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Variability in functional brain networks predicts expertise during action observation.

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Abstract: Observing an action performed by another individual activates, in the observer, similar circuits as those involved in the actual execution of that action. This activation is modulated by prior experience; indeed, sustained training in a particular motor domain leads to structural and functional changes in critical brain areas. Here, we capitalized on a novel graph-theory approach to electroencephalographic data [1] to test whether variability in functional brain networks implicated in Tango observation can discriminate between groups differing in their level of expertise. We found that experts and beginners significantly differed in the functional organization of task-relevant networks. Specifically, networks in expert Tango dancers exhibited less variability and a more robust functional architecture. Notably, these expertise-dependent effects were captured within networks derived from electrophysiological brain activity recorded in a very short time window (2 s). In brief, variability in the organization of task-related networks seems to be a highly sensitive indicator of long-lasting training effects. This finding opens new methodological and theoretical windows to explore the impact of domain-specific expertise on brain plasticity, while highlighting variability as a fruitful measure in neuroimaging research.

Keywords and phrases: Functional networks, EEG, Predicting expertise, Statistics on networks.

1. Introduction

Expertise can be conceptualized as a set of specific skills or abilities acquired through sustained training, which supports outstanding performance in a particular artistic, athletic, professional, or otherwise cognitive domain. Understanding what is special in the expert brain provides a unique window into experience-dependent plasticity changes and learning mechanisms. Several studies have shown that expert deployment of specific functions induces structural changes in brain areas devoted to them. For example, relative to non-expert controls, experienced taxi drivers have greater grey matter volume in the posterior hippocampus, a region subserving navigational skills [2]. Moreover, expertise may change long-range cortical connections, allowing top-down control mecha-

nisms to modulate the states (and multiply the function) of sensory and motor circuits [3, 4, 5]. In this sense, expertise may involve the functional reorganization of a brain region originally specialized for different domains. For instance, expertise in recognizing cars and birds is associated with activity in the fusiform face area, a cortical region normally specialized in face recognition [6].

While these notions have some degree of generalization, how they are instantiated depends on each specific domain and form of expertise. Two interesting questions thus emerge: (a) can a general signature of expertise be reliably identified; and, if so, (b) which could be a suitable approach for its detection and measurement? Fruitful answers may be derived from functional connectivity methods [7]. In particular, graph-theory metrics have been proposed as powerful tools for quantifying properties in complex brain networks [8, 9]. Interestingly, this approach allows capturing inter- and intra-individual variation during task performance. Although variability is an inherent property of the human brain, neuroimaging research has largely neglected its importance or interpreted it as the result of various confounds [10]. However, an increasing body of evidence suggests that variability measures constitute a powerful index to study human brain functions (for a review, see [10]). In line with this idea, we propose that variability in functional brain networks derived from a task-evoked condition would be a natural candidate to track this general signature of expertise. Notably, intense training has been specifically linked to a decrease in variability [11], with some demonstrations of a causal role between temporal variability and learning [12, 13]. Furthermore, naturalistic everyday stimuli (which can be conceived as stimuli for which we all are naturally experts) evoke highly reliable brain activity across observers, both at the neuronal [14, 15] and at the macroscopic [16] scales.

Here, we test the hypothesis that expertise results in more reproducible patterns of brain activation across individuals, and that these connectivity patterns can be used as an index to classify participants according to their expertise.

Based on the notion that action observation and execution depend on partially shared circuits [17, 18, 19], and that only those actions performable by the observer are mapped onto his/her own motor system [20, 21], we focused on Tango dancers as a model of expertise. Using high-density electroencephalography (EEG), we recorded neural activity from expert and beginner Tango dancers as they observed videos depicting a couple of dancers performing various Tango steps. Importantly, by using videos of dance movements which vary in time and are well-known by the observers, we aimed to measure the reliability of task-evoked functional networks.

Overall, we predicted that: (i) brain functional networks engaged during the dance observation task [22] would show lower variability in experts than in beginners; and that (ii) network variability would serve as a classifier to identify the observers degree of expertise.

2. Materials and Methods

Participants

The study comprised 53 Tango dancers recruited from three Tango schools: DNI, the *Flor de Milonga* and the *DivinoEstudio del Abasto*. Twenty-five (14 female) were expert dancers (mean age = 29, $SD = 6.2$), and 28 (15 female) were beginner dancers (mean age = 29.5, $SD = 5.8$). The groups were matched for age, education level, gender, and executive skills. Furthermore, previous studies on action observation suggest that empathic abilities may affect action simulation [23, 24, 25], including the observation of dance movements [26]. Therefore, to ensure that expertise-related differences between groups were not confounded by such a factor, we controlled for it using the Interpersonal Reactivity Index (IRI) questionnaire (Table 1).

