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Time to Tango: Expertise and contextual anticipation during action observation

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A B S T R A C T

Predictive theories of action observation propose that we use our own motor system as a guide for anticipating and understanding other people's actions through the generation of context-based expectations. According to this view, people should be better in predicting and interpreting those actions that are present in their own motor repertoire compared to those that are not. We recorded high-density event-related potentials (ERPs: P300, N400 and Slow Wave, SW) and source estimation in 80 subjects separated by their level of expertise (experts, beginners and naïves) as they observed realistic videos of Tango steps with different degrees of execution correctness. We also performed path analysis to infer causal relationships between ongoing anticipatory brain activity, evoked semantic responses, expertise measures and behavioral performance. We found that anticipatory activity, with sources in a fronto-parieto-occipital network, early discriminated between groups according to their level of expertise. Furthermore, this early activity significantly predicted subsequent semantic integration indexed by semantic responses (N400 and SW, sourced in temporal and motor regions) which also predicted motor expertise. In addition, motor expertise was a good predictor of behavioral performance. Our results show that neural and temporal dynamics underlying contextual action anticipation and comprehension can be interpreted in terms of successive levels of contextual prediction that are significantly modulated by subject's prior experience.

Introduction

Our proactive brain appears to interpret incoming sensorimotor and contextual information in terms of prior experience to *predict* the future course of others' actions and intentions (Arnal and Giraud, 2012; Bar, 2007; Buckner and Carroll, 2007). People are more accurate in comprehending actions that are present in their own motor repertoire compared to those actions that are not (Buccino et al., 2004). Moreover, this ability increases with motor expertise (Calvo-Merino et al., 2005). For example, recent studies comparing elite athletes to novices revealed that experts predict earlier and more efficiently those actions for which they possess sporting excellence by using a 'resonance' mechanism that allows for the embodied mapping of action kinematics (Aglioti et al., 2008; Tomeo et al., 2012).

Dance is a fertile domain to investigate the neurophysiology of motor expertise. A handful of neuroimaging studies have found that the intensity of a dancer's brain activity is modulated by motor experience in mirror areas during observation of trained versus untrained movements (Cross et al., 2006) with style and gender specificity (Calvo-Merino et al., 2005, 2006; Orgs et al., 2008).

Here, we capitalize on one of the primary advantages of dancing: its fine temporal and rhythmic assembly with patterns that conform to highly structured movements (Brown et al., 2006). Specifically, we focus on Tango. First, it is a very popular dance in Argentina and, currently, worldwide. Second, it involves high levels of synchronization and coordination in close proximity to another body. Third, it involves joint improvisation, which forces the dancer to develop expertise in

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reading the partner's body kinematics online to appropriately respond to changes in speed and direction.

We investigated the dynamics of anticipation and comprehension of complex joint actions by using an ecological paradigm in which 80 participants with different levels of dance expertise (experts, beginners and naïves) watched realistic videos of Tango steps while we recorded the electroencephalogram (EEG) and the event-related potentials (ERPs) of the observers. We focused our analyses on four temporal windows: early anticipation (250 ms preceding stimulus onset), P300 (234–305 ms), N400 and Slow Wave (SW, 347–410 ms and 750–900 ms, respectively). These temporal windows were chosen to test the assumption that neural and temporal signatures underlying action observation and comprehension would be modulated by subject's motor expertise in terms of successive levels of prediction. Specifically, we expected that early cortical responses (anticipation) would facilitate subsequent meaning construction indexed by modulations in those ERPs responses linked to semantic-related processes (such as N400 and SW). Conversely, we expected that those ERPs not primarily involved in the processing of semantic meaning, but rather in stimulus frequency (such as P300), would not be affected by motor expertise.

In addition, we performed a path analysis of brain–behavior relationships (Herzmann et al., 2010; Ibanez et al., 2013; Shipley, 2002) to infer a causal relationship between expertise, ongoing anticipatory brain activity, semantic responses of ERPs and behavioral performance.

We found that anticipatory neural responses (with sources in the fronto-parieto-occipital reconstruction of the high-density electroencephalogram) discriminated motor expertise and errors detection at early stages. Furthermore, this activity was a good predictor of subsequent meaning-processing and expertise. Second, cortical evoked responses to semantic violations (N400 and SW) with sources in temporal and motor regions were affected by the participant's degree of accuracy and expertise. Importantly, these ERPs predicted the participant's motor expertise, and, in turn, motor expertise was a good predictor of behavioral performance in error detection. Thus, our results highlight the influence of expertise on proactive brain activation and its influence on cortical ongoing activity, evoked responses and behavior.

Materials and methods

Participants

Eighty Argentine right-handed participants, as defined by the Edinburgh Inventory (Oldfield, 1971), completed the full assessment. Twenty-five expert Tango dancers (M = 29 years old, SD = 6.2 years, 14 females), twenty-eight beginner Tango dancers (M = 29.5 years old, SD = 5.8 years, 15 females), and twenty-seven naïves (M = 28.2 years old, SD = 5.5 years, 14 females) took part in this study. Expert Tango dancers and beginners were obtained from the *DNI*, the *Flor de Milonga* and the *Divino Estudio del Abasto* Tango schools. The three groups were matched for age, level of education, proportion of males to females, executive function and empathy levels (a summary of the sample characteristics is presented in Table 1). All participants possessed normal or corrected-to-normal vision and reported no past neurological or psychiatric history during an initial interview. All participants 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.

Neuropsychological assessment and expertise level

To control for potentially relevant individual differences that are not directly related with expertise but that could affect task performance (e.g., executive functions and empathy), all participants completed a neuropsychological assessment. The INECO Frontal Screening test (Torralva et al., 2009) was used to assess executive function via several sub-tasks: Motor Programming, Conflicting Instructions, Verbal Inhibitory Control, Abstraction, Backwards Digit Span, Spatial Working Memory, and Go/No Go. In addition, empathy scores were obtained using the Interpersonal Reactivity Index (IRI, Davis, 1980).

Participants also completed a self-rating questionnaire composed of twenty items to evaluate their degree of expertise (Table 2). The items explore different domains, such as Tango practicing, dance practicing and Tango teaching. Immediately after the EEG session, the participants also completed a brief post-task questionnaire to evaluate their familiarity with the observed videos.

Stimulus construction

Originally, 330 videos were recorded using two Canon EOS 550D video cameras. Afterward, they were converted to grayscale and muted, and they persisted for exactly the same duration (video length was 5.04 s and was presented at a rate of 30 frames per second, for a total of 150 frames) using Adobe Premier Pro CS3 3.0 software.

All video clips depicted a pair of expert Tango dancer's full-body centered performance of ten classical steps of Tango Salon style (Ballroom Tango): *Salida Básica*, *Sandwichito*, *Americana*, *Cambio de Frente*, *Salida de 40*, *Gancho*, *Sentadita*, *Calesita*, *Barrida* and *Sacada*. The dance was choreographed by Diego Pérez and Soledad Cantarini, the finalists in

Table 1
Descriptive statistics and comparisons between groups. Mean (M), standard deviations (SD) and *p* values for demographics, empathy and executive function scores obtained from experts, beginners and naïves.

		Experts (25)	Beginners (28)	Naives (27)	*p*	*p* (Tukey's post hoc)		
		M (SD)	M (SD)	M (SD)		Exp vs Beg	Exp vs Naïve	Naïve vs Beg
Demographics	Age (years)	29.08 (6.20)	29.57 (5.85)	28.25 (5.51)	NS	NS	NS	NS
	Gender (M: F)	11:14	13:15	13:14	NS			
	Education (years)	17.4 (3.59)	18.25 (3.40)	18.11 (3.37)	NS	NS	NS	NS
	Handedness (L:R)	0:25	0:28	0:27	NS			
Empathy	IRI Global Score	95.72 (10.81)	101 (8.07)	95.40 (13.98)	NS	NS	NS	NS
	Perspective taking	26.76 (4.09)	28.82 (3.43)	24.77 (5.39)	<0.01	NS	NS	<0.01
	Fantasy	23.16 (4.57)	23.67 (3.43)	24.33 (6.50)	NS	NS	NS	NS
	Empathy	31.6 (3.90)	33 (3.03)	24.77 (4.31)	NS	NS	NS	NS
	Personal distress	14.2 (3.50)	15.5 (3.97)	15.22 (4.55)	NS	NS	NS	NS
Executive functions	IFS Global Score	26.16 (2.3)	26.64 (1.9)	26.51 (2.11)	NS	NS	NS	NS
	Motor series	2.76 (0.66)	2.92 (0.26)	2.85 (0.60)	NS	NS	NS	NS
	Conflicting instructions	2.92 (0.27)	3 (0)	2.88 (0.32)	NS	NS	NS	NS
	Go–no go	2.84 (0.37)	2.96 (0.18)	2.96 (0.19)	NS	NS	NS	NS
	Backward digits span	4.28 (0.84)	4.28 (0.18)	4.29 (0.19)	NS	NS	NS	NS
	Verbal working memory	1.84 (0.37)	1.82 (0.47)	1.96 (0.97)	NS	NS	NS	NS
	Spatial working memory	3.32 (0.69)	3.28 (0.65)	2.92 (0.78)	NS	NS	NS	NS
	Abstraction capacity	2.8 (0.32)	2.75 (0.65)	2.88 (0.78)	NS	NS	NS	NS
	Verbal inhibitory control	5.4 (0.81)	5.60 (0.62)	5.66 (0.78)	NS	NS	NS	NS

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Table 2
Questionnaire to evaluate expertise in Tango. Self-rating questionnaire composed of twenty items to evaluate subjects' expertise degree in three different domains: Tango practicing, Dance practicing and Tango teaching.

Questions to evaluate expertise degree	Posible answers
a) Tango practicing	
1—Do you currently dance Tango?	Yes/no
2—For how long have you been dancing Tango?	Specified in years, months and weeks
3—How many hours per week do you dance Tango?	Specified in hours
4—How many hours per month do you dance Tango?	Specified in hours
5—Have you ever received formal Tango instruction?	Yes/No
6—For how long have you received formal Tango instruction?	Specified in years, months and weeks
7—What style of Tango do you usually perform?	1—Salon/2—Milonguero/3—Free style/4—Electronic/5—Other
b) Dance practicing	
8—Do you performance any other style of dance?	Yes/no
9—Have you ever received formal instruction in any other style of dance?	Yes/no
10—For how long have you received formal instruction in any other style of dance?	Specified in years, months and weeks
11—Do you dance for hobby (at discos, parties, etc.)?	Yes/no
12—How many hours per week do you dance for hobby?	Specified in hours
c) Tango teaching	
13—Do you teach others to dance Tango?	Yes/no
14—How many hours per week do you teach Tango?	Specified in hours
15—Does your main income derive from teaching Tango?	Yes/no
16—Do you consider yourself as a professional Tango dancer?	Yes/no
17—Do you consider yourself as a(n):	1—Naive/2—Beginner/3—Intermediate/4—Expert
d) Familiarity with observed videos	
18—Which is the degree of familiarity that you have with the Tango steps previously observed in the videos?	1—None/2—Know 1 or 2 steps/3—Know half of the steps/4—Know most of the steps/ 5—Know all of the steps
19—How often do you execute the Tango steps previously observed in the videos?	1—Never/2—Few times a year/3—Few times a month/4—Few times a week/5—Everyday
20—How well do you know Tango Salon style?	1—Not at all/2—Very little/3—Moderately 4—Pretty well/5—Perfectly well

the category "Tango Salon" of the Tango World Championship celebrated in Buenos Aires, Argentina, in August 2010. Before video recording, several training sessions were performed. Finally, video clips were filmed in a theater scenario with a black backdrop with no additional objects or furniture in the scene to prevent potential distractions. Dancers were dressed in light-colored clothes to favor figure-ground contrast, and the costume remained consistent during the whole session. Additionally, the dancers were instructed to suppress any salient facial gestures or expressions to avoid emotional processing in the observers.

Each of the ten dance steps was recorded in five different variations. More specifically, each step was either correctly or incorrectly executed and, in this latter case, the error could be performed either by the male or the female, and it could be gross or subtle. Gross errors were defined as disruptions in the Tango step performance that could be noticed by any person irrespective of their Tango knowledge (e.g., stepping on others' feet). Subtle errors were defined as mistakes that could only be noticed by Tango dancers, given that they represent violations in the structure of the step (e.g., an incorrect position of the feet at the end of a step). Importantly, errors were always located in the legs or the feet of the dancers regardless of whether the error was gross or subtle or performed by the male or the female. Accordingly, five categories were constructed for each figure: congruent (Cong), incongruent male gross error (IncoMG), incongruent male subtle error (IncoMS), incongruent female gross error (IncoFG) and incongruent female subtle error (IncoFS). Afterward, a rating study was conducted to statistically validate these categories and select the most appropriate samples (see below).

