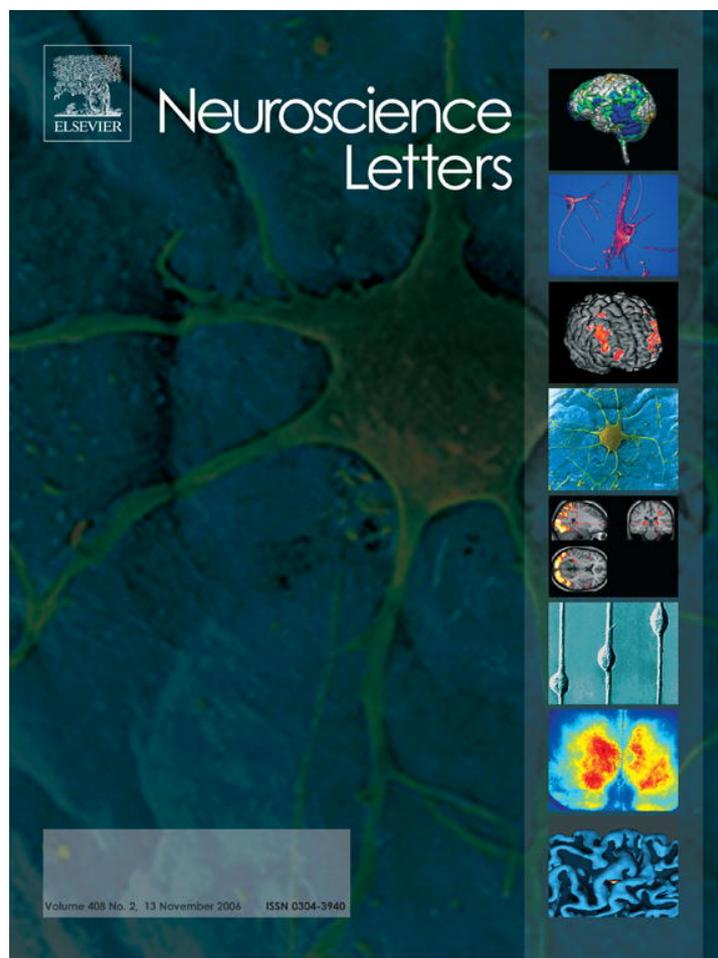


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Neural correlates of fast stimulus discrimination and response selection in top-level fencers

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Abstract

Flexible adaptation of behaviour is highly required in some sports, such as fencing. In particular, stimulus discrimination and motor response selection and inhibition processes are crucial. We investigated the neural mechanisms responsible for fencers' fast and flexible behaviour recording event-related potentials (ERPs) in discriminative reaction task (DRT, Go/No-go task) and simple reaction task (SRT) to visual stimuli. In the DRT, in addition to faster RTs measured in fencers with respect to control subjects, three main electrophysiological differences were found. First, attentional modulation of the visual processing taking place in the occipital lobes and reaching a peak at 170 ms was enhanced in the athletes group. Second, the activity in the posterior cingulate gyrus, associated with the stimulus discrimination stage, started earlier in fencers than controls (150 ms versus 200 ms) and the peak had larger amplitude. Third, the activity at the level of the prefrontal cortex (time range: 250–350 ms), associated with response selection stage and particularly with motor inhibition process, was stronger in fencers. No differences between athletes and controls were found in the SRT for both ERPs and RTs. Concluding, the fencers' ability to cope to the opponent feint switching quickly from an intended action to a new more appropriate action is likely due to a faster stimulus discrimination facilitated by higher attention and by stronger inhibition activity in prefrontal cortex.

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Rapid environmental changes require flexible adaptation of behaviour. This condition is frequent in some sports, such as fencing. Fencers respond quickly to their opponent's fast actions; to cope to the opponent's feint they switch quickly from an intended action to a new more appropriate action. Thus, stimulus discrimination and motor response selection and inhibition processes are crucial. In the present study, we investigated the neural mechanisms responsible for fencers' fast and flexible behaviour using an experimental condition which, although in an oversimplified form, mimics the fencing condition.

The Go/No-go paradigm was widely used to study the neural basis of motor response execution and inhibition. In this paradigm, the subject has to produce a motor response to a target, and to refrain from responding to a non-target. The paradigm

involves multiple perceptual and motor processing stages such as stimulus processing, stimulus discrimination, selection of the appropriate response, and response output or response inhibition.