All participants were right-handed, as confirmed with the Edinburgh Inventory [27], and possessed normal or corrected-to-normal vision. None of them

reported a history of neurological or psychiatric disorders. Each participant read and signed a consent form in agreement with the Declaration of Helsinki and the Ethics Committee of the Institute of Cognitive Neurology (INECO), which approved this study.

TABLE 1
The average and the standard deviation is presented within parentheses.

		Experts (25) <i>M(SD)</i>	Beginners (28) <i>M(SD)</i>	<i>p</i> -value
Demographics	Age (years)	29.08 (6.20)	29.57 (5.85)	0.76
	Gender (M: F)	11:14	13:15	0.85
	Education (years)	17.4 (3.59)	18.25 (3.40)	0.38
	Handedness (L:R)	0:25	0:28	1.00
Empathy	Perspective taking	26.76 (4.09)	28.82 (3.43)	0.07
	Fantasy	23.16 (4.57)	23.67 (3.43)	0.49
	Empathy	31.6 (3.90)	33 (3.03)	0.11
	Personal distress	14.2 (3.50)	15.5 (3.97)	0.23
Executive functions	IFS Global Score	26.16 (2.3)	26.64 (1.9)	0.66
	Motor series	2.76 (0.66)	2.92 (0.26)	0.57
	Conflicting instructions	2.92 (0.27)	3 (0)	0.62
	Go / no go	2.84 (0.37)	2.96 (0.18)	0.44
	Backward digits span	4.28 (0.84)	4.28 (0.18)	0.81
	Verbal working memory	1.84 (0.37)	1.82 (0.47)	0.95
	Spatial working memory	3.32 (0.69)	3.28 (0.65)	0.83
	Abstraction capacity	2.8 (0.32)	2.75 (0.65)	0.64
	Verbal inhibitory control	5.4 (0.81)	5.60 (0.62)	0.42

Stimuli and procedure

The stimuli comprised realistic videos of two Tango dancers (one man and one woman), captured from head to toes, performing Tango Salon dance sequences. Each step could be either correctly or incorrectly executed. In the latter case, the error could be performed either by the man or the woman, and it could be gross or subtle. Stimuli were constructed and validated in a previous study [22]. In that original report, the videos lasted 5000 ms and error onset always occurred 200 ms before the end of each video i.e., the time at which the last move to complete the Tango step began. However, in the present study we considered only 2000 ms from the second to the fourth second. This window excludes

the last segment associated to EEG activity during error perception, which guarantees that potential between-group differences would be specifically due to Tango observation, and not to confounds inherent to stimulus categorization (i.e., error detection). Furthermore, in our previous study [22], we found that expertise-related differences in an ongoing wave indexing anticipatory activity (predictions) started at 4600 ms after video onset but not before this time point. Therefore, by selecting a segment not containing the last second of the video, where those differences were observed, we ensured that any early modulations in brain activity related to error prediction would also be excluded. Note that this creates stringent measurement conditions, given the difficulties of finding relevant network metrics to discriminate groups based on a two-second signal.

Also, while our previous study included three groups (naïve, beginner, and expert dancers), only the latter two were considered here. This way we ensured that our comparison would be driven by the samples amount of training rather than the development of visuo-motor skills. Unlike naïve subjects, beginners share basic procedural and declarative knowledge with experts but they lack long-lasting practice. In other words, as beginners possessed task-relevant visuo-motor knowledge, they afforded a more suitable baseline to assess training-induced changes. Note that Tango dancing expertise involves exposure to both motor and visual aspects of this style. Indeed, acquiring dance expertise requires not only the long-lasting practice of specific movements but also an increased visual exposure to them [28, 29, 30]. Thus, relative to beginners, experts are likely to have developed both higher motor expertise and increased task-relevant visual skills (e.g., through observational learning). Accordingly, both aspects could jointly contribute to any observed effect.

EEG recordings

Participants sat in a dimly lit, electrically shielded room. During the action observation task, EEG activity was recorded with a Biosemi 128-channel Active Two system (Amsterdam, NLD). The sampling rate was set at 1024 Hz, and signals were band-pass filtered between 0.1 and 100 Hz. Data were filtered off-line between 0.3 and 40 Hz and down-sampled to 512 Hz. During recording, the reference was set as default to link mastoids. Two bipolar derivations monitored vertical and horizontal ocular movements. Artifacts such as oculo-motor or muscle activity were rejected offline through Independent Component Analysis (ICA) and visual inspection. Only artifact-free segments were used to obtain the functional networks (trial rejection rates were 22% for experts and 21% for beginners). The number of rejected ICA components was not statistically different between groups (p -value $> .05$). Note that finding group differences in smaller EEG channel systems is a challenging issue. In this main document we show results for the set of 128 electrodes. Results obtained from the set of 20 electrodes of the 10-20 systems are shown as Supplementary Material.