All of the videos were structured in a similar manner: the execution of a Tango step represented the context, and the end of the step (which could be correctly or incorrectly executed) represented the target scene. Importantly, error onset was always located −200 ms before the end of each video, the time at which the last move to complete the Tango step began. The end of this movement, which completed and closed the Tango step, was matched with the end of the video. We were careful to ensure that the onset of the final movement always took place during this critical point (−200 ms), and not preceding it, via thorough editing of the video. This critical point was determined by examining each video, frame by frame, using Adobe Premier Pro CS3 3.0 software and was subsequently used to time-lock ERP recording (for a similar methodology, see Cornejo et al., 2009; Ibanez et al., 2010, 2011; Sitnikova et al., 2003).

Stimulus validation

A rating study was performed to validate each stimulus. Ten professional Tango dancers (M = 26.7 years old, SD = 1.7 years, 6 females) with a mean of 8.8 years of Tango training and twenty-two novices (M = 21.1 years old, SD = 2.3 years, 15 females) participated in the study. After viewing the 330 videos, subjects were instructed to classify it as "correct", "masculine incorrect" or "feminine incorrect" by selecting one of those three possible options in a forced-choice questionnaire. In addition, subjects were asked to evaluate the Degree of correctness (DC) of each video via a 7-point Likert scale (1-totally correct to 7-totally incorrect).

A qualitative criterion was established to select the videos. According to this criterion, the congruent category (C) was constructed by choosing those videos with high accuracy (>80%) and a high degree of correctness (DC < 2) in both groups (experts and novices). To construct the gross categories (IFG and IMG), videos with high accuracy (>80%) and a very low degree of correctness (DC > 5) in both groups were selected. The subtle categories (IFS and IMS) were constructed by selecting those videos with high accuracy (>80%) and a moderate low degree of correctness (DC < 4) only in the Tango Group. A one-way analysis of variance (ANOVA) was performed, comprising the entire final video selection (150 videos), to calculate significant differences between categories ($F(4, 14) = 1193.9$, $p < 0.001$). Post-hoc comparisons (Tukey HSD, MS = 0.07, df = 145.00) further confirmed that the degree of correctness of the congruent category (mean = 1.24; SD = 0.10) was significantly lower than that of the incongruent categories (all $p < 0.001$). In addition, the gross categories (IncoFG, mean = 5.35; SD = 0.29; IncoMG, mean = 5.4; SD = 0.39) displayed a higher degree of correctness (all $p < 0.001$) than the subtle categories (IncoFS, mean = 3.53; SD = 0.22; IncoMS, mean = 3.57; SD = 0.25). Finally, no significant differences were detected between male and female gross ($p = 0.94$) neither subtle categories ($p = 0.97$).

According to this selection, 150 videos (30 per category) were selected for use in the final experimental task (see online Supplementary material for examples of the videos).

Experimental task

In a two-alternative forced-choice (2AFC) task, participants were instructed to watch the videos and classify them into one of two categories (correct or incorrect) as quickly and accurately as possible (see Fig. 1). Each video was repeated twice, resulting in a total of 300 stimulus presentations throughout the entire experiment. Trials were presented pseudo-randomly (the sequence was counterbalanced, ensuring that no more than two trials of the same category came consecutively) after a brief practice session (15 video clips that were not included in the experimental trials). Videos were presented at a rate of 30 frames per second on a 19-inch ViewSonic CRT screen at a resolution of 1024 × 768 pixels and a refresh rate of 100 Hz. The presentation of the videos was centered on a black background at a viewing distance of 60 cm and subtended approximately 22.61 visual angle horizontally and 12.83 vertically. Each trial began upon presentation of the video. A fixation cross appeared in the quadrant of the screen where the Tango step would finish (beginning at 2500 ms after video onset and lasting 500 ms).

Target scene onset (the time point of the video at which the error could appear) was identified using a red frame surrounding the video display, similar to the one used in a subset of studies conducted by Sitnikova et al. (2003, 2008). This red frame was used in the entire video presentation (including videos used during the practice session) and participants were aware of it. ERPs were time-locked to the error onset, which always took place −200 ms before the end of the video. In this task, participants were instructed to press either key 1 or 2 (congruent or incongruent, respectively) with their right hand and had to wait until the clip ended to respond. After each response, an interval of 1500 ms preceded the next trial. No feedback was given

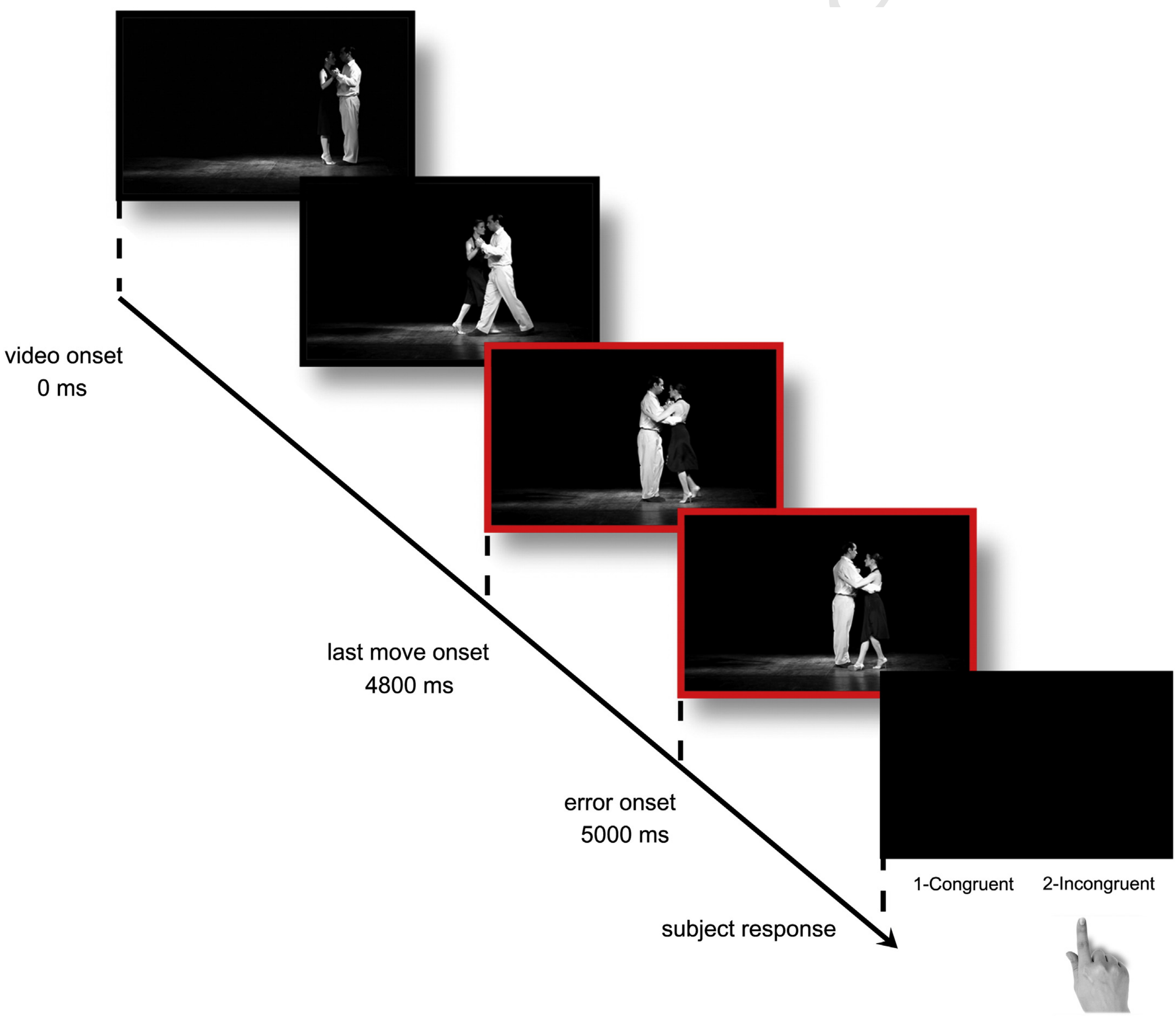

Fig. 1. Example of the experimental task. In a two-alternative forced-choice (2AFC) task, participants watched the videos and classified them as congruent or incongruent by pressing either key 1 or 2 with their right index finger. Each trial began upon presentation of the video (video onset). ERPs were time-locked to the last move onset, which always took place 200 ms before the end of the video. The end of this move, which completed and closed the Tango step, was matched with the end of the video (5000 ms).

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to the participants during the task. There were no breaks during the task.

Eye-tracking recording

Eye movements were recorded to control that the subjects were actually looking at the feet/legs of the dancers during the task. The task was carefully designed to control eye movements by using a small display and a red frame surrounding the target scene in order to focus participant's attention on the body part and time frames were the error could appear. Therefore, we did not expect to detect significant differences between groups in their eye-tracking patterns. In addition, ocular measures ensured that the observed differences in the ERPs could not be explained by differences in eye movement patterns as it has been reported that microsaccades can bias ERPs (Dimigen et al., 2009). For more detailed information regarding eye-tracking recording, pre-processing and analysis see the Supplementary material.

EEG recording and pre-processing

Participants were seated in an electrically shielded, dimly lit room. The EEG was recorded using 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. Then, data were filtered off-line to remove any undesired frequency components between 0.3 and 40 Hz and were 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 (EOG).

Continuous EEG data were segmented from −5000 ms to 1000 ms after stimulus onset to explore anticipatory modulations and from −200 ms to 1000 ms after stimulus onset to examine ERP modulations. All segments with eye movement contamination were removed from further ERP analysis using Independent Component Analysis (ICA) and visual inspection. Only artifact-free segments were averaged to obtain ERPs. All conditions possessed a trial rejection rate of <22% and no differences between the groups with respect to ERP trial rejection rates were observed in any condition. Four ERP responses were identified: anticipation, P300, N400 and SW. Brain potentials were built according to the content of the clip. The amplitude of each component was measured for each condition. Time windows encompassing the maximum amplitude difference between the conditions were selected, and the mean amplitude was calculated in the epochs: from −250 ms to the stimulus onset for anticipation; 234–305 ms for P300; 347–410 ms for N400; and 750–900 ms for SW. In the case of anticipation, this epoch was chosen based on data visual inspection and the theoretical assumption that this activity would occurred preceding target scene onset (the time point of the video at which the error could appear). Therefore, the anticipation window (~200 ms before error onset) corresponds to the time at which the last move to complete the Tango step is performed. In the case of the P300, N400, and SW responses, the epochs were selected based on visual inspection of the data and previous literature which suggest a convergence around centro-posterior sites (Lau et al., 2008; Polich, 2007).

Data analysis

Executive function, empathy and expertise

The neuropsychological data and the expertise measures derived from the questionnaire were compared between groups using one-way ANOVA or mixed repeated measures ANOVA (RM-ANOVA). Post-hoc analyses (Tukey Honestly Significant Difference, HSD) were performed for multiple pairwise comparisons. When analyzing categorical variables, the Pearson chi-square (χ^2) and the maximum likelihood χ^2 tests were applied.

Behavioral data analysis of the paradigm

The behavioral data (accuracy) were compared between groups using RM-ANOVA. Estimates of the effect size were obtained using eta squared. Post-hoc analyses (Tukey HSD) were performed for multiple comparisons. For each comparison, one between-subjects factor (group variable with 3 levels: experts, beginners, or naïves) and one within-subjects factor (condition variable with five levels: Cong, IncoFG, IncoFS, IncoMG, IncoMS) were used.

ERP analyses

To analyze the scalp topography of the ERP components, regions of interest (ROIs) were chosen after visual inspection of each component as recommended for dense arrays. In order to avoid a loss of statistical power (Ibanez et al., 2012a; Oken and Chiappa, 1986), groups of eight electrodes were collapsed into specific regions. The selection of ROIs was conducted in several steps. During an initial visual inspection, several effects were observed all over the scalp. After a preliminary analysis, we selected four centro-parietal ROIs (see ERPs figures for localization of the scalp electrodes) where the effects were most prominent: the Cz ROI (around the vertex: A1, C1, C2, D1, D2, C21, C22, C23), the PL ROI (parietal left: A6, A7, A8, D17, D26, D27, D28, D29), the Pz ROI (parietal central: A3, A4, A5, A18, A19, A20, A31, A32) and the PR ROI (parietal right: B3, B4, B5, B13, B16, B17, B18, B19).

