were certified by the internationally renowned Basque Culinary Center, and 5 of the 14 were enrolled in graduate-level enology programs at the time of our study. Nonetheless, discrepancies between our results and those of past studies may be influenced by socioeconomic, cultural or lifestyle factors that differentially affect each population (Gauthier et al., 2020; Stevenson et al., 2016). (c) *Wine variety*. All wines in this study were produced in Spain and mostly contained typical Spanish varietals, though our selection drew from various regions with continental and Mediterranean climates. Given our Sommeliers were drawn from a Spanish culinary institute, they were likely especially familiar with Spanish wines. The effect of familiarity is difficult to assess as

participants were only asked about wine complexity rather than their general thoughts on each wine. Future studies may consider using an international selection or more obscure wine to account for the possible effects of familiarity.

5 | CONCLUSION

The current study represents one of only a handful of experiments that have examined sommelier brain structure and function during tastings. We improve on prior studies by assessing the influence of wine complexity in a comparably larger sample size and correcting for multiple comparisons during our analysis. Our results show differences between sommeliers and controls in brain structure, functional response to both wine and wine complexity, as well as functional connectivity. Sommeliers generally displayed greater activation and functional connectivity of temporal areas, whereas controls had greater activation and functional connectivity of frontal areas. Specifically, the functional connectivity profile of sommeliers included regions associated with both taste and language. Sommeliers, but not controls, also demonstrated differential activation patterns when tasting wines with high complexity compared to wines with low complexity. Collectively, these results suggest that sommeliers may benefit from automatized retrieval of lexicosemantic information during wine tasting, as well as the ability to recognize the numerous flavor components in a complex wine. In contrast, increased frontal involvement in control participants may represent effortful retrieval of lexicosemantic information evoked by wine tasting. Our results indicate that experience and expertise in wine tasting likely modulate both the tasting and language circuits to produce superior flavor recognition abilities, as displayed by sommeliers during blind tastings.

AUTHOR CONTRIBUTIONS

Manuel Carreiras and Ram Frost designed the research. Ileana Quiñones data acquisition, curation, and analysis, figure design, presentation of results, writing of different sections, corresponding author. All authors contributed to the interpretation of the data, to the writing of the paper, and reviewed the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Following BCBL data sharing policy, all data used in this study has been shared upon specific request to the authors and according to a

formal data sharing agreement (https://www.bcbl.eu/DataSharing/HBM2022_Sommeliers).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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