Few events related potentials (ERPs) studies investigated group differences in the Go/No-go paradigm. Reduced components were reported in children with attention-deficit/hyperactivity-disorder (e.g. [16]), in subjects with impulsive-violent behaviour [3] and in patients with obsessive compulsive disorder [4]. Data were interpreted in terms of difficulties with inhibition of prepotent behaviour characteristic of these individuals. The present study focus on the opposite side of the population distribution, i.e., fencers with excellent skills in switching from one movement to another.

To our knowledge, the paradigm associated with ERPs recording has been used only once in fencers [18], and the results were limited to N2 and P3 components in the Go condition. The motor inhibition condition (No-go) was ignored and no information was given about other ERPs components. Based on behavioural data [18,21], we expected shorter RTs in

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fencers than control subjects. At the electrophysiological level, we expected that the perceptual and motor experience involved in fencing would modulate ERPs components related to perceptual and motor processing stages. First, we expected a group effect on attention-related components, and one question of the study was whether it would be generalized to any visuo-motor tasks, including those not requiring stimulus discrimination, such as Simple Response Task (SRT). Second, we expected to find group differences in N2 and P3 components. These components are characteristically modulated in a Go/No-go task, being larger for No-go than Go trials (e.g., [1]). Group differences would be an expression of processing difference in fencers and control subjects. To evaluate separately stimulus discrimination stage and motor selection stage, we studied difference waves [17] using a Discriminative Response Task (DRT) and a control SRT. Special care was devoted to localizing the neural substrate of electrophysiological components.

Twelve students (mean age 24.9 years; S.D. 3.5) and 12 fencers (mean age 25.2 years; S.D. 5.4) with at least four years of fencing and international championships experience partici-

pated in the study. Ten students and 10 fencers had right hand dominance. All subjects provided written informed consent to participate in the experiment after the procedures (approved by local ethics committee) had been fully explained to them.

The fixation point was a cross ($0.3 \times 0.3^\circ$ of visual angle) in the center of the computer monitor. Squared configurations made of vertical and horizontal bars subtending $4 \times 4^\circ$ (see Fig. 1 inset) were presented for 200 ms on a dark grey background. The stimulus lower edge was centered 1° above the fixation point in order to stimulate the upper hemifield only and to avoid concurrent activity that in visual areas with opposite geometry (as V1) could lead to reduction of some ERP components (see [5] for more details). The four configurations were displayed randomly with equal probability ($p=0.25$); onset asynchrony varied from 1 to 2 s.

In separate runs subject performed two tasks: DRT and SRT. In DRT, two configurations were defined as targets and two non-targets. The subjects had to press a button with their right hand, as quickly as possible, when target appeared on the screen (Go stimuli; $p=0.5$) and withheld the response when non-target appeared