For each comparison, a mixed RM-ANOVA was used, with one between-subjects factor (group variable: experts, beginners and naïves) and two within-subject factors: condition (Cong, IncoFG, IncoFS, IncoMG, IncoMS) and ROI (Cz, PL, Pz and PR). We proceed with splitting in more simple design ANOVA to explore complex interactions within each group. The interactions with the factor ROI were tested in separated follow-up ANOVAs within each group (thus representing a second-level interaction between condition × group). Estimates of effect size were obtained using the eta squared value, and post-hoc analyses (Tukey HSD) were performed for multiple comparisons. The EEGLab-Matlab toolbox was used for EEG off-line processing and analysis (Delorme and Makeig, 2004).

Source reconstruction analysis

Cortical current density mapping of subject-wise averaged ERPs for conditions of interest were reconstructed using the Brain Storm package (Tadel et al., 2011). The forward model was calculated using the OpenMEEG Boundary Element Method (Gramfort et al., 2010) on the cortical surface of a template MNI brain (colin27 atlas) with a 1 mm resolution. The inverse model was constrained using weighted minimum-norm estimation (wMNE) (Baillet et al., 2001) to estimate source activation in picoampere-meters (pA m). Relative activation values per subject and condition were normalized by calculating z-scores at each time-point relative to the baseline activity within the −200 to 0 ms window. These z-scores were used to plot cortical maps and to extract the ROIs that were visually identified in the cortical maps.

Source reconstructions were performed on the waves obtained from the grand-average of the incongruent conditions (collapsing IncoFG, IncoFS, IncoMG and IncoMS) in two time windows, one for estimating the neural generators of the anticipatory effect (−1000–0 ms) and the other for estimating the generators of P300, N400 and SW (0–1000 ms). The statistical analysis was performed using cluster-based permutation tests (Maris and Oostenveld, 2007) and was implemented in the FieldTrip toolbox for M/EEG analysis (Oostenveld et al., 2011). We selected this statistical analysis to handle the multiple comparisons problem of EEG data. In this analysis, the statistical metric of the original data was computed with independent samples. T-statistics and clusters were identified based on t-values that were at the 2.5-th and the 97.5-th quartiles of the two-sided *t*-test. Afterwards, the selected t-values were combined into connected sets based on their temporal adjacency, and cluster-level statistics were calculated by taking the sum of the t-values within each cluster. The data were later permutated by applying 2000 permutation draws to generate a

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histogram called the Monte Carlo approximation of the permutation distribution. To calculate the differences between our data and this distribution, we used the Monte-Carlo estimation of the permutation p-value, which is the proportion of random partitions in which the observed test statistic is larger than the value drawn from the permutation distribution. If this p-value is smaller than the critical alpha-level of 0.05, then it is concluded that the data between the two groups are significantly different. This Monte Carlo method generated a non-parametric estimate of the p-value, representing the statistical significance of the originally identified cluster. For a similar methodology, please see Chennu et al. (2013).

Several scouts, BrainStorm jargon for the ROIs that are defined as a subset of vertices of the surface, were selected from an atlas (Tzourio-Mazoyer et al., 2002). In addition, some scouts were manually constructed using the BrainStorm toolbox to improve surface segmentation (we identified these regions using the MNI space). Selection of the ROIs for source analysis was based on previous fMRI, evoked magnetic fields and intracranial recording studies that reported the neural generators of anticipation-related processes and the ERPs that were analyzed in the current study. Based on previous studies of action observation and anticipation, we expected to observe activity for (a) the anticipatory window in fronto-parietal regions (e.g., BA 10, IFG and AG), the extrastriate body area (EBA) and motor and/or premotor regions (Abreu et al., 2012; Aglioti et al., 2008; Grupe et al., 2012; Kilner et al., 2004; Tomeo et al., 2012). In the case of (b) P300 (P3b), we expected to observe activity in the medial temporal lobe, the superior temporal sulcus, the superior parietal cortex and the prefrontal cortex (Baudena et al., 1995; Brazdil et al., 1999; Halgren et al., 1995, 1998, 2011; Polich, 2007). For the (c) N400, we expected to observe activations primarily in the temporal regions, such as the superior temporal gyrus (STG), the middle temporal gyrus (MTG), the superior temporal sulcus (STS), the anterior medial temporal lobe (AMTL), the inferior parietal angular gyrus (AG) and the inferior frontal gyrus (IFG) (Halgren et al., 1994, 2002; Helenius et al., 1998, 2002; Ibanez et al., 2012b; Maess et al., 2006; McCarthy et al., 1995). In addition, as we were analyzing action-related semantic violations, we also expected to observe activations in the motor and/or premotor regions (Amoruso et al., 2013). Finally, in (d) the case of SW, we expected to observe similar activations to those observed for N400, as we assumed that meaning is not something constructed at once but rather a process that emerges over time. Deep structures, such as the hippocampus and amygdala (involved, for example, in the generation of P300), are not reported here.

Path model analysis

To determine the relationships between anticipation, ERPs (P300, N400 and SW), expertise and error detection performance, we used a path analysis (Shipley, 2002). This analysis relies on a theoretical model that characterizes relationships between a set of variables. These relationships are specified a priori (following a given theoretical criterion) and further tested by exploring how successfully the model explains the pattern of correlations between the targeted variables (Ibanez et al., 2013). Based on this approach, we have proposed two competing models which aim to predict the expertise effect in view of ongoing activity and evoked responses. One of the models is based on the semantic processing of the observed actions and their processing frequency; therefore, it includes not only the N400 and SW modulations but also the P300 ones (Model 1). Conversely, the second one is exclusively based on the semantic processing of the observed actions (Model 2), considering only N400 and SW modulations (see below).

The theoretical path model developed in the present study states that ongoing anticipatory activity would directly predict the evoked cortical responses (N400 and SW) and motor expertise. Furthermore, depending on their timing (N400 first and SW later), these evoked cortical responses would also predict motor expertise. In addition, motor expertise would predict subjects' behavioral responses (e.g., performance on error detection). More specifically, the predictions of our theoretical model are the following:

(a) Anticipation → N400/SW: If ongoing activity reflects the acquisition and maintenance of information to interpret, predict, and respond more efficiently to environmental demands (Raichle, 2010), then this activity would anticipate the meaning of the observed action and directly impact on the N400 and SW modulations through a congruency effect.
(b) Anticipation → Motor Expertise: If the ability to predict others' actions ahead of their execution depends on previous motor experience with the observed action, then ongoing anticipatory activity should predict and discriminate the observer's expertise level at early stages.
(c) N400 → SW: If the late positive activity (SW) that usually follows the N400 reflects a re-analysis of the previous semantically inconsistent situation indexed by the N400 (Munte et al., 1998), then a congruency effect in the N400 would predict further SW modulations in a similar direction.
(d) N400/SW → Motor Expertise: If a congruency effect in the N400 and the SW reflects enhanced ability to semantically process the observed action, then these modulations in the evoked responses would predict a higher degree of expertise in the observers.
(e) Motor Expertise → Error Detection Performance: If previous motor experience with the observed action tunes the perceptual abilities of the observer (Aglioti et al., 2008; Calvo-Merino et al., 2010a), then experts and (to a lesser extent) beginners should be better than naïves in detecting dance performance errors. Therefore, we would expect expertise to predict error detection in a gradual fashion.
(f) P300 → N400/SW: If the P300 indexes a frequency effect (linear accumulation of information) relevant for cortical semantic processing, then the modulations observed in this component would predict further semantic processing of the observed action as indexed by N400/SW modulations.
(g) P300 → Motor Expertise: If the P300 indexes a frequency effect (not relevant for action observation and understanding), then the modulations observed in this component would not predict the observer's expertise level.

In short, we propose that individual differences in early (anticipatory) and later (ERPs semantic responses) brain activity will be robust enough for predict the expertise profiles of the individual. As in recent studies (e.g., Ibanez et al., 2013) testing the robustness of brain activation as input for correct classification of relevant behavioral differences in a task, the present model aims to test the assumption that brain activity by itself is able to predict subject's expertise. Moreover, we propose that the ongoing brain activity elicited during video observation (and before error execution) in each group will predict both, the evoked responses and the expertise level.

The set of hypothesis tested in the present study is based on the idea that the brain is a proactive organ that is constantly benefiting from prior experiences and current contextual information to make accurate predictions in anticipating the meaning of future events (Amoruso et al., 2011, 2013; Bar, 2007, 2009; Ibanez and Manes, 2012). Moreover, this ability appears to be tuned by the individual's motor repertoire, and experts are thought to possess greater resources for generating appropriate predictions in their specific domains (Cheung and Bar, 2012). As mentioned above, one of the core aspects of this predictive ability is that it highly relies on the semantic knowledge derived from our prior sensorimotor experiences with the world. Therefore, we expected that those ERPs that index semantic-related processes (such as N400 and SW) would be affected by the subject's expertise. In fact, it has been suggested that the N400 component could be indexing 'embodied' or 'grounded' activation in the sense that the retrieval of sensorimotor information clearly modulates meaning-related processes indexed by this component (Chwilla et al., 2007, 2011; Collins et al., 2011; Hald

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Table 3
Expertise questionnaire results. P values of the RM-ANOVA and the post-hoc comparisons (Tukey's Honestly Significant Difference, HSD) obtained from the three groups in the Tango expertise questionnaire. The columns on the right specify the comparisons between groups. For the categorical variables, the Pearson χ^2 and the maximum likelihood χ^2 tests were applied.

Expertise questions	Results						
	Chi-Square (2)	ML-Chi-Square (2)	F (2, 77)	p	p (Tukey's post hoc)		
					Exp vs Beg	Exp vs Naïve	Naïve vs Beg
–Do you currently dance Tango?	80	102.29		<0.001			
–For how long have you been dancing Tango?			91.24	<0.001	<0.001	<0.001	<0.05
–How many hours per week do you dance Tango?			33.80	<0.001	<0.001	<0.001	<0.05
–How many hours per month do you dance Tango?			122.91	<0.001	<0.001	<0.001	<0.001
–For how long have you received formal Tango instruction?			59.02	<0.001	<0.001	<0.001	a
–Do you dance for hobby?	2.10	2.32		NS			
–How many hours per week do you dance for hobby?			11.00	<0.001	NS	<0.001	<0.001
–Do you teach others to dance Tango?	71.69	87.88		<0.001			
–How many hours per week do you teach Tango?			73.21	<0.001	<0.001	<0.001	NS
–Does your main income derive from teaching Tango?	39.81	41.46		<0.001			
–Which is the degree of familiarity that you have with the Tango steps previously observed in the videos?			271.63	<0.001	<0.001	<0.001	<0.001
–How often do you execute the Tango steps previously observed in the videos?			134.01	<0.001	<0.001	<0.001	<0.001
–How well do you know Tango Salon style?			214.96	<0.001	<0.001	<0.001	<0.001

(a) No variance was observed in the Naïves group, all values for Tango instruction in this group were 0.

et al., 2011). On the other hand, we expected that those ERPs that are not primarily involved in the processing of semantic meaning, but rather in stimulus frequency (such as P300), would not be affected by motor expertise.

To test this hypothesis, we developed two alternative models (Model 1 and Model 2, respectively). Both models incorporated modulations in anticipation, N400 and SW as well as the two behavioral variables, motor expertise and error detection performance. However, while Model 1 incorporated modulation in P300, Model 2 did not. We included six variables. For anticipation, P300, N400 and SW, we estimated congruent-minus-incongruent gross actions as subtractions from the relevant ERP waveforms. Motor expertise was measured via partial scores obtained from the self-rating questionnaire used to evaluate the Tango skills of the participants (see Table 2). We defined this latent variable as the sum of the most significant scores obtained by the participants in the following items: a) How many hours per week do you teach Tango? b) What degree of familiarity do you have with the Tango steps previously observed in the videos? c) How often do you execute the Tango steps previously observed in the videos? The reliability for three items was $\alpha = 0.88$. Finally, error detection performance was measured by calculating each participant's total accuracy score (%) for incongruent categories: IncoFG, IncoMG, IncoFS and IncoMS.