Eye-tracking recording and analysis

Eye movements were recorded to ensure that between-group differences in EEG activity could not be explained by discrepancies in their eye movement patterns [31]. Eye movement data were recorded using an Eye-Link 1000 system (SR Research, Ontario, Canada). The data were fed directly into the EEG through a digital-to-analog converter card in the Eye-Tracker, and the analog signal was input preceding the digitization of the EEG data by a Biosemi measurement system. The EEG and eye movements were synchronized, and the sampling rate was equivalent for both. The eye tracker was calibrated at 13 points spanning the central part of the screen, where the stimuli were presented. Before detecting saccades, voltages in the extra analog channels in each dataset were rescaled

to pixels. An adapted version of the algorithm of Engbert and Kliegl [32] was implemented to detect the saccades from the continuous eye movements. We set the relevant parameters based on the literature and on inspection of the raw data, including the minimum duration of the (micro)saccade (3 ms), the velocity threshold (6 times the mean velocity), and the minimum inter-saccadic interval (50 ms). All saccades were considered in the analysis, including microsaccades.

We estimated saccades at time T in non-overlapping bins of 75 ms for each subject as the sum of saccades initiated in that bin divided by the total number of saccades performed in the time window of interest, and then we normalized the trace. To ensure that ocular patterns were similar across subjects, we performed a Wilcoxon test within each bin. Importantly, the number of saccades in each participant remained largely constant throughout the video segment used to construct the networks. The Wilcoxon test revealed a non-significant effect of group (p -value $> .05$), indicating comparable eye-tracking patterns irrespective of expertise.

Data analysis

Data were analyzed through a novel statistical framework for devised to examine sequences of networks [1]. Functional networks were constructed considering a time window of 2 to 4 seconds during video observation. The Spearman (rank) correlation matrix was calculated for each of the 400 hundred trials. The networks were constructed by framing each electrode as an individual node. EEG signals were obtained from each electrode for every trial in each subject. These signals were used to construct an association matrix between pairs of electrodes. This matrix represents the strength of the association between each pair, which can be quantified by different metrics of functional coupling, such as the rank correlation coefficient between the EEG signals of the electrodes, which we adopted in the present study. The matrix was then thresholded to generate

binary networks by using two criteria. First, we used a fixed correlation threshold affording networks with varying numbers of links. Second, we established a fixed number of links, in which case a specific threshold was chosen for each trial; in other words, a link between a pair of electrodes was added if thresholds exceeded a given value in each case.

Having determined the network criteria, for each subject (say, subject E_1) we obtained a network per trial, leading to a full sample of networks $G_1^{E_1}, G_2^{E_1}, \dots, G_t^{E_1}$. In what follows, expert and beginner Tango dancers are represented by E and B , respectively. Each group will be next characterized by its functional networks,

$$G_1^{E_1}, \dots, G_t^{E_1}, G_1^{E_2}, \dots, G_t^{E_2}, \dots, G_1^{E_n}, \dots, G_t^{E_n},$$

and

$$G_1^{B_1}, \dots, G_t^{B_1}, G_1^{B_2}, \dots, G_t^{B_2}, \dots, G_1^{B_m}, \dots, G_t^{B_m}.$$

Figure 1 illustrates the temporal evolution of functional networks in each group based on the 20 electrodes of 10-20 system. Here, we show 20 electrodes only for visual issues. Note that each subject has its own central network, and there is large variability between trials.

As shown in [1], key properties of networks can be captured by introducing a natural distance between graphs to establish their mean and dispersion, and to implement classification methods. In the present analysis, the central (subset) network or average network is defined as the one that minimizes the edit distance between all empirical networks,

$$\hat{C}_\ell = \arg \min_{H \in \mathcal{G}} \frac{1}{\ell} \sum_{i=1}^{\ell} d(G_i, H),$$

where \mathcal{G} is the space of networks and d is the edit distance between two networks.

Given two networks G_1, G_2 , the edit distance is given by the minimum number of links we have to add and subtract in order to transform G_1 into G_2 . More precisely, if T_{ij} is the inversion operator of the link (i, j) , which interchanges 1