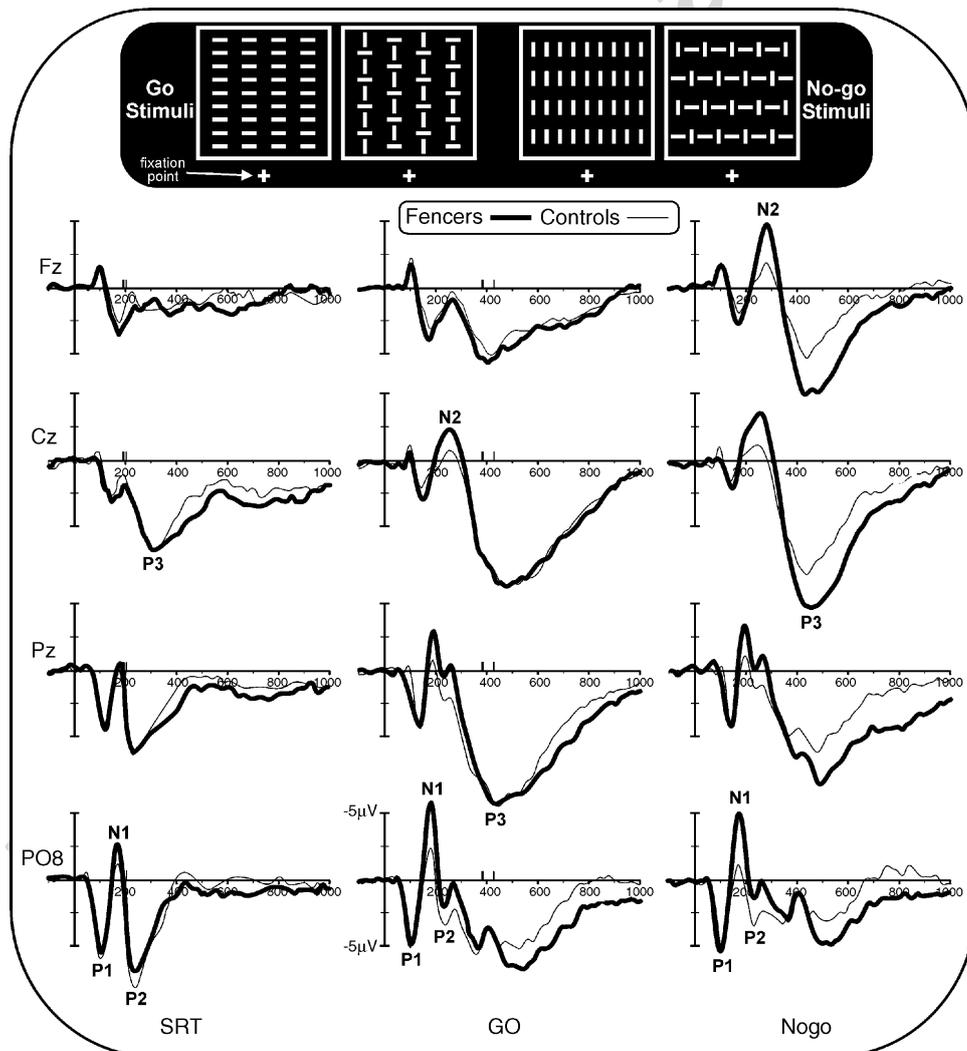


Fig. 1. Grand-average ERPs waveforms in the SRT, Go and No-go conditions. Selected channels show the major components in the two groups. Small vertical bars on the time scale indicate the motor reaction times for SRT and Go conditions. Fencers and controls are represented by thick and thin lines, respectively. The inset on the top shows the stimuli used in present experiment for Go (left) and No-Go (right) tasks.

(No-go stimuli; $p = 0.5$). The mapping of stimulus features to Go or No-go responses counterbalanced over subjects. In SRT the subjects had respond to any of the four configurations. Four runs of SRT and eight runs of DRT consisted of a sequence of 400 SRT, Go and No-go trials each. The order of tasks was counterbalanced. Only trials followed by a correct response in the 100–900 ms window were considered. The first trial of each run was excluded from further analysis to avoid orienting response contamination; warm-up trials were included. The order of presentation was randomised across subjects. The duration of each run was 2 min with a pause interleaved (total duration about 30 min).

EEG was recorded using BrainVision™ system with 64 electrodes referenced to the left mastoid (see [5]). Horizontal eye movements blinks and vertical eye movements were recorded. The EEG was digitized at 250 Hz, amplified (bandpass of 0.01–60 Hz including a 50 Hz notch filter) and stored for off-line averaging. Computerized artifact rejection was performed prior to signal averaging in order to discard epochs contaminated by artefacts (13% of the trials were rejected). ERPs were averaged in epochs starting 100 ms prior the stimulus onset and lasting for 1100 ms. To further reduce high and low frequency noise, the time averaged VEPs were band-pass filtered from 0.05 to 25 Hz. To visualize the voltage topography of the ERPs components, spline-interpolated 3D maps were constructed using the BESA 2000 software.

ERPs from SRT and DRT runs were sorted into three categories: (1) ERPs for SRT stimuli, (2) ERPs for No-go stimuli and (3) ERPs for Go stimuli. Peak amplitudes (measured with respect to 100 ms pre-stimulus baseline) and latencies of major ERPs component were calculated for each subject in the following time window: P1 (80–150 ms), N1 (130–200 ms), P2 (180–300 ms), N2 (200–350 ms) and P3 (250–500 ms). Data of each time window were evaluated with a separate ANOVA for SRT, Go and No-go stimuli. In order to isolate ERPs components associated to stimulus discrimination, we subtracted the SRT from Go ERPs (Go minus SRT). In order to isolate ERPs components associated to response selection, we subtracted the Go from No-go ERPs (No-go minus Go). ANOVAs were performed on the difference waves components. The electrode sites included in the analysis were selected according to the component peak amplitude. For each component, the independent factor was the Group (fencers versus controls). Greenhouse-Geisser correction was applied. The significance level was set at $p < 0.05$.