The analysis was conducted using MPlus 7.0 software to estimate model parameters and to assess the adequacy of the proposed model (Muthen and Muthen, 2001). The extent to which the model fit the empirical data was quantified using the following goodness of fit statistics: (1) χ^2 values and their associated p-values (which should not be significant if there is a good model fit); (2) the Root Mean Square Error of Approximation (RMSEA), which measures the degree to which the model fits the data in the correlation matrix (values that are <0.06 are considered indicative of a good fit) (Hu and Bentler, 1999); (3) the comparative fit index (CFI), which compares the performance of the specified model to the performance of a baseline (null or independent) model (values >0.95 are considered to be consistent with an acceptable model fit) (Hu and Bentler, 1999); (4) the normed-fit index (NFI),which compares the χ^2 value of the model to the χ^2 of the null model (recent studies suggest that the cut-off criteria should be NFI ≥ 0.95) (Hu and Bentler, 1999); and (5) the standardized root mean square residual (SRMR), which is defined as the standardized difference between the observed correlation and the predicted correlation. A value less than 0.08 is generally considered a good fit (Hu and Bentler, 1999). Finally, the Akaike (AIC) and Bayesian (BIC) information criteria were used to compare the two models estimated with the same data (Bollen, 1989; McDonald and Ho, 2002; Mueller and Hancock, 2008, 2010). The AIC and the BIC are comparative measures of fit, and they are meaningful only when two different models are tested. Lower values indicate a better fit, so the model with the lower AIC and BIC is the best fitting model. Importantly, the models' parsimony addressed by the AIC and BIC measures does not depend on the number of variables used in the

Table 4
Accuracy in error detection. Percentages of correct answers for each condition in the three groups.

	Experts (25)	Beginners (28)	Naives (27)
Congruent	95.12 (4.44)	93.47 (8.57)	90.61 (7.28)
Incongruent female gross error	97.06 (2.07)	91.38 (10)	67.63 (23.69)
Incongruent male gross error	82.93 (10.17)	78.30 (10.85)	65.10 (15.13)
Incongruent female subtle error	75.45 (12.34)	61.34 (21.08)	33.97 (19.67)
Incongruent male subtle error	64.66 (16.86)	54.95 (16.59)	42.35 (18.54)

Table 5
Electrophysiological measures. Mean amplitudes (in μV) and standard deviations (SD) for the anticipatory responses, the P300, the N400 and the SW evoked potentials obtained for each of the five conditions from each group.

	Experts (25)	Beginners (28)	Naives (27)
	M (SD)	M (SD)	M (SD)
Anticipatory window			
Congruent	−1.18 (0.34)	−0.94 (0.32)	−0.88 (0.33)
Incongruent female gross error	2.17 (0.42)	−0.62 (0.39)	−0.64 (0.40)
Incongruent male gross error	1.24 (0.30)	−0.05 (0.28)	−0.52 (0.29)
Incongruent female subtle error	−0.04 (0.33)	−1.18 (0.31)	−0.60 (0.31)
Incongruent male subtle error	0.83 (0.29)	−0.40 (0.28)	−0.13 (0.28)
P300			
Congruent	1.29 (0.21)	0.20 (0.20)	0.13 (0.20)
Incongruent female gross error	2.76 (0.37)	1.58 (0.35)	1.82 (0.85)
Incongruent male gross error	1.87 (0.27)	0.71 (0.25)	1.17 (0.26)
Incongruent female subtle error	2.87 (0.33)	0.93 (0.31)	1.08 (0.31)
Incongruent male subtle error	0.99 (0.25)	0.78 (0.23)	0.79 (0.24)
N400			
Congruent	3.10 (0.52)	0.77 (0.49)	1.45 (0.50)
Incongruent female gross error	0.17 (0.63)	2.16 (0.60)	3.39 (0.61)
Incongruent male gross error	1.72 (0.50)	0.82 (0.47)	2.61 (0.48)
Incongruent female subtle error	3.71 (0.61)	1.94 (0.58)	2.58 (0.59)
Incongruent male subtle error	1.53 (0.47)	1.24 (0.44)	1.16 (0.45)
SW			
Congruent	3.79 (0.65)	1.70 (0.61)	2.15 (0.62)
Incongruent female gross error	−2.19 (0.54)	0.79 (0.51)	1.45 (0.52)
Incongruent male gross error	0.13 (0.52)	1.36 (0.49)	2.07 (0.50)
Incongruent female subtle error	2.28 (0.58)	1.97 (0.55)	2.16 (0.56)
Incongruent male subtle error	1.03 (0.42)	1.14 (0.40)	1.68 (0.41)

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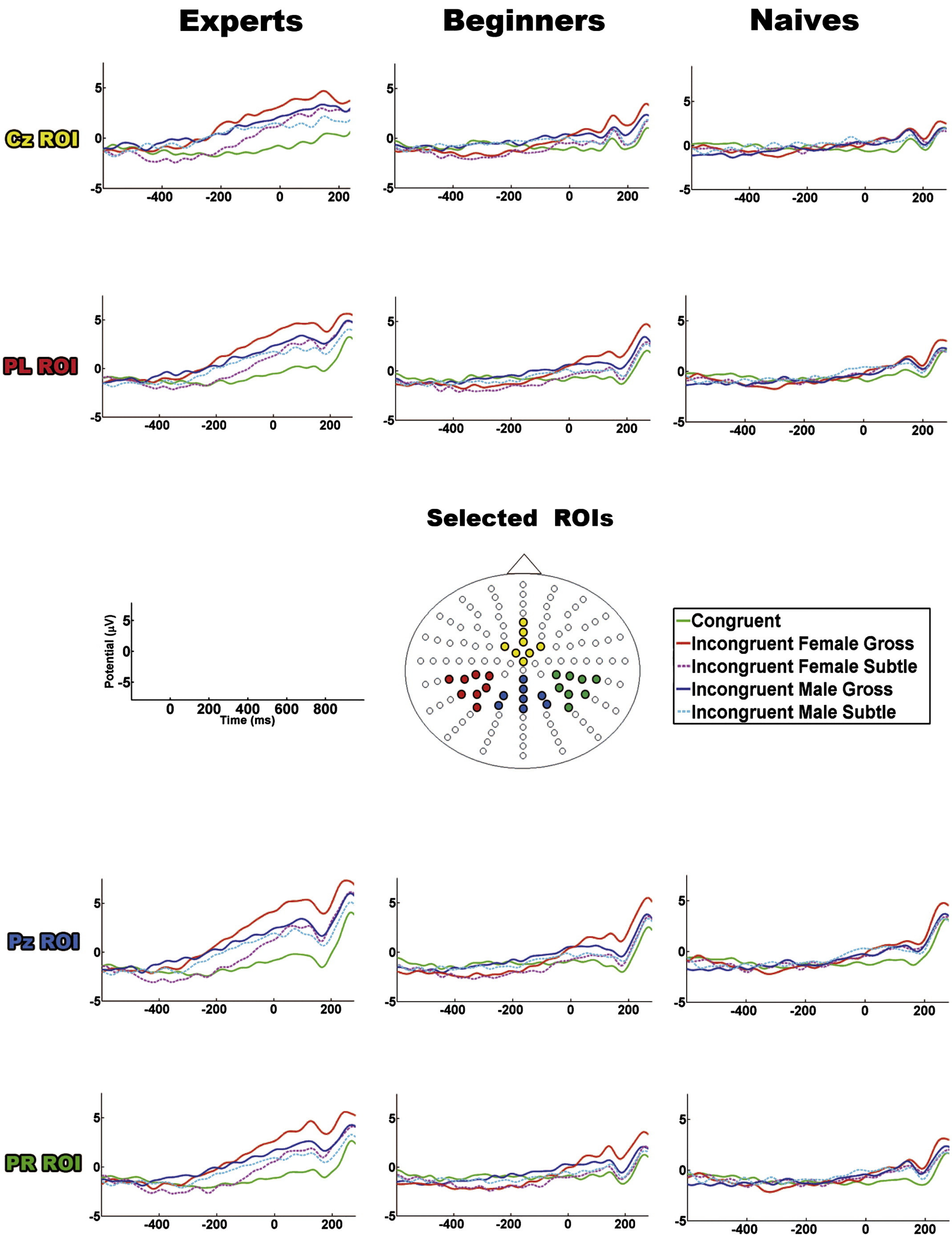

Experts
Beginners
Naives
Cz ROI
PL ROI
Selected ROIs
Potential (μV)
Time (ms)
Congruent
Incongruent Female Gross
Incongruent Female Subtle
Incongruent Male Gross
Incongruent Male Subtle
Pz ROI
PR ROI

tested models. What is primarily considered by the AIC and BIC is the statistical goodness of fit—as well as the power of estimated parameters (Byrne, 1994; Hair and Anderson, 2010; McDonald and Ho, 2002; Mueller and Hancock, 2008). Therefore, when comparing two models, the best fitting value yielded by AIC and BIC is independent of the number of variables in each model.

Results

Individual differences

Empathy and executive functions

No group effect ($F(2,77) = 2.23$, $p = 0.11$) or empathy global score × group interaction ($F(6, 23) = 1.77$, $p = 0.1$) was observed. Likewise, no group ($F(2, 77) = 0.36$, $p = 0.69$) or executive function global score × group interaction was found ($F(16, 61) = 0.62$, $p = 0.86$). In addition, in both tests, no significant interactions were observed for the subscale items (see Table 1). In summary, all groups presented similar neuropsychological profiles, with equivalent total and subtotal scores in both tests. Importantly, these findings serve as a control, as they ensure that differences between groups can only be explained by expertise and not by any of the socio-cognitive variables explored with respect to the empathy and executive function measures.

Expertise questionnaire

Multiple significant effects and significant differences were observed between the groups for several measures of expertise. Experts exhibited higher scores in those items concerning Tango practicing (e.g., hours per week dancing Tango), Tango teaching (e.g., hours per week teaching Tango) and familiarity with the observed videos. Beginners displayed intermediate scores, and naïves displayed null scores (see Table 3 for detailed statistical results).

Behavioral data

Eye-tracker results

All participants focused their attention on the dancers' legs/feet. Moreover, the probability of each participant to perform a saccade at a given time remained largely constant throughout the entire video (see Supplementary Fig. 1). The ANOVAs revealed non-significant effects of expertise and errors (see supplementary material).

Accuracy

Table 4 shows the percentages of correct responses obtained by each group.

An ANOVA of the percentage of correct responses yielded a main effect of group ($F(2, 77) = 43.63$, $p < 0.001$), and further post-hoc analysis (Tukey HSD, MS = 421.72 df = 77) revealed significant differences between subjects (experts > beginners > naïves; $p < 0.001$ and $p < 0.01$, respectively). In addition, a main effect for condition ($F(4, 30) = 55.79$, $p < 0.001$) was observed. Follow-up comparisons (Tukey HSD, MS = 160.16 df = 308) indicated that, in general, subjects were less accurate in detecting incongruent conditions compared with congruent conditions, and for incongruent conditions, subjects were less accurate in detecting subtle errors compared with gross errors (Cong > IncoFG > IncoMG > IncoFS > IncoMS, all $p < 0.01$). Finally, the group × condition interaction ($F(8,30) = 8.40$, $p < 0.001$) indicated that expertise significantly modulated error detection. Post-hoc comparisons (Tukey HSD, MS = 212.47 df = 309.86) confirmed that congruent trials were correctly classified by the three groups. However, incongruent trials were significantly better detected by experts and beginners (although to a lesser degree in the second case) than by naïves ($p < 0.001$). In addition, experts were more accurate than beginners in detecting subtle errors ($p < 0.01$).

In brief, the accuracy data reveal that while all groups were able to process congruent steps in a similar manner, gross inconsistencies in Tango steps were better detected by experts and beginners than by naïves. Finally, experts were better than beginners in detecting subtle inconsistencies, suggesting that expertise modulates action perception in a gradual fashion.

Cortical measures

Table 5 shows the means and standard deviations of all effects, and Figs. 1 and 2 illustrate the anticipatory and evoked (P300, N400 and SW) responses, respectively.

Anticipatory window

A main effect for group was observed ($F(2, 77) = 7.17$, $p < 0.01$, $\eta2 = 0.15$). Post-hoc comparisons (Tukey HSD, MS = 35.01 df = 77) indicated that, compared to beginners and naïves (both $p < 0.01$), experts elicited more positive waveforms during this epoch. However, no significant differences were detected between beginners and naïves.

A main effect was also found for condition ($F(4, 30) = 17.98$, $p < 0.001$, $\eta2 = 0.18$). Further analysis (Tukey HSD, MS = 5.91 df = 308) revealed that, in general, incongruent actions (IncoFG, IncoMG and IncoMS, all $p < 0.001$) elicited a more positive waveform than congruent ones. In addition, gross errors elicited greater amplitudes than subtle ones (IncoFG > IncoFS; IncoMG > IncoFS, both $p < 0.001$).