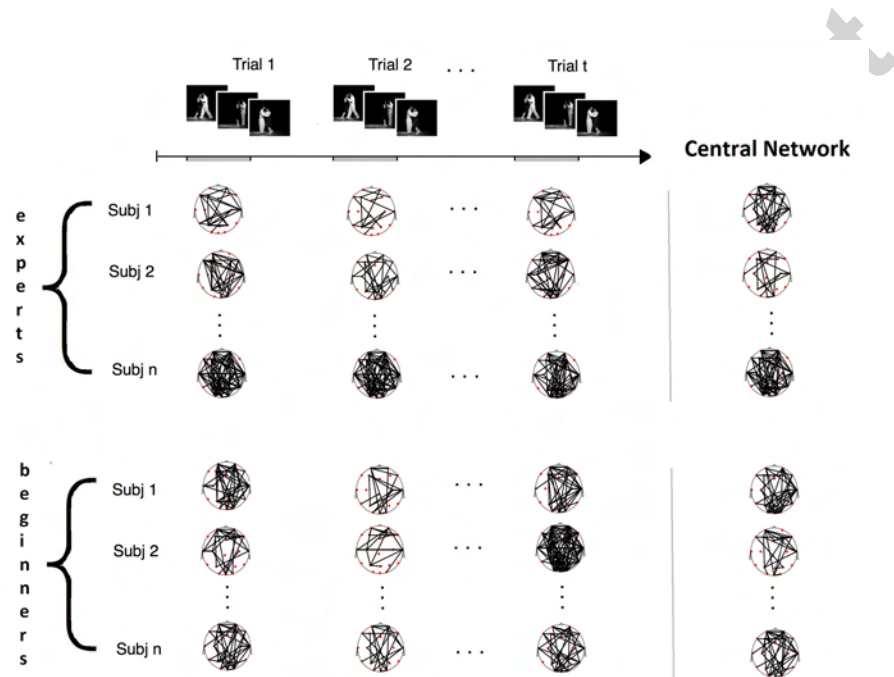


Fig 1: Brain functional networks.

with 0 on the (i, j) entry of the adjacency matrix of the graph, and A_1, A_2 are the adjacency matrices of G_1 and G_2 (respectively), the distance is defined as

$$d(G_1, G_2) = \min\{k : T_{i_1 j_1} T_{i_2 j_2} \dots T_{i_k j_k} A_1 = A_2\}. \quad (2.1)$$

With this distance definition, the central network can be ascertained as the network that contains only links that are observed more than half of the times [1]. Once the central network is calculated, the diversity or dispersion of the population of networks $\hat{\sigma}$ is computed as the average edit distance between the empirical networks and the central network.

$$\hat{\sigma} := \frac{1}{\ell} \sum_{i=1}^{\ell} d(G_i, S^*). \quad (2.2)$$

where S^* is the central network.

The central network and the dispersion coefficient defined above are a natural extension of traditional one-dimensional measures. The nearest neighbors method based on the distance defined in eq. 2.1 was applied for supervised classification. A training sample comprising half of the networks was used for classifying the rest of the networks (test sample). The performance of the classification method was evaluated by the receiver operating characteristic (ROC) curve.

Finally, to test for between-group differences in terms of network probability law ($H_0 : P(\mathbf{G}^E = G_i) = P(\mathbf{G}^B = G_i)$ for all networks G_i), we used the projective method described in [1]. Briefly, we chose a random direction in the Euclidean space containing the space of networks, and then we projected the graphs on that direction. A (one-dimensional) Kolmogorov-Smirnov test was performed on this random direction. To improve statistical power, we repeated the procedure 100 times and studied the percentage of rejected tests. Under the null hypothesis, we expect to obtain a 5% of rejected tests at a significance threshold of .05.

Supplementary Analyses

Note that our functional connectivity analysis was performed on broadband data. However, it is also interesting to assess whether variability in brain functional networks for experts and beginners also differs upon consideration of other frequency bands. To this end, we conducted an additional analysis on four other bands of interest (8-40 Hz, 8-12 Hz, 12-30 Hz, 30-40 Hz).

Finally, to better illustrate how variability behaves across groups, we zoomed in on a portion of the data. We focused on fronto-occipital connections, which can exhibit a differentially fast coupling in experts, favoring early prediction of upcoming movements. Specifically, for each trial within each group, we computed the proportion of links connecting distant electrodes from frontal to occipital (P_{F-O}) regions and studied its distribution. We tested equal distributions with the Kolmogorov test for all the numbers of links and correlation thresholds studied.

3. Results

A comparison between both groups revealed small central network differences for a correlation threshold of up to .95 (Figure 2A). However, an analysis with a fixed correlation threshold of 250 links showed fewer connections in the experts central network (Figure 2B). The latter result reflects the fact that links in the expert group were mostly the same across subjects, because only recurrent links appear in the central network. This suggests that experts more frequently activated the same type of (sub)networks, while beginners recruited more diverse ones. Hence, the central network of experts was more robust and featured less variability.

Moreover, the networks engaged during video observation were more similar among experts than beginners. Consistent with our hypothesis, the variability of the networks (eq. 2.2) of the expert group was smaller than the one from

beginners.

This was observed through both analysis criteria (Figures 2C and 2D), which supports the idea that experts have developed more focused and systematic predictions for Tango dance observation [22]. The reduction of variability is also evident when we zoom in to a portion of the data indexed by long-range fronto-occipital connections (See Supplementary Results and Figure A2). Accordingly, their networks would feature less variability since they would be calling on similar processing mechanisms. This is compatible with the idea that experts are more precise in action execution, so that exposure to repeated or similar stimuli would yield less variability.

