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ORIGINAL ARTICLE

Females are more proactive, males are more reactive: neural basis of the gender-related speed/accuracy trade-off in visuo-motor tasks

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Abstract

In the present study, we investigated neural correlates associated with gender differences in a simple response task (SRT) and in a discriminative response task (DRT) by means of event-related potential (ERP) technique. 120 adults participated in the study, and, based on their sex, were divided into two groups matched for age and education level. Behavioral performance was assessed with computing response speed, accuracy rates and response consistency. Pre- and post-stimulus ERPs were analyzed and compared between groups. Results indicated that males were faster than females in all tasks, while females were more accurate and consistent than males in the more complex tasks. This different behavioral performance was associated with distinctive ERP features. In the preparation phase, males showed smaller prefrontal negativity (pN) and visual negativity (vN), interpreted as reduced cognitive preparation to stimulus occurrence and reduced reliance on sensory proactive readiness, respectively. In the post-stimulus phase, gender differences were present over occipital (P1, N1, P2 components) and prefrontal (pN1, pP1, pP2 components) areas, suggesting allocation of attentional resources at distinct stages of information processing in the two groups. Overall, the present data provide evidence in favor of a more proactive and cautious cognitive processing in females and a more reactive and fast cognitive processing in males. In addition, we confirm that (1) gender is an important variable to be considered in ERP studies on perceptual processing and decision making, and (2) the pre-stimulus component analysis can provide useful information concerning neural correlates of upcoming performance.

Keywords Gender differences · Speed–accuracy trade-off · Motor behavior · Proactive control · Decision making · Predictive brain

Introduction

"Men Are From Mars, Women Are From Venus" is the famous John Gray's book (Gray 1992) suggesting that males and females rely on different mindsets. Differences between males and females in cognition and behavior have been largely explored, especially in the 90s. Literature highlighted higher visual-spatial and mathematical abilities in males (e.g., Benbow and Stanley 1980; Voyer et al. 1995) and higher verbal and social-cognitive skills in females (e.g., Erwin et al. 1992; Hyde and Linn 1988). However, gender differences were also found in simple cognitive tasks, where a different speed–accuracy trade-off was shown: males have usually faster but less accurate responses than females in both simple (SRT) and discriminative response tasks (DRT) (see Fozard et al. 1994 for data of a large sample). This trend was present also in children (Torpey et al. 2012), possibly suggesting an early acquisition of distinctive response styles. In contrast to the view supporting a more "cautious" style in females, adult females showed faster RTs to deviant stimuli in a two-choice oddball task (Yuan et al. 2008). This could be due to females' higher ability in inhibiting the prepotent motor response in case of deviant stimuli compared to males. Further, intra-individual response variability was explored at behavioral level (for a review, see Dykiert et al. 2012). Deary and Der (2005) and Der and Deary (2006) found higher variability in females than males from middle adulthood onwards in both SRT and choice reaction task (CRT); Bielak et al. (2014) found higher variability in young

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adult females than males, but only in SRT. Overall, results are not consistent, and how task complexity may modulate gender differences in intra-individual RT variability remains an open question (Ghisletta et al. 2018).

In relation to neuroanatomy, gender differences in gray and white matter were reported (e.g., Allen et al. 2003; Gur et al. 1999; Szeszko et al. 2003), pointing to a higher percentage of gray matter in females. Further, compared to males, females' brain showed enhanced interhemispheric