A significant condition × group interaction ($F(8, 30) = 7.95$, $p < 0.001$, $\eta2 = 0.17$) was detected within groups (Fig. 2).

Among experts, a main effect of condition ($F(4, 96) = 18.53$, $p < 0.001$, $\eta2 = 0.32$) further indicated (Tukey HSD, MS = 8.82 df = 96) that participants elicited larger amplitudes for incongruent actions (IncoFG, IncoMG and IncoMS all $p < 0.001$) than for congruent ones. This effect was maximal at the parietal-midline site, where a significant condition × ROI interaction ($F(12, 28) = 4.38$, $p < 0.001$, $\eta2 = 0.04$) was detected, suggesting that experts were able to anticipate and discriminate early between categories. Importantly, only experts were able to distinguish, at early stages, between different types of errors, presenting greater amplitudes for gross errors than subtle ones (IncoFG > IncoFS, $p < 0.001$; IncoFG > IncoMS; IncoMG > IncoFS, both $p < 0.05$).

Among beginners, a main effect of condition ($F(4, 10) = 4.03$, $p < 0.01$, $\eta2 = 0.12$) was further explored (Tukey HSD, MS = 5.48 df = 108), indicating that the only comparisons that reached statistical significance were IncoMG > Cong ($p < 0.05$) and IncoMG > IncoFS ($p < 0.01$). No further interactions were detected.

Finally, no main effects or interactions were detected among naïves, suggesting a complete lack of anticipation in this latter group.

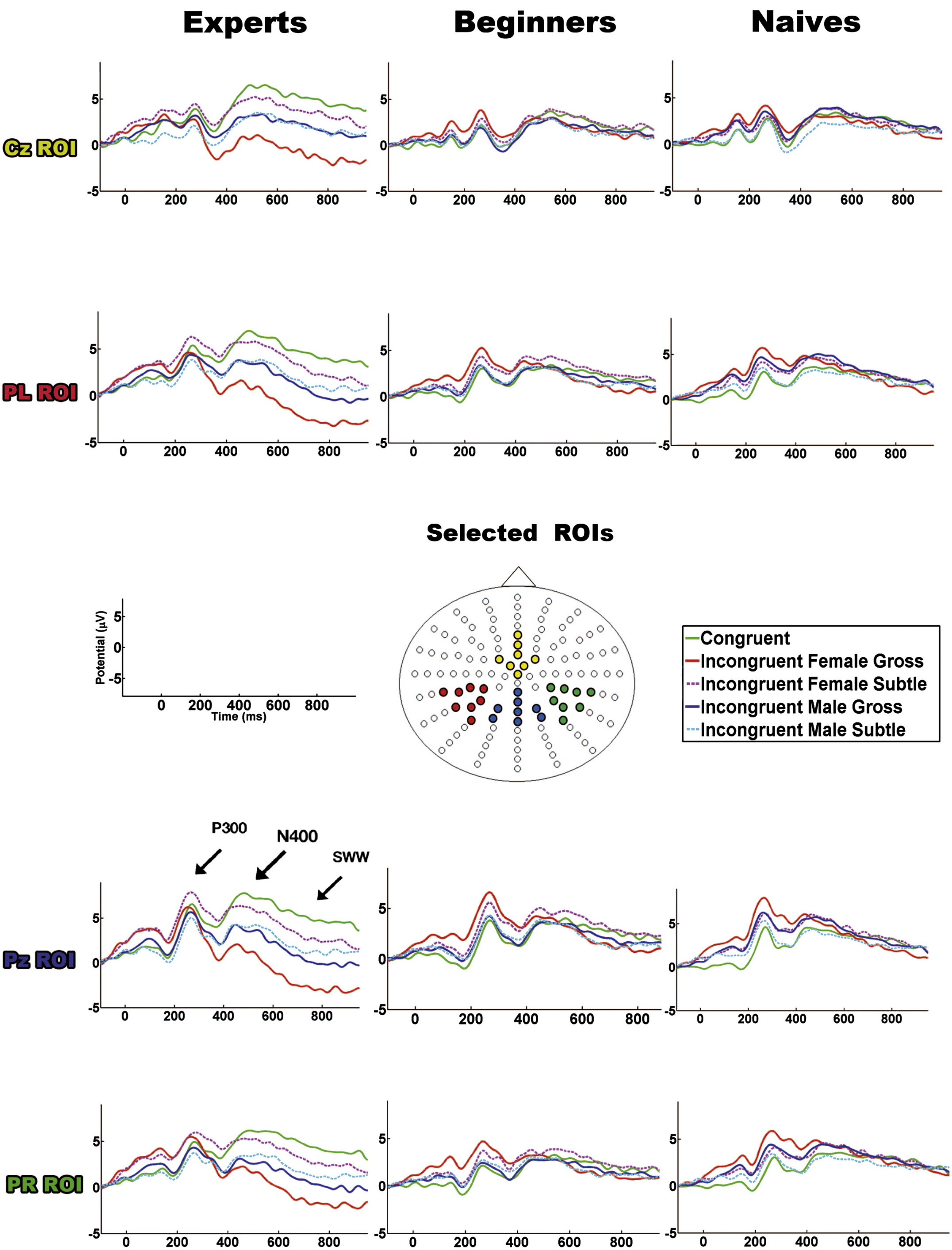
In brief, these results demonstrate that only experts were able to anticipate and detect both types of incorrect actions (gross and subtle ones) during this time window, suggesting that expertise significantly modulates action perception and motor expectations.

P300

During the P300 epoch, a main effect of group ($F(2, 77) = 10.36$, $p < 0.001$, $\eta2 = 0.21$) was observed. Post-hoc comparisons (Tukey HSD, MS = 18.14 df = 77) revealed that, compared to beginners ($p < 0.001$) and naïves ($p < 0.01$), experts elicited a greater overall P300. No significant differences were detected between beginners and naïves.

Among experts, an effect of condition ($F(4, 96) = 9.28$, $p < 0.001$, $\eta2 = 0.27$) further revealed (Tukey HSD, MS = 7.68 df = 96) that

Fig. 2. Anticipatory window. Anticipatory responses elicited by experts, beginners and naïves in the five conditions: congruent (green), female gross (red), female subtle (pink dotted line), male gross (blue) and male subtle (light blue dotted line). Shown are the anticipatory activities at the four selected ROIs: Cz, Parietal Left, Pz and Parietal Right. Time zero corresponds to the end of the video.


Experts
Beginners
Naives
Cz ROI
PL ROI
Selected ROIs
Potential (µV)
Time (ms)
Congruent
Incongruent Female Gross
Incongruent Female Subtle
Incongruent Male Gross
Incongruent Male Subtle
P300
N400
SWW
Pz ROI
PR ROI

high-skilled participants elicited a greater P300 response for IncoFG and IncoMG (both $p < 0.01$) compared to Cong. This effect was maximal over the parietal-midline electrodes ($p < 0.001$), which was confirmed by a condition × ROI interaction ($F(12, 28) = 3.31$, $p < 0.001$, $\eta2 = 0.08$). Follow-up comparisons of this interaction (Tukey HSD, MS = 0.30 df = 288) also indicated that IncoFG and IncoMG (both $p < 0.001$) elicited larger P300 amplitudes compared to IncoMS for the same electrode sites.

Among beginners, an effect of condition ($F(4, 10) = 5.53$, $p < 0.001$, $\eta2 = 0.17$) was also detected. Post-hoc analysis (Tukey HSD, MS = 5.01 df = 108) indicated that the processing of incongruous actions elicited greater P300 amplitudes than congruent actions. However, only IncoFG ($p < 0.001$) reached statistical significance. A condition × ROI interaction ($F(12, 32) = 1.94$, $p < 0.05$, $\eta2 = 0.06$) further confirmed (Tukey HSD, MS = 0.21 df = 324) that this effect was maximal over the parietal-midline and right parietal electrode sites (both $p < 0.001$).

A similar pattern was observed among naïves. A main effect of condition ($F(4, 10) = 6.73$, $p < 0.001$, $\eta2 = 0.20$) was further explored (Tukey HSD, MS = 6.03 df = 104), indicating that the processing of incongruent actions (IncoFG $p < 0.001$; and IncoMG $p < 0.05$) elicited greater P300 amplitudes compared to Cong. A condition × ROI interaction ($F(12, 31) = 3.36$, $p < 0.001$, $\eta2 = 0.11$) further indicated (Tukey HSD, MS = 0.24 df = 312) that this effect was maximal over the parietal-midline and right parietal electrode sites (all $p < 0.001$).

In brief, similar responses to action processing were observed within this time window in the three groups, with more incongruent actions eliciting greater amplitudes than congruent ones (see Fig. 2). This suggests that subjective probability modulated the P300 amplitude (see Discussion section).

N400

During the N400 epoch, no main effect of group was observed. A main effect of condition ($F(4, 30) = 6.24$, $p < 0.001$, $\eta2 = 0.07$) was detected, and post-hoc comparisons (Tukey HSD, MS = 14.24 df = 308) revealed significant differences between the conditions (IncoFS > Cong; IncoFS > IncoMG both $p < 0.01$; and IncoFS > IncoMS $p < 0.001$).

A significant condition × group interaction ($F(8, 30) = 8.55$, $p < 0.001$, $\eta2 = 0.18$) was further explored within each group.

Among experts, a main effect of condition ($F(4, 96) = 11.46$, $p < 0.001$, $\eta2 = 0.32$) revealed that the N400-like signal was affected in amplitude by action congruence, with lower ERPs for all incongruent actions (except IncoFS) than for congruent actions. However, post-hoc comparisons (Tukey HSD, MS = 16.92 df = 96) revealed that only IncoFG ($p < 0.001$) reached statistical significance. In addition, IncoFG ($p < 0.001$), IncoMG and IncoMS (both $p < 0.01$) presented more negative amplitudes compared to IncoFS. A condition × ROI interaction ($F(12, 28) = 3.39$, $p < 0.001$, $\eta2 = 0.12$) indicated that this effect was maximal in the left and parietal-midline regions (both $p < 0.001$).

A main effect of condition was also found in beginners ($F(4, 10) = 3.56$, $p < 0.01$, $\eta2 = 0.11$). This group exhibited an opposite ERP pattern, with congruent actions eliciting more negative amplitudes than incongruent ones. Post-hoc comparisons (Tukey HSD, MS = 17.73 df = 108) yielded significant differences between IncoFG < Cong and IncoMG < IncoFG (both $p < 0.05$). This effect was localized to the parietal-midline regions, as indicated by the condition × ROI interaction ($F(12, 32) = 2.44$, $p < 0.01$, $\eta2 = 0.08$).

Finally, naïves exhibited a similar pattern to that observed in beginners. A main effect of condition was detected ($F(4, 10) = 6.81$, $p < 0.001$, $\eta2 = 0.20$). Further comparisons (Tukey HSD, MS = 13.33 df = 104) revealed significant differences between IncoFG < Cong ($p < 0.01$), IncoFG < IncoMS ($p < 0.001$), IncoFS < IncoMS and IncoMG < IncoMS (both $p < 0.05$) at the parietal-midline electrode sites, which was confirmed by the condition × ROI interaction ($F(12, 31) = 3.25$, $p < 0.001$, $\eta2 = 0.11$).

In summary, while experts presented more negative amplitudes for incongruent compared to congruent actions, beginners and naïves exhibited the opposite pattern, with enhanced amplitudes for congruent compared to incongruent actions (see Fig. 3). Taken together, these findings suggest that only the N400 of high-skilled participants was able to properly process a semantic distinction of the observed actions.

SW

No main effect of group ($F(2, 77) = 1.20$, $p = 0.3$) was detected. However, a main effect of condition ($F(4, 30) = 18.63$, $p < 0.001$, $\eta2 = 0.19$) was found. Post-hoc analysis (Tukey HSD, MS = 16.41 df = 308) revealed that, in general, the congruent condition elicited a greater ERP amplitude than incongruent conditions (IncoFG; IncoMG both $p < 0.001$ and IncoMS $p < 0.01$). In addition, incongruent conditions differed in their amplitudes (IncoFS > IncoFG, $p < 0.001$; IncoMG > IncoFG; IncoMS > IncoFG, both $p < 0.01$; and IncoFS > IncoMG, $p < 0.05$).

A significant condition × group interaction ($F(8, 30) = 7.99$, $p < 0.001$, $\eta2 = 0.17$) was further explored within groups.