We also compared the network distribution in each group. Both the correlation threshold and the fixed-number-of-links criteria yielded similar results (Figures 3A and 3B). Interestingly, task-relevant networks derived from Tango observation significantly differed in their graph distribution for experts and beginners. Specifically, we tested the hypothesis that both groups had the same functional networks probability law by generating 500 random directions. Nearly 100% of the tests showed that this was not the case, obtaining a p -value $< 10^{-20}$. Finally, ROC spaces were generated to determine the maximum sensitivity and specificity to classify experts and beginners. Classification was almost perfect based on both the correlation threshold (Figure 3C) and the number-of-links (Figure 3D) criteria. As Figure 3 further shows, this was true considering different correlation thresholds or numbers of links. This last result is in accordance with the second hypothesis posed in the Introduction.

Importantly, when the analyses were performed with the set of 20 electrodes from the 10/20 system, variability, testing, and classification results remained largely the same (see Figure A1 in the Appendix). This finding provides strong support for both of our hypotheses.

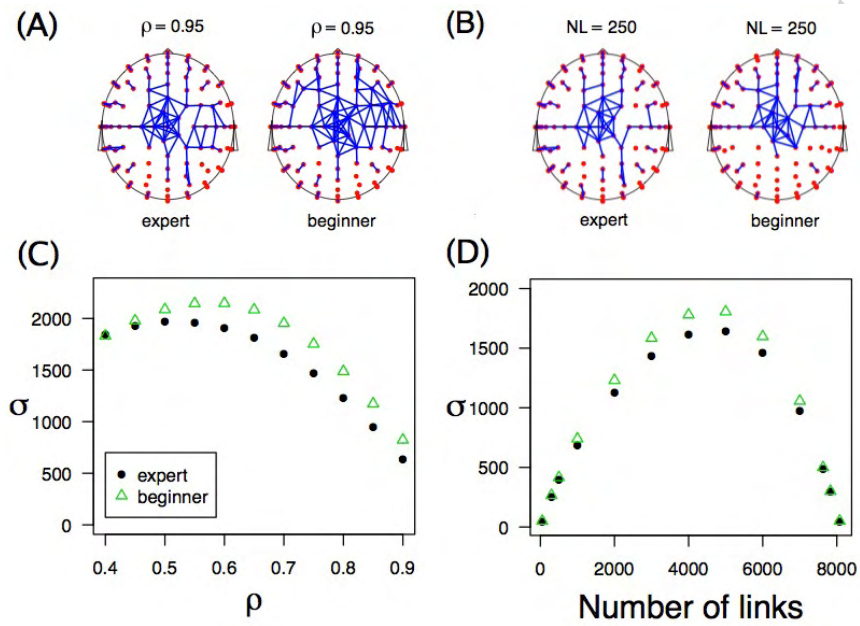


Fig 2: **Network statistics:** Central network for: (A) the fixed correlation criteria and (B) the fixed number of links criteria. (C) Network variability as a function of the correlation threshold. (D) Network variability as a function of the number of links fixed in all networks.

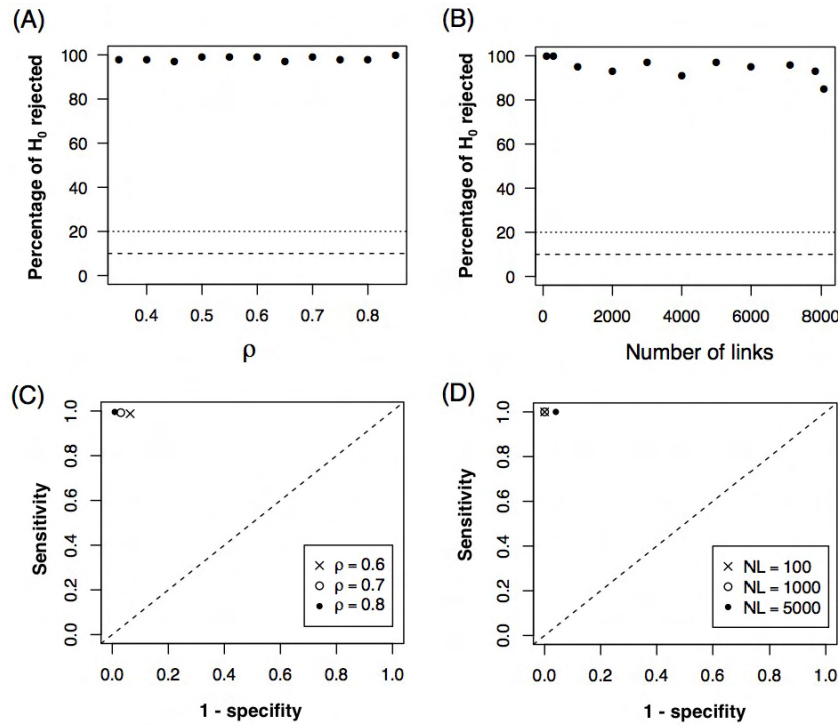


Fig 3: Network testing and classification: Percentage of projective tests rejected at a significance level of 5% as a function of (A) the correlation threshold, and (B) the number of links. The null hypothesis tested is that both beginners and experts have the same network probability law. Receiver operating characteristic space (sensitivity vs. 1-specificity) for classifying experts and beginners using (C) a fixed correlation threshold criterion, or (D) a fixed links criterion. Results for different values of the correlation threshold and the number of links are shown.