Estimation of dipolar sources of differential ERP components was carried out using Brain Electrical Source Analysis (BESA 2000 version 5.14). BESA algorithm estimates location and orientation of multiple equivalent dipolar sources by calculating scalp distribution that would be obtained for a given dipole model (forward solution) and comparing it to actual ERP distribution. Interactive changes in location and orientation in the dipole sources lead to minimization of residual variance between the model and the observed spatio-temporal ERP distribution. Electrode position was digitized and averaged across subjects. The three-dimensional coordinates of each dipole in the BESA model were determined with respect to the Talairach axes, scaled

according to brain size. Details of the technique are given elsewhere [6].

Given the wide medial or bilateral scalp topography of differential ERPs, pairs of dipolar sources were fit over specific latency ranges (given below) to account for major ERP difference waves features derived averaging fencers and control data. Dipole pairs were fit sequentially to the distinctive components in the waveform. Latency-ranges for fitting were chosen to minimize overlap among successive, topographically distinctive components. Dipoles accounting for earlier portions of the waveform were left in place as additional dipoles were added. The reported dipole fits were found to remain consistent for different starting positions. Dipole fitting strategy was as follows: for Go minus SRT difference three bilateral mirror symmetric dipoles pairs were sequentially fit to the component at 240, 300 and 500 ms, respectively. These multi-dipole models accounted for more than 96% of the variance in scalp voltage topography over the 200–550 ms time range. For No-go minus Go difference two bilateral mirror symmetric dipoles pairs were sequentially fit to the component at 280 and 450 ms, respectively, accounting for more than 97% of the variance in scalp voltage topography over the 250–500 ms time range.

Missing errors were nearly absent in both groups (SRT 1.6%, DRT 1.2%). In DRT the false alarms were 12.8% and 9.5% in fencers and controls, respectively. These group differences resulted not significant ($F_{1,11} = 1.58$ $p = 0.23$). RTs for correct trials were analyzed in the 100–900 ms window. Median RTs were submitted to ANOVA with two factors as Group (fencers versus controls) and Task (SRT versus DRT). Post-hoc comparisons were conducted with Tukey Honest Difference test. Overall alpha value was fixed at 0.05.

No difference was found between groups in the SRT. RTs were comparable (fencers 204 ms, controls 189 ms), and amplitudes and latencies of all ERPs components were similar. Group ERPs are shown in Fig. 1; components peak latencies, amplitudes and group comparisons are reported in Supplementary Table 3. Components topography is shown in Supplementary Fig. 1. Fencer advantage was present only when the experimental task was more complex (DRT); in this case fencers' RTs were faster than non-athletes' RTs (386 versus 435 ms; $p < 0.05$).

No group ERP differences were present at the earliest visual processing level i.e., P1 component (peak latency 100 ms); but the N1 component (peak latency 170 ms; occipital lobes distribution) to Go and No-go stimuli was two-to-four times larger in fencers than controls ($p < 0.05$).

The N2 (peak latency 260 ms) and P3 (peak around 450 ms) components are typically considered in Go/No-go studies (e.g., [2]). In agreement with literature, N2 was larger for No-go than Go trials ($p < 0.05$). No-go N2 is thought to originate in prefrontal areas as the anterior cingulate cortex [1] while Go N2 had more posterior sources. This latter component was not detectable in SRT. Group comparison showed that fencers' No-go N2 was larger than controls' N2. No significant group difference was found for Go stimuli.

P3 was larger in Go/No-go task than in SRT ($p < 0.05$). For No-go stimuli, P3 distribution suggested multiple bilateral sources in temporo-parietal and frontal areas. For Go stimuli, the

distribution was more posterior (see [7]) suggesting sources in temporo-parietal and occipital areas (similar to SRT sources). Group comparisons showed that fencers' P3 amplitude was larger than controls' P3 for No-go stimuli. No difference was found for Go trials (or SRT). Overall, results of N2 and P3 indicate that the group difference was maximal in the inhibitory (No-go) condition.