Importantly, a main effect of condition ($F(4, 96) = 23.55$, $p < 0.001$, $\eta2 = 0.49$) was only detected among experts. Post-hoc comparisons of this effect (Tukey HSD, MS = 21.66 df = 96) confirmed that SW amplitudes were strongly affected by action congruence, with greater ERPs for congruent vs. incongruent actions (IncoFG, IncoMG and IncoMS, all $p < 0.001$) at the left parietal and parietal-midline sites, as indicated by Tukey's comparisons (MS = 0.708 df = 288) of the condition × ROI interaction ($F(12, 28) = 3.97$, $p < 0.001$, $\eta2 = 0.14$). For beginners and naïves, no main effects of condition or any further interactions were detected.

In brief, the results indicate that the SW amplitudes are significantly modulated by action congruence only among experts, suggesting again that only high-skilled participants were able to properly perform a semantic re-analysis of the observed actions (see Fig. 3).

Source reconstruction

Fig. 4 shows the overall pattern of activation within the different temporal dynamics (anticipation, P300, N400 and SW) for the three groups. The overall activity corresponding to each of these windows was averaged and plotted as relative activation z-scores (positive and negative values) for visualization purposes. Note that higher positive values indicate an enhancement of positive activity in a given brain area, while negative ones indicate an enhancement of negative activity within that area.

Fig. 5 shows the cluster analysis of the source reconstruction. As detailed below, the z-score normalized cortical maps of source activation were grouped by significant differences between groups during the specific time windows for anticipation, P300, N400 and SW activation.

Anticipatory window

As expected, significant activation was observed in the occipital, frontal and parietal regions. This activity was significantly more negative for experts compared to naïves in the right motor cortex (MC, cluster t = −120.74, $p < 0.05$), the left inferior (cluster t = −293.34, $p < 0.05$) and left middle occipital cortices (MOC, cluster t = −290.23, $p < 0.05$), the left EBA (cluster t = −400, $p < 0.01$) and the anterior portion of the right orbitofrontal cortex (antOFC, cluster t = −385.31, $p < 0.05$). In addition, we observed a tendency toward

Fig. 3. Overall average waveforms for P300, N400 and SW. ERPs elicited by experts, beginners and naïves in the five conditions: congruent (green), female gross (red), female subtle (pink dotted line), male gross (blue) and male subtle (light blue dotted line) time-locked to 200 ms before the end of the Tango video ending (error onset). Shown are the waveforms at the four selected ROIs: Cz, Parietal Left, Pz and Parietal Right.

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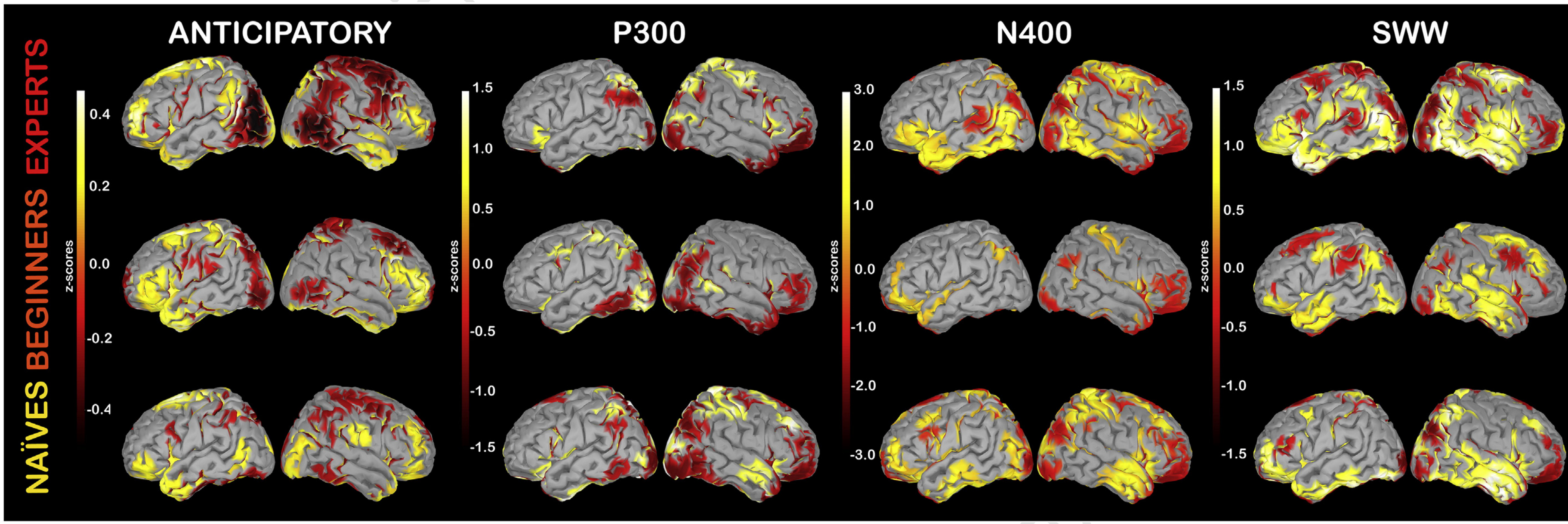

Fig. 4. Source reconstruction of cortical responses. The figure reflects the mean source activation for each group (experts, beginners and naïves) in each of the four time windows of interest: anticipation (250 ms before stimulus onset), P300 (234–305 ms), N400 (347–410 ms) and SW (750–900 ms). The activity corresponding to each of these windows was averaged and presented as a relative activation value (positive or negative) for visualization purposes.

more negative activation in the right BA 10 (cluster t = −83.03, p = 0.06) and in the right superior parietal lobe (SPL, cluster t = −118.06, p = 0.05).

More positive activity for experts compared to naïves was also detected in the left (cluster t = 234.98, $p < 0.05$) and right lingual gyri (cluster t = 267.20, $p < 0.05$), the left (cluster t = > 400, $p < 0.05$) and right fusiform gyri (FUS, cluster t = >400, $p < 0.01$), the right inferior MC (cluster t = 130.44, $p < 0.05$) and the right medial parietal lobe (cluster t >400, $p < 0.01$). In addition, compared to beginners, experts exhibited more negative activation in the right MC (cluster t = −110.00, $p < 0.05$).

Finally, naïves exhibited more negative activity in the left lingual gyrus (cluster t = −131.63, $p < 0.05$) and the right FUS (cluster t = −203.22, $p < 0.05$) and more positive one in the MOC (cluster t = 119.28, $p < 0.05$) compared to beginners.

P300

Significant activation was observed in temporal regions. This activity was significantly more negative for experts compared to beginners in the right superior temporal gyrus (STG, cluster t = −113.57, $p < 0.05$) and more positive for naïves compared to beginners in the medial temporal gyrus (MTG, cluster t = 104.19, $p < 0.05$).

N400

Significant activation was observed in the temporal, motor and premotor regions. This activity was significantly more negative for experts than beginners in the right STG (cluster t = −81.77, $p < 0.05$).

Compared to naïves, the activity of experts was more negative in the right STG (cluster t = −104.19, $p < 0.05$), the left MTG (cluster t = −117.74, $p < 0.05$) and the more anterior parts of the right temporal lobe (ATL, cluster t = −88.17, $p < 0.05$). Importantly, compared to beginners and naïves, experts exhibited significantly more negative activity in the right MC (both cluster t = <−400, $p < 0.01$) and more positive activity in the right premotor cortex (PMC, cluster t for beginners = 206.50 and for naïves > 400; both $p < 0.01$).

SW

During this time window, significant activation was observed in the frontal, pre-frontal, temporal and parietal regions. These activations were more negative for experts than for naïves in the right inferior parietal cortex (IPC, cluster t = <−400, $p < 0.01$), the left inferior frontal gyrus (IFG, cluster t = −111.95, $p < 0.05$) and the left MTG (cluster t = −125.36, $p < 0.05$). Again, compared to beginners and naïves, experts exhibited a more negative activation in the right MC (both cluster t = <−400, $p < 0.01$) and a more positive one in the right PMC (cluster t = −131.59, $p < 0.05$ and cluster t < −400, $p < 0.01$, respectively). In addition, naïves exhibited lower activity in the right PMC compared to beginners (cluster t = −102.35, $p < 0.05$).

Path analysis modeling

In Model 1 (Fig. 6), the χ^2 test statistic was not significant, suggesting that the model fit was acceptable (χ^2 (7, N = 80) = 10.58, p = 0.16). Overall, the fit indices were good; however, the RMSEA index was somewhat weak (NFI = 0.92; GFI = 0.96; CFI = 0.97; RMSEA = 0.08; IC = 0.00; .172; SRMR = 0.04). All paths among variables were significant except the paths between the P300 modulation and motor expertise (p = 0.41) and between the P300 and N400 modulations (p = 0.09). The path coefficients, direct and indirect effects and p values are provided in Table 6.

Model 2, without P300 (Fig. 7), displayed a better overall fit compared to that of Model 1 (χ^2 (4, N = 80) = 2.66, p = 0.62). Moreover, excellent indicators, including RMSEA, were calculated in this second model (NFI = 0.98; GFI = 0.98; CFI = 1.00; RMSEA = 0.00, IC = 0.00; .140; SRMR = 0.02). Importantly, all paths among variables were significant. An examination of the standardized and non-standardized coefficients (Table 6) revealed that anticipation had a direct negative effect on motor expertise (−0.35), N400 (−0.23) and SW (−0.18). In turn, SW displayed a positive effect on motor expertise (0.28). Additionally, N400 had a direct positive effect on SW (0.61). Finally, motor expertise predicted the error detection performance (0.61). The path coefficients; direct, indirect and total effects; and p values are shown in Table 7.

Finally, we compared both models using different measures of fit (Table 8). Essentially, this procedure is recommended for examination of competing theoretically plausible models (Bollen, 1989; McDonald and Ho, 2002; Mueller and Hancock, 2008, 2010). The results indicate that our path analysis without the P300 modulation fits better, suggesting that Model 2 is the more parsimonious model.

Discussion

Our study provides novel evidence regarding the following issues: 1) Early anticipatory ongoing brain activity (with sources in the fronto-parieto-occipital regions) discriminated motor expertise and error detection. 2) The causal model demonstrated that this anticipatory activity was a significant predictor of subsequent evoked neural responses of meaning-processing as well as motor expertise. Furthermore, semantic processing also accurately predicted subjects' motor expertise, and in turn, motor expertise was a good predictor of behavioral performance in error detection. 3) Evoked cortical responses not directly involved in semantic processing (P300) were similar among groups and did not predict expertise. Although the overall P300 was more positive within experts, the three groups showed greater P300 amplitudes for incongruent actions compared to congruent ones. 4) ERPs sensitive to the semantic aspect of the observed actions (N400 and SW) were affected by the degree of congruence and expertise. 5) Accuracy in error detection during action observation was significantly influenced by motor expertise. Together, our findings provide novel insights into action observation and motor expertise by integrating the behavioral and neural dynamics that underlie action processing in terms of their causal interactions.

Behavioral and neural signatures of expertise regarding action observation

As expected, analogous levels of accuracy were observed for congruent steps in the three groups. Conversely, error identification was influenced by the expertise level of the observers. Importantly, similar to previous studies on dancing expertise (Calvo-Merino et al., 2010a; Cross et al., 2006), discrimination of errors was significantly better in experts than in the other two groups, suggesting that fine motor expertise directly affects action observation.

In addition, similar ocular patterns were observed across subjects, suggesting that the differences in neural responses between groups that were elicited during action observation were not due to differences in peripheral ocular movements.

As hypothesized, differences in ERPs associated with expertise x congruence interaction were only observed for those components sensitive to the semantic aspect of the action (N400 and SW). Although the N400 was initially described following the onset of incongruent verbal stimuli (Kutas and Hillyard, 1980), it has been also recently detected for incongruent non-verbal stimuli referring to actions (for a review, see Amoruso et al., 2013).