Supplementary Results

Figure A2 illustrates a network with 12 links, four of which connect frontal and occipital regions. In this example, the proportion of P_{F-O} equals 1/3. The P_{F-O} distributions are significantly different between groups (Kolmogorov tests, all p -values $< 10^{-6}$). In particular, the standard deviation of the P_{F-O} differs between experts and beginners when considering the networks constructed either with the fixed correlation (panel C) or with the number of links criterion (panel B). Beginners show increased variance in their functional networks, sometimes expressed with a small P_{F-O} and sometimes with a larger one. Panels D and E correspond to the histograms of P_{F-O} (analyzing all trials in each group) for networks featuring 60 (fixed) links (panel C). Values plotted in the histograms correspond to the filled symbols shown in panel C, as indicated by the solid (experts) and dotted (beginners) arrows.

Figure A3 depicts network variability for experts and beginners as a function of the correlation threshold and the number of links in the four frequency bands of interest (8-40 Hz, 8-12 Hz, 12-30 Hz, 30-40 Hz). Importantly, the main result remained across all bands studied: networks still showed less variability in experts than in beginners.

4. Discussion

In this study, we applied a novel graph-theory approach [1] to examine whether EEG functional networks derived from the observation of actions for which the observers have expertise, could discriminate between groups with different levels of expertise in performing those actions. The functional organization of task-relevant networks significantly differed between experts and beginners. Importantly, expertise-dependent effects were captured by considering EEG activity recorded in a very short time window (2000 ms). To our knowledge, this is the first study to show expertise-dependent changes in functional network properties

derived from EEG data.

More specifically, we found that networks in expert Tango dancers exhibited less variability and a more robust functional architecture. This pattern suggests that the development of style-specific knowledge leads to a more efficient organization of task-related mechanisms. Such an interpretation aligns well with reports showing that experts exhibit less variability across repeated skilled movements [33] and greater activation in networks subserving their execution [34, 35].

Our careful sampling procedure allowed us to rule out broad cognitive or affective factors as possible confounds, a problem that has undermined previous studies on expertise effects. Indeed, both groups were matched for demographic variables (gender, age, education, handedness) as well as affective (empathy) and cognitive (executive functioning) skills. Thus, the observed differences seem reasonably attributable to their levels of expertise.

Ample evidence from studies in monkeys and humans [18, 36, 37, 38, 39] shows that when participants observes an action, the neural circuits subserving the execution of that action are automatically engaged (for a review, see [40]). In brief, these studies indicate that action-related representations stored in the primary motor and somatosensory cortices become active by both action-execution and action-observation conditions, suggesting that the observer recruits simulation mechanisms which contribute to understanding others behaviors. Furthermore, people are more accurate in comprehending actions that are present in their own motor repertoire as compared to those actions that are not [41], and this ability is known to increase with expertise [42]. Our findings corroborate the relevance of action observation tasks to track plasticity effects due to long-lasting training [21, 22, 43, 44] and further show their impact on functional connectivity [45].

Furthermore, our findings align well with sparse yet robust evidence of expertise-induced changes on functional brain networks. For instance, in a comparison between expert and less experienced improvisers, the former exhibited lower ac-

tivity in fronto-parietal association areas involved in musical creativity, as well as greater functional connectivity among prefrontal, premotor, and motor regions during improvisation [46]. Also, relative to non-musicians, musicians performing an audiovisual task displayed greater connectivity within a more distributed auditory cortical network and enhanced network-level processing efficacy [47]. Moreover, as compared with novice controls, grandmaster and master level Chinese chess players exhibited enhanced integration between the caudate nucleus (an area recruited by professional chess players during quick generation of the best next move) and the default mode network (characterized by deactivation during goal-directed behavior and increased activity in chess-relevant domains, such as self-referential processing and theory of mind). Finally, Wang et al. [48] found that taxi drivers, as compared to nondrivers, evince stronger functional connectivity between high-order (fronto-parietal) and sensory (primary visual) resting-state networks, suggesting better integration capacities across processing levels in the former group. Interestingly, a recent study [49] showed that taxi drivers are characterized by reduced variability of functional connectivity within brain areas involved in the vigilance network. According to the authors, this decrease may indicate more stable functional interactions within vigilance-related regions subserving a core cognitive ability necessary for driving. Overall, these studies provide strong evidence that functional brain connectivity is reorganized due to field-specific expertise, further suggesting that training-related modulations reflect more efficient interaction within relevant brain areas. Furthermore, in line with our findings, one of these studies [49] suggests that reduced variability in functional connectivity networks may reflect the effects of long-term training. In line with previous literature, the present data further nurture the view that sustained practice in a specific domain hones the efficiency of relevant neural resources, further showing that this is true even when a spectatorial role is assumed.