To study the N2 and the P3 effects, subtraction procedures are useful [7,15,17,19]. Subtracting the activity evoked by targets (Go trials) from activity evoked by non-target stimuli (No-go trials), ERPs associated with movement execution/inhibition were enhanced. Subtracting SRT from Go trial waves the activity related to stimulus discrimination was enhanced, because discrimination was required only in the Go trials.

Difference waves for the two groups are shown in Fig. 2; component peak latency and amplitude and group comparisons are displayed in Supplementary Tables 1 and 2. Components topography is shown in Supplementary Fig. 2. The Go minus SRT wave had a first negative peak at 240 ms on medial parieto-occipital sites (Pz in Fig. 2); a second negative peak at 270–300 ms on medial central sites (Cz in Fig. 2); a large positive deflection around 440 ms on parietal site; and a positive component peaking on central sites at 500 ms. Groups' comparisons

showed that the negative component in Cz started and peaked earlier ($p < 0.05$) in fencers (onset 170 ms, peak 270 ms) than controls (onset 200 ms, peak 300 ms). This component and the positive component at 500 ms were larger ($p < 0.05$) for fencers than controls. No other group differences were found on difference waves associated to stimulus discrimination stage.

ERPs subtraction waveform associated to response selection stage (No-go minus Go) showed a first negative component starting at 200 ms and peaking at 280 ms on frontal site. At 450 ms a bipolar component showed a positive focus peaking on medial frontal sites and a simultaneous positive distribution on medial parieto-occipital sites. Groups comparisons showed that at 280 and 450 ms the frontal components were larger in fencers than controls ($p < 0.05$).

Dipole modeling was carried out on the two difference waves (Go minus SRT and No-go minus Go) of fencers and controls that were averaged together (Fig. 3) because preliminary analysis showed no group differences in dipole locations. Source analysis suggested that a minimum of three neural structures were involved in the stimulus discrimination stage (Fig. 3a). First, the superior temporal gyrus started its activity at 150 ms and peaked at 240 ms; second, the posterior cingulate gyrus started at 180 ms and peaked at 280 ms; third, the fusiform gyrus started at 300 ms