Nevertheless, a relevant question remains: to what extent can the observed N400 modulations be explained by differences in silent verbalization instead of motor expertise? In other words, the N400 component may be modulated by verbal labels for the observed steps—e.g., "Sandwichito" or "Salida básica", in Lunfardo (the Tango dialect), which are present in the experts' but not in the naïves' vocabulary. While the present data are not conclusive, important factors suggest that this is not the case. First, to our knowledge, there is no evidence that silent verbalization of action observation can elicit a congruency

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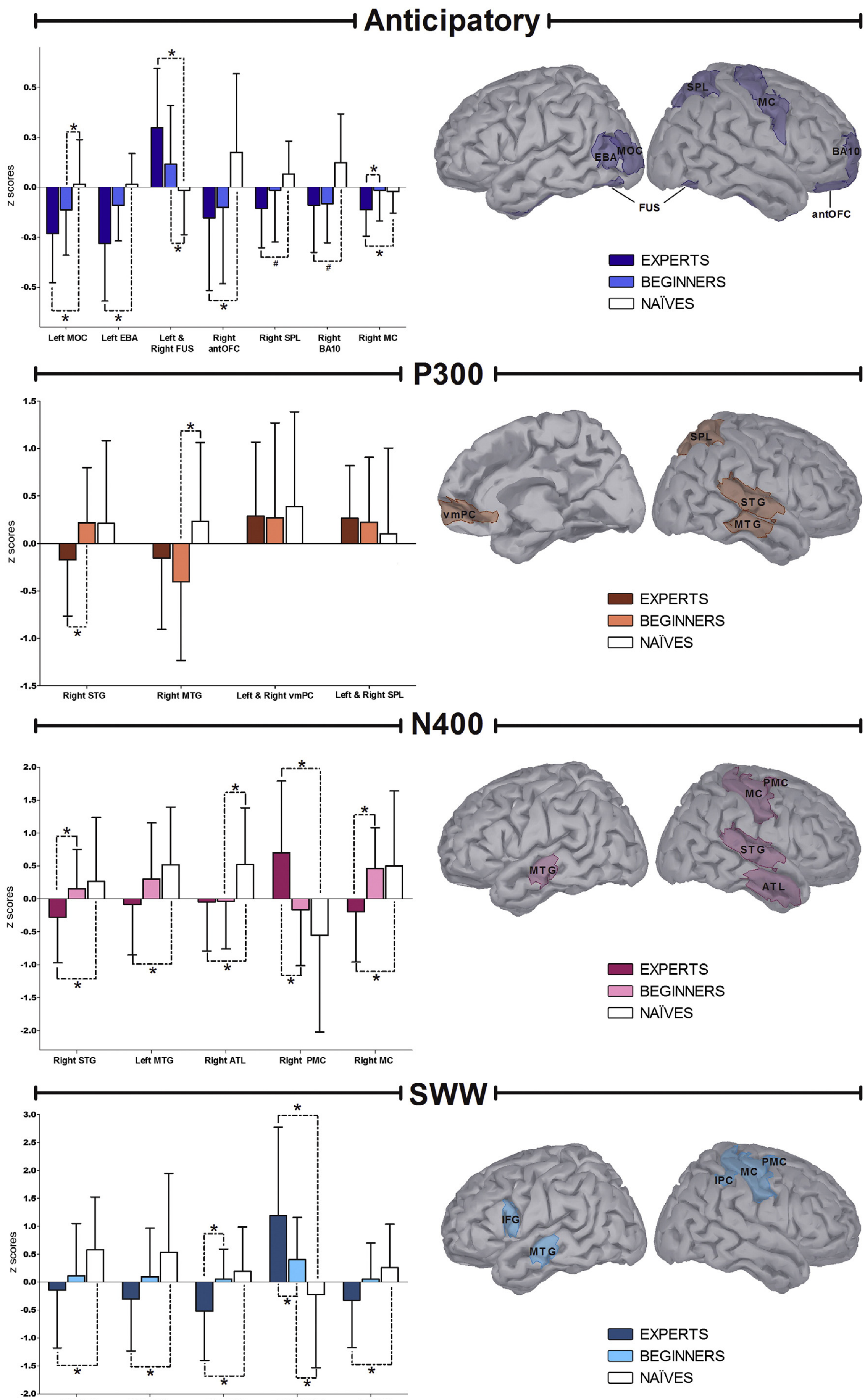
Anticipatory
z scores
Left MOC
Left EBA
Left & Right FUS
Right antOFC
Right SPL
Right BA10
Right MC
SPL
MC
EBA
MOC
BA10
FUS
antOFC
EXPERTS
BEGINNERS
NAÏVES
P300
z scores
Right STG
Right MTG
Left & Right vmPC
Left & Right SPL
vmPC
SPL
STG
MTG
EXPERTS
BEGINNERS
NAÏVES
N400
z scores
Right STG
Left MTG
Right ATL
Right PMC
Right MC
MTG
PMC
MC
STG
ATL
EXPERTS
BEGINNERS
NAÏVES
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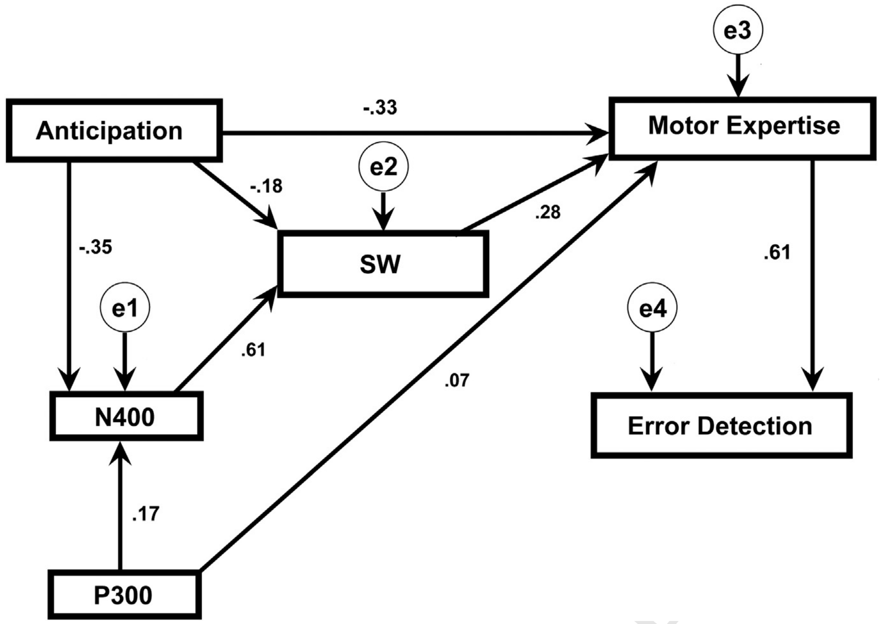

Fig. 6. Model 1. Path analysis model used to test the relationships between anticipation, ERPs (P300, N400 and SW), expertise and error detection performance. Each standardized coefficient in the diagram was statistically significant ($p < 0.01$). The "e" in the path represents the error terms of the factors not included in the model (including measurement error).

N400 effect by itself. Note that, even if this were the case, such an effect would not constitute an intrinsic limitation of our study, as it would also apply to previous N400 studies on action observation (e.g., Proverbio and Riva, 2009, Proverbio et al., 2010; Wu and Coulson, 2005; Sitnikova et al., 2003). Second, if ERP modulations actually reflected the vocabulary differences in question, no N400 effect should be observed in the naïve group. However, naïves did exhibit N400 modulations—albeit with an opposite pattern, showing enhanced amplitudes for congruent relative to incongruent actions. This finding suggests that although they were able to differentiate between categories at some level, they did not properly process semantic distinctions between the actions.

Be that as it may, there is emerging evidence that the N400 can be elicited by action observation only (for a review see Amoruso et al., 20013). Importantly, current N400 models of action assume a partial overlapping between verbal and non-verbal semantic processing. Therefore, since label assignment would depend on the observers' experience, both interpretations may actually be compatible. This interesting issue should be assessed by future studies explicitly designed to test the effect of silent verbalization on action observation.

Most of N400 studies on action observation also reported that modulations in this component are usually followed by modulations in a late positive potential (SW), which appears to reflect different types of cognitive closure such as syntactic violations (Osterhout and Holcomb, 1992), decision-making (Wu and Coulson, 2005), or re-analysis of the previous semantic inconsistent situation (Munte et al., 1998).

Interestingly, previous electrophysiological studies in other expertise domains reported modulations in both the N400 and the SW components. For example, Francois and Schön (2011) showed that musicians were better at learning musical (and linguistic) structures than non-musicians—this was indexed by a familiarity N400-like effect with greater amplitudes for musicians than non-musicians. Similarly, Besson and Faïta (1995) reported that incongruities in melodies (whether familiar or unfamiliar) elicited a larger late wave in musicians than in non-musicians. In addition, N400 expertise-like effects have been observed within the sports domain (Proverbio et al., 2012). Taken together, these studies suggest that both components (N400 and SW) are suitable to detect expertise effects.

As expected, the evoked responses that were not directly influenced by prior semantic knowledge (P300) exhibited similar modulations across groups. It is well-known that the P300 is involved in general stimulus categorization, with low-probability target items eliciting higher amplitudes than non-target (or "standard") items. Several factors, such as attentional demands, stimulus salience, and novelty are closely related to this broader process (Polich, 2007). In the present study, however, task demands remained constant throughout the experiment and stimuli had similar physical properties and were equiprobably distributed. Therefore, it seems unlikely that P300 modulations can be explained by a general process of categorization. Notably, the definition of "category" is determined by how subjects are asked to classify stimuli during a given task (Van Petten and Luka, 2012). In other words, the frequency effect on the P300 amplitude depends not only on the objective probability of the stimulus but also on the category to which events are assigned by the subjects—that is, on the subjective probability associated with the personal categorization of the eliciting event (Johnson and Donchin, 1980; Rosenfeld et al., 2005). In our study, subjects were less accurate in detecting incongruent subtle

Fig. 5. Cluster analysis of source reconstruction. Shown is a Z-score normalized cortical map of source activation for those periods that reached significant differences between groups within the windows of interest (anticipatory, P300, N400 and SW). For the anticipatory window, this activity was significantly more negative among experts compared to naïves in the right motor cortex (MC), the left middle occipital cortex (MOC), the left extrastriate body area (EBA) and the anterior portion of the right orbitofrontal cortex (antOFC). A tendency in the above-mentioned direction was detected in the right BA10 and the right superior parietal lobe (SPL). More positive activity among experts compared to naïves was detected in the left and right fusiform gyrus (FUS). In addition, compared to beginners, experts showed a more negative activation in the right MC. Finally, naïves exhibited more negative activity in the right FUS and more positive activity in the MOC compared to beginners. For P300, the activity was significantly more negative for experts compared to beginners in the right superior temporal gyrus (STG) and more positive for naïves compared to beginners in the right middle temporal gyrus (MTG). During the N400 window, experts, compared to naïves, exhibited negative activation in the right STG, the left MTG and the right anterior temporal lobe (ATL). Importantly, compared to beginners and naïves, experts exhibited significantly more negative activity in the right MC and more positive one in the right premotor cortex (PMC). Finally, for the SW window, more negative activation among experts compared to naïves was observed in the right inferior parietal cortex (IPC), the left inferior frontal gyrus (IFG) and the left MTG. Compared to beginners and naïves, experts exhibited a more negative activation in the right MC and a more positive one in the right PMC. In addition, naïves exhibited more negative activity in the right PMC compared to beginners.

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Table 6
Model 1. Path coefficients of the model with P300. All paths among variables were significant except the path between the P300 modulation and motor expertise and the path between P300 and N400, indicating that the P300 modulations were not able to predict the subjects' level of expertise and the cortical measures of semantic processing, respectively.

Effects	Non standardized			Standardized	
	Coef	SE	p	Coef	SE
Anticipation → N400	−0.53	0.15	<0.001	−0.35	0.09
P300 → N400	0.39	0.23	NS	0.17	0.10
N400 → SW	0.72	0.10	<0 .001	0.61	0.07
Anticipation → SW	−0.33	0.15	<0.05	−0.18	0.08
SW → Motor Expertise	0.38	0.13	<0.01	0.28	0.10
Anticipation → Motor Expertise	−0.79	0.24	<0.001	−0.33	0.10
P300 → Motor Expertise	0.27	0.33	NS	0.07	0.09
Motor Expertise → Error Detection Performance	2.05	0.29	<0.001	0.61	0.06
Anticipation → SW → Motor Expertise	−.0.12	0.07	NS	−0.05	0.03
Anticipation → N400 → SW	−0.38	0.12	<0.01	−0.21	0.06
Anticipation total effect on Motor Expertise	−1.06	0.23	<0.001	−0.45	0 .09
Anticipation total effect on SW	−0.71	0.18	<.001	−0.40	0.09
P300 total effect on Motor Expertise	0.38	0.34	NS	0.11	0.09
P300 total effect on SW	0.28	0.17	NS	0.10	0.06

steps compared to congruent ones. Therefore, although conditions were equally distributed, an infrequent P300 effect was observed for incongruent actions. This reflects that, in many cases, primarily among the beginner and naïve groups, subjects processed IncoMS and IncoFS as if they were Cong.