The robustness of our results was confirmed by the excellent classification rate

we obtained. In this sense, the method developed in [1] shows great potential, as it allows analyzing networks without “network mining” techniques, such as looking for differences in local network properties (with the statistical problems involved). In this first application to EEG data, the method yielded consistent results for the 128-channel montage and the 20-channel montage corresponding to the 10/20 system. By obtaining very similar patterns independently of the number of EEG sources, our study jointly highlights the sensitivity of functional network analysis to capture expertise effects and the suitability of our novel approach to such an end. Future implementations of this framework could yield even more robust results (for example, by comparing task-relevant networks against resting-state data).

Finally, although functional networks derived from high-density EEG recordings have provided a reliable means to investigate brain network configurations, they require a channel-level connectivity analysis with limited spatial resolution (as compared to that provided by other neuroimaging techniques). Furthermore, although action observation tasks are suitable to capture experience-dependent effects, more ecological approaches are needed to translate laboratory work into realistic everyday settings. Promisingly, functional near-infrared spectroscopy (fNIRS) has recently proven to be a powerful means to quantify dance training-dependent effects in brain activity during the online performance of a dance simulation gameplay [50, 51]. For instance, measures of pre-post dance training effects with this technique indicate that motor-skill learning suppressed activity in the frontopolar cortex (FPC), a region involved in prospective memory and top-down regulation [51]. This finding suggests that the FPC might change its activity in response to improvements in motor performance and could reliably index acquired motor automaticity. Based on our current findings, we hypothesize that high-performance dancers would show relatively small variance in FPC activity, as compared to low-performance dancers. Future studies using complementary fNIRS measures could extend our knowledge about the neurofunctional

dynamics of networks sensitive to expertise effects.

5. Conclusion

In conclusion, the present study shows that task-based EEG functional networks are sensitive to field-specific expertise. We suggest that these differences, reflected in terms of network variability, reveal the impact of long-lasting training on brain functional connectivity. Promisingly, we have further shown that this effect can be captured and measured with graph-theory tools. This way, our study opens new avenues to investigate experience-dependent functional plasticity via action observation paradigms.

6. Acknowledgement

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7. Appendix

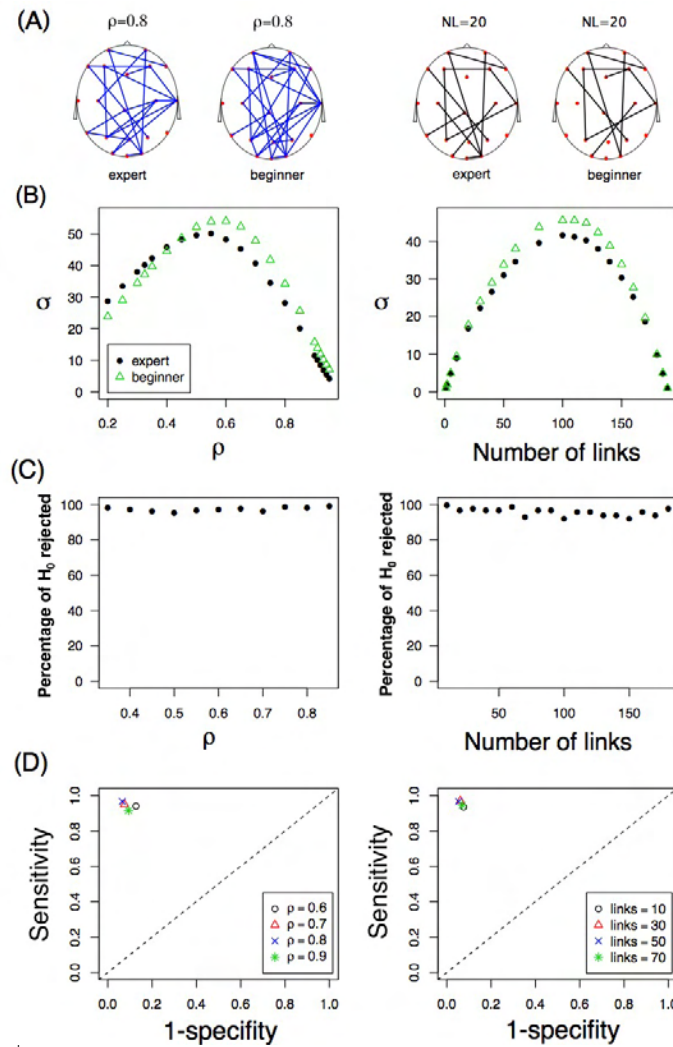


Fig A1: **Twenty electrode networks:** (A) Central network of experts and beginners dancers for a correlation threshold of .95. (B) Network variability. as a function of the correlation threshold and the number of links. (C) Percentage of projective tests where H_0 was rejected at a significance level of 5%. (D) Receiver operating characteristic space for classifying experts and beginners. The results shown on the left (right) column corresponds to the fixed correlation threshold (fixed number of links) criterion.