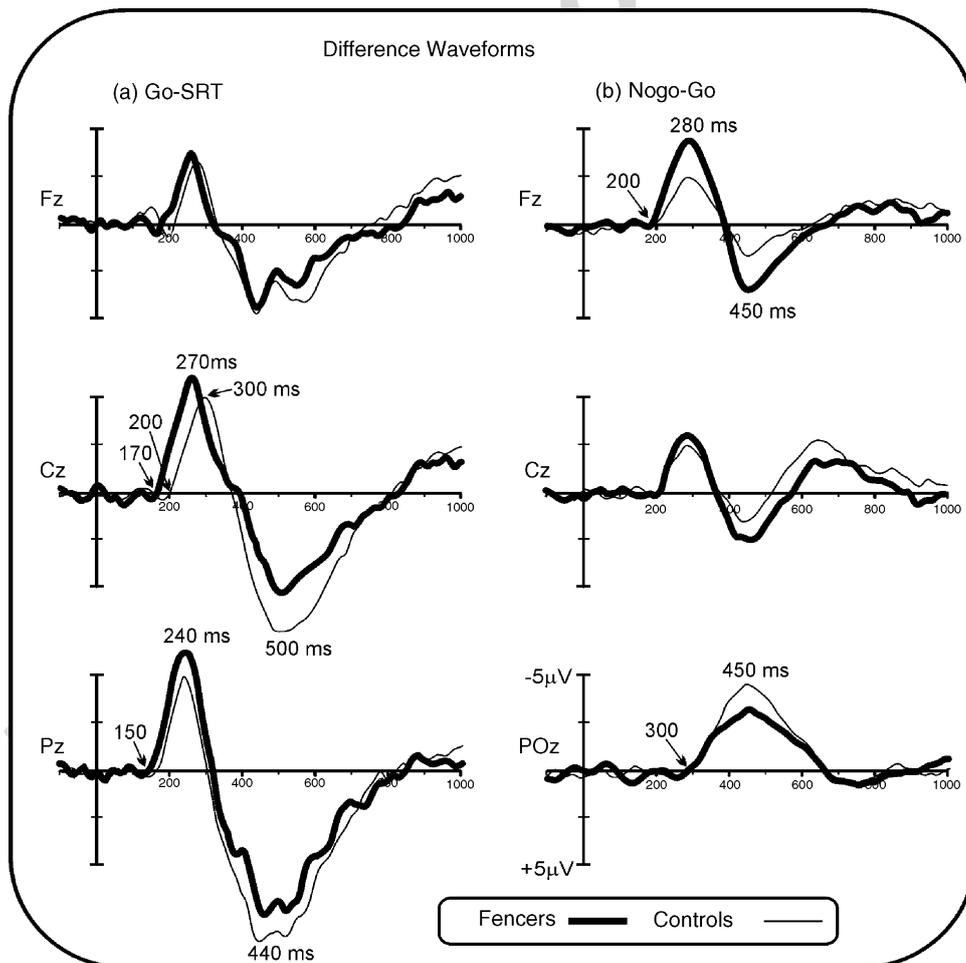


Fig. 2. Difference waves obtained in the Go minus SRT (left) and in the No-go minus Go (right) subtractions. Onset and peak latencies are labelled on selected channels showing the major components. Fencers and controls are represented by thick and thin lines, respectively.