Overall, our findings suggest that meaning is shaped by the observer's experience with respect to the observed action. Some studies (Chwilla et al., 2007, 2011) have highlighted the sensorimotor-grounded nature of N400. Current models of N400 have proposed that this signal would originate from a distributed network, including storage (MTG, STG, ITC, and STS), multimodal (IFG) and control retrieval areas (DLPFC) (Baggio and Hagoort, 2011; Lau et al., 2008). Based on the specific N400 models of action observation (Amoruso et al., 2013), the motor and premotor regions, such as domain-specific regions, would also be recruited, together with the temporal regions classically associated with semantic memory (ATL, MTG, STG). As expected, a source reconstruction of the N400-related activity indicated that the motor and premotor regions, together with temporal regions (e.g., STG), were significantly involved within this time window.

Activations observed during the SW window displayed a similar pattern, with the subsequent contribution of the IFG and the IPC. Thus, the significance of an action event would be achieved via integration of the sensorimotor information from previous experiences (the premotor/motor regions), with learned semantic associations stored in temporal regions (e.g., the MTG). This integration is mediated by multimodal and cross-modal brain regions located in the frontal and parietal cortices (IFG and IPC), which work in parallel. Within this framework, the IFG implements a mechanism that matches the observed actions to one's motor repertoire (Avenanti and Urgesi, 2011; Kilner et al., 2009), and the IPC works as an interface between sensorimotor and semantic information to contextually represent action significance (Seghier, 2013). Notably, experts showed a more negative activity in the STG compared to beginners and naïves. This area has been reported to be involved in the perception of biological motion (Fraiman et al., 2014; Howard et al., 1996; Vaina et al., 2001), suggesting that skilled subjects were better in reading body cues. Our findings are consistent with the aforementioned network but are directly modulated by the subjects' expertise.

Finally, our path model revealed that early ongoing anticipatory activity was a significant predictor of further semantic processing, suggesting that anticipation facilitates subsequent meaning construction along successive temporal levels. Moreover, this anticipatory activity also accurately predicted the subjects' motor expertise. Thus, our model highlights the anticipatory nature of our brains.

Action anticipation: contextual predictions

Theoretical models of action perception, object recognition and even social cognition have emphasized that our brain constantly generates predictions about future events by minimizing discrepancies between context-based expectations and current experience (Bar, 2007, 2009; Ibanez and Manes, 2012; Melloni et al., 2013).

In neuroanatomical terms, these models suggest that the frontal regions would be involved in updating contextual information and

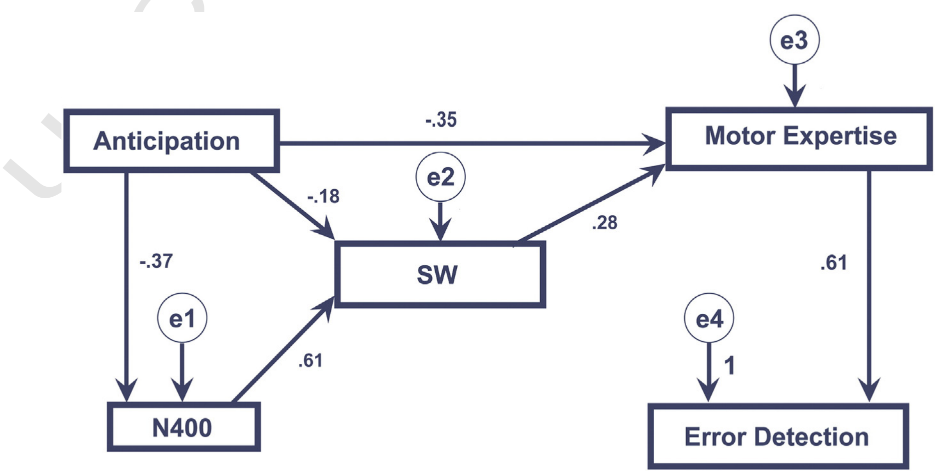

Fig. 7. Model 2. Path analysis model used to test the relationships between anticipation, ERPs (N400 and SW), expertise and error detection performance. Each standardized coefficient in the diagram was statistically significant (p < 0.01). The “e” in the path represents the error terms of factors not included in the model (including measurement error).

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Table 7
Model 2. Path coefficients of the model without P300. Anticipation had a direct negative effect on motor expertise, N400 and SW. In turn, SW displayed a positive effect on motor expertise. Additionally, N400 had a direct positive effect on SW. Finally, motor expertise predicted error detection performance.

Effects	Non standardized			Standardized	
	Coef	SE	*P*	Coef	SE
Anticipation → N400	−0.57	0.15	<0.001	−0.37	0.09
N400 → SW	0.72	0.10	<0.001	0.61	0.07
Anticipation → SW	−0.33	0.15	<0.05	−0.18	0.08
SW → Motor Expertise	0.37	0.13	<0.01	0.28	0.10
Anticipation → Motor Expertise	−0.82	0.24	<0.001	−0.35	0.09
Motor Expertise → Error Detection Performance	2.05	0.29	<0.001	0.61	0.06
Anticipation → SW → Motor Expertise	−0.12	0.07	<0.05	−0.05	0.03
Anticipation → N400 → SW	−0.41	0.12	<0.01	−0.23	0.06
Anticipation total effect on Motor Expertise	−1.10	0.23	<0.001	−0.46	0.08
Anticipation total effect on SW	−0.74	0.18	<0.001	−0.41	0.09

generating focused predictions, integrating incoming information with prior knowledge stored in temporal regions. Thus, patterns of observed movements embedded in specific contexts can trigger motor expectations about upcoming steps in an action sequence. In the present study, when the triggered expectations did not fit with the current information, the anticipatory activity and the N400 amplitudes were significantly enhanced; suggesting higher contextual anticipation and integration of target endings, respectively (see Ibanez et al., 2006). Moreover, these modulations were greater among experts, suggesting that, based on their prior experience with the observed actions; they were able to construct early expectations that were further disconfirmed upon error observation.

From the predictive coding perspective (Friston, 2012; Friston et al., 2011; Kilner, 2011; Kilner et al., 2007), the actions that are present in our own motor repertoire can be more accurately understood through the generation of an internal forward model (minimizing the prediction error at different cortical hierarchies). Briefly, an action can be described at four levels, from more concrete to more abstract aspects of action representation: the kinematic, motor, goal and intentional levels (Kilner, 2011). For example, given an expectation of the goal of a person who we are observing, we can predict, based on our own action system, the motor commands of that action, and given this, we can predict their kinematics. Therefore, if predictions are based on our own motor system, skilled subjects should be better at predicting the future steps of those actions in which they have motor excellence by the *early* generation of an error signal at the kinematic level. We observed that experts exhibited an enhancement of positive activity in a temporal window preceding the execution of the error that was further supported by the main effect of group and the condition x group interaction (anticipatory window). Similar to previous studies of motor expertise in the sporting domain (Abreu et al., 2012; Aglioti et al., 2008; Tomeo et al., 2012; Urgesi et al., 2012), this anticipatory activity might reflect that experts were able to successfully use kinematic cues, in this particular case of Tango movements, to predict the final goal of the observed action, possibly by using a 'resonance' mechanism.

One problem regarding this interpretation, however, is that people who have motor expertise in the execution of a given movement usually have visual expertise on that movement. In other words, experts not only had more experience with the observed actions but also with watching them. Additionally, it has been recently shown that visual experience in dance is able to increase motor resonance with the observed movements without motor experience (Jola et al., 2012). Thus, it remains unclear whether experts performed better because of their motor, visual expertise or both.

In fact, these two aspects have been previously dissociated as subserving two different brain mechanisms for understanding others' actions from their observed movements. Briefly, while some argue that action comprehension depends on a matching mechanism (motor simulation or motor resonance) in which observed actions are directly mapped onto one's own motor system (Gallese et al., 1996), others emphasize that this is achieved through general processes of visual inference (Saxe, 2005). Nevertheless, recent accounts suggest that both mechanisms have a complementary role and cannot be longer considered as mutually exclusive (Aziz-Zadeh et al., 2012; de Lange et al., 2008). In line with this later assumption, we suggest that, in the present study, experts benefited of both mechanisms with the anticipatory activity indexing a simulated pre-reflective representation of the action and the evoked semantic responses a more elaborate stage of processing related to meaning construction.

Source reconstruction within the anticipatory window revealed that the brain regions of the extrastriate visual cortex that are highly sensitive to the perception of human bodies/body parts (e.g., the EBA) (Amoruso et al., 2011; Calvo-Merino et al., 2010b; Urgesi et al., 2007), together with the frontal areas that are involved in top-down contextual prediction (the BA 10), were activated during this time window, primarily in the expert group. This finding suggests that experts most likely benefit from fast coupling between the visual and frontal areas, which enables them to generate early expectations based on kinematic information. Moreover, it has been suggested that EBA is also involved in imagining movements of the observer's hand or foot (Astafiev et al., 2004); therefore, the EBA activity found in experts might suggest the possible involvement of motor imagery of the body triggered by video observation.

Action features can be represented in two separate pathways (Kilner, 2011). While abstract levels (e.g., the goal) are encoded by the MTG and the IFG via a ventral pathway, more concrete aspects (e.g., kinematics) are encoded by the premotor, superior temporal and inferior parietal sites via a dorsal pathway. Our results are consistent with this proposal, as we detected MTG and IFG activity during the N400-SW window and PM-IPC activity during the anticipatory window.

In addition, our results indicated that ongoing anticipatory activity affected the subsequent evoked responses. It has been proposed that

Table 8
Model comparison. Comparison between the proposed model (without the P300) and the rival model (with the P300) using fit indices.

Model	χ^2	*p*	RMSEA	90% RMSEA	CFI	SRMR	AIC	BIC
Proposed model	2.66	0.62	0.00	(0.00; 0.14)	1.00	0.02	2251.38	2284.73
Rival model (P300)	10.58	0.16	0.08	(0.00; 0.17)	0.97	0.04	2542.24	2589.88

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ongoing brain activity could reflect the acquisition and maintenance of information to interpret, respond and predict environmental demands (Raichle, 2010). Interestingly, our results revealed that the amplitude of ongoing brain activity was a good predictor of cortical evoked responses and the subjects' ability to accurately interpret upcoming information. The link between ongoing brain activity and upcoming evoked responses might be predictive in nature.

Limitations

The present study is not without limitations. First, since no visual control condition was included in the experimental design, we cannot exclude the possibility that ERP discrepancies between groups may reflect differences in the allocation of visual selective attention in time and space. However, three factors suggest that this is not the case. First, if ERP differences were explained by an attentional rather than an expertise effect, then naïves should have performed poorly in all conditions. However, all groups achieved equal levels of accuracy for the control condition (Congr). Second, neurocognitive profiles in attention and executive functions were measured with a neuropsychological battery and no differences were observed between groups. Finally, eye-tracking results showed that all groups were similar in their ocular patterns (saccadic eye-movements analysis); this suggests that the three groups panned the scene similarly and focused their attention where appropriate, that is, on the dancers' legs/feet (see also Supplementary Fig. 1A). This is relevant because shifts of visuo-spatial attention and saccadic eye-movements patterns are closely intertwined (Corbetta et al., 1998; Hoffman and Subramaniam, 1995; Zhao et al., 2012). These three factors notwithstanding, future studies are needed to further elucidate the relationship between action observation and attention.

Second, ERP source analysis has well-known limitations for localizing the neural generators of the observed activity due to the 'inverse problem' inherent to scalp EEG recording (Luck, 2005). As done in previous studies (Lynne et al., 2008; Mishra et al., 2007; Proverbio et al., 2009, 2012), we have used labels such as EBA and STG to identify the regions where the source localizations were significant. Note, however, that these labels denote functionally-defined regions with fuzzy, partially overlapping anatomical boundaries (e.g., EBA overlaps with motion region hMT+). Therefore, these labels should be considered as approximations rather than strict topographical landmarks.

Conclusions

Although other studies have previously examined the role of motor expertise in action processing and understanding, this is the first study to provide a causal model that connects expertise, ongoing anticipatory brain activity, semantic responses of ERPs and behavioral performance within a predictive contextual coding framework. Neural signatures underlying action observation can be interpreted in terms of successive levels of contextual prediction that are crucially modulated by the subject's prior experience.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2014.05.005.

Uncited references

Bernstein et al., 2008

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Conflict of interest

The authors declare no competing financial interests.

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