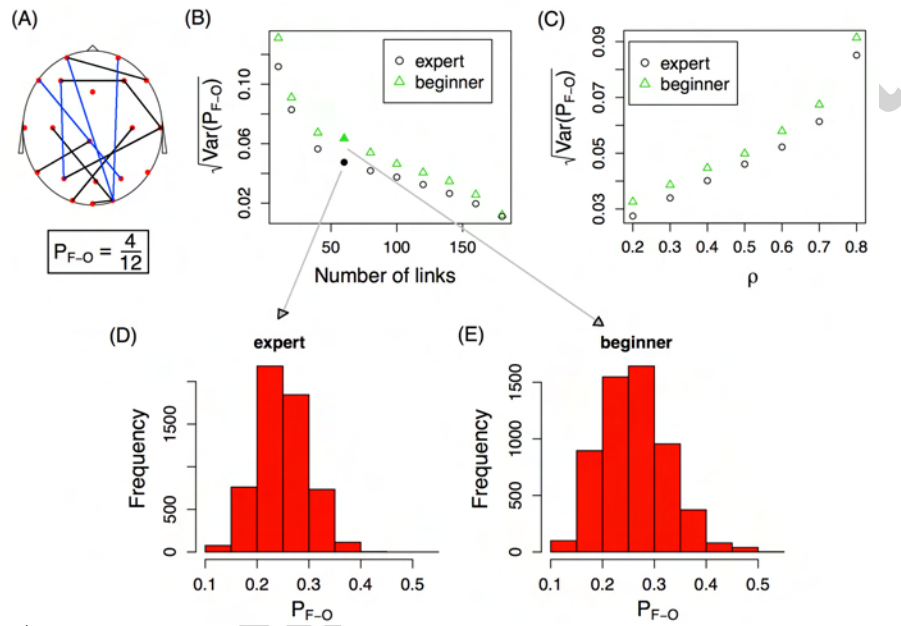


Fig A2: **Twenty electrode networks:** (A) Scheme of a network with 12 links, four of which connect frontal and occipital regions. The proportion of P_{F-O} equals $1/3$. Standard deviation of the P_{F-O} when considering the networks constructed either with the fixed correlation (B) or with the number of links criterion (C). Histograms of P_{F-O} for networks featuring 60 links of the group of experts (D) and beginners (E). Values plotted in the histograms correspond to the filled symbols shown in C.

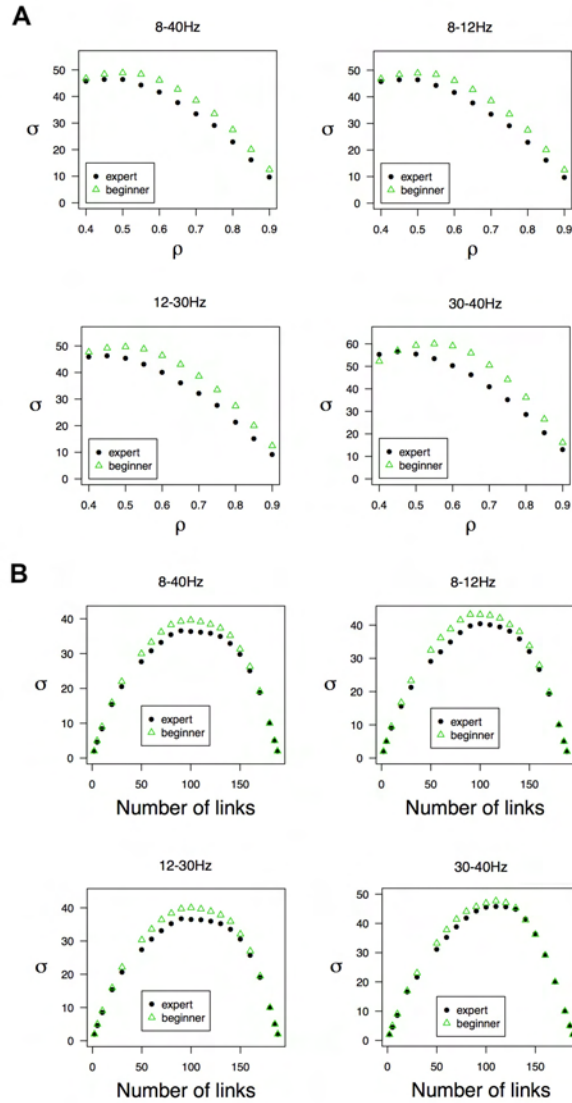


Fig A3: **Twenty electrode networks:** Network variability across frequency bands. Comparison between experts and beginners in terms of correlation threshold and number of links in four separate frequency bands (8-40 Hz, 8-12 Hz, 12-30 Hz, 30-40 Hz).

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