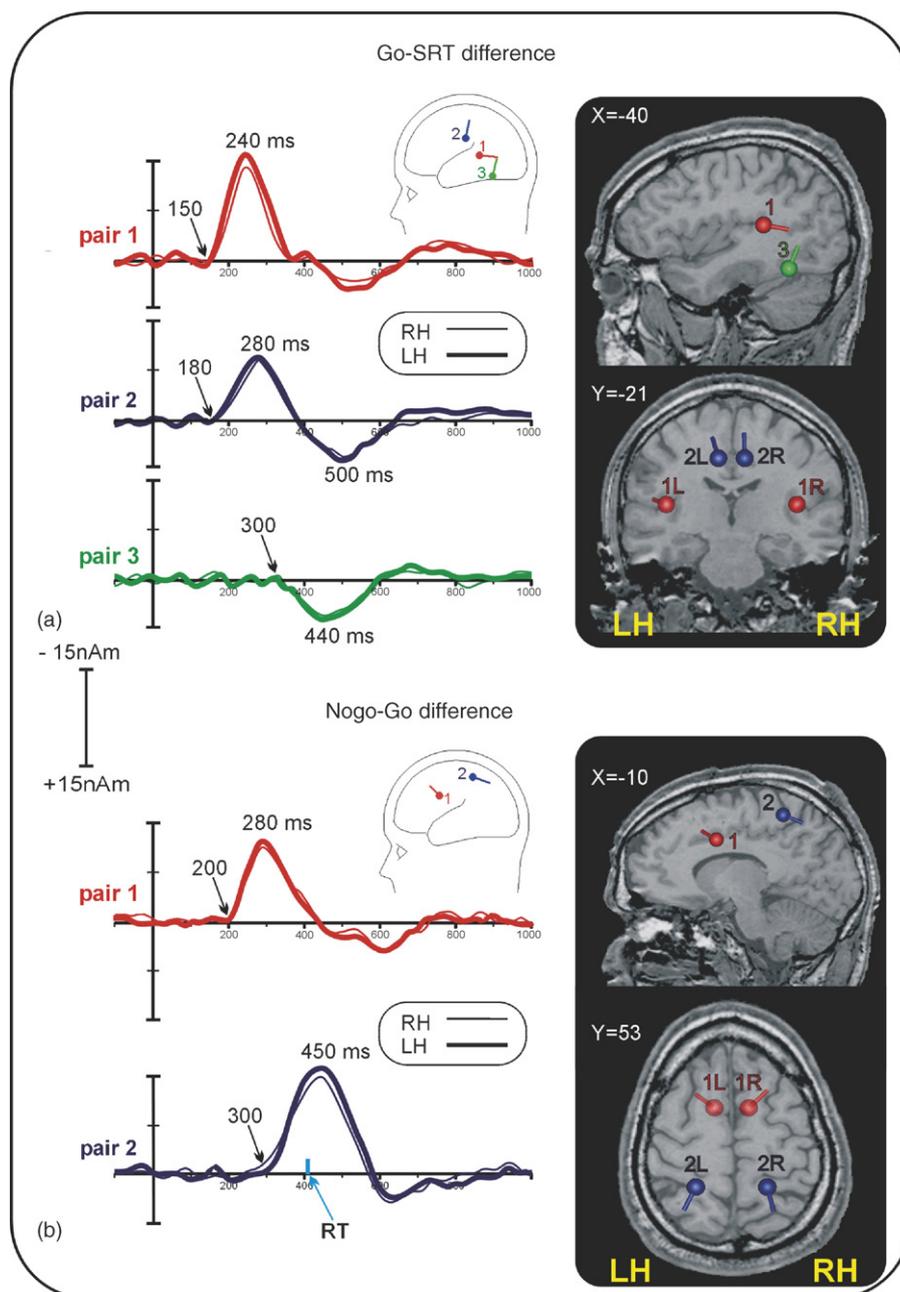


Fig. 3. Source analysis of the ERPs obtained in the Go minus SRT and in the No-go minus Go differences. Waveforms on the left show the time course of the source activity localized in the cerebral areas represented by spheres in the head model and in the MR image template (right). Vectors represent the source orientation. Source onset and peak latency are labelled. Left and right hemispherical activity represented by thick and thin lines, respectively.

and peaked at 440 ms. Based on this model and on group data (Fig. 2a), the activity in the posterior cingulate gyrus associated with discrimination processing was 30 ms faster and more intense in fencers than controls.

Source analysis of the response selection stage (Fig. 3b) indicated the involvement of prefrontal and parietal cortex. Activity started at 200 ms and peaked at 280 ms in the anterior cingulate gyrus; subsequent activity at 450 ms (onset 300) involved dorsal superior parietal cortex. According to source model and to the data of Fig. 2b, the activity at level of the anterior cingulate gyrus associated to inhibition processing was more intense in fencers than controls.

Good fencing requires the reflexes of a boxer, the legs of a high-jumper, and the concentration of a tournament chess player. Although the experimental condition in this study was designed to test a limited portion of the multiple fencers' skills, it offers the view of how brain activity can be shaped by an enormous number of hours of training (3–4 h per day for 5 to 10 years).

Three main differences in brain activity were found between fencers and controls. Specifically, there were no differences in the simple reaction task (SRT); differences emerged only when the experimental task was more complex (DRT), somewhat mimicking the processing required by the sport-specific condition. This general rule hold through also for RTs.

The first difference was a stronger attentional modulation of the early visual processing in fencers. Consistent with a general finding (e.g. [1]), attentional effect was marked by a larger N1 component peaking at 170 ms.

The second difference was associated with the stimulus discrimination stage (as indicated by Go minus SRT wave). The activity in the posterior cingulate gyrus – known to be crucial for visuospatial transformations and consciousness (e.g. [20]) – started earlier in fencers than controls (150 ms versus 200 ms) and the peak (latency 270 and 300 ms for fencers and controls, respectively) had larger amplitude (ca. 3 μ V, 50%).

The third group difference regards the response selection stage (as indicated by No-go minus Go wave). Stronger activity was found in fencers' prefrontal cortex at the level of the anterior cingulate gyrus. Within this time range (250–350 ms), difference wave is known to be related to selection of motor output (execution or inhibition). In the same time window, the dominant ERP component (not the difference wave) was the N2, and this component was found to be larger in fencers only in the No-go trials. According to these data, the main difference between groups was related to the response inhibition process. However, differences in processing related to detection of conflict and attentional modulation cannot be excluded (for a discussion of the confounding activity in the difference waves and the use of a different procedure, see [1]). Present findings are in agreement with neuroimaging data showing that response inhibition is associated with activity in the dorso-lateral prefrontal cortex [8,10,11,14] and regions of the lateral parietal cortex, possibly reflecting stored potential motor responses to external inputs [9,13]. fMRI studies also showed involvement of the right posterior inferior frontal gyrus (IFG) in response inhibition [8,10,11]. The failure to detect IFG involvement was likely due to the limited spatial resolution of ERP in areas distant from the scalp or masked by other sources.

The lack of a group difference in the Go condition contrasts with the shorter N2 and P3 latency reported for fencers [18]; the difference may be due to the use of auditory versus visual channels or to the different probability of the target stimulus. Low Go versus No-go trial frequency, as used in [18] should maximize conflict between event types [12,15].

Concluding, the fencers' ability to cope to the opponent feint switching quickly from an intended action to a new more appropriate action is likely due to a faster stimulus discrimination facilitated by higher attention, and to a stronger inhibition activity in prefrontal cortex.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neulet.2006.08.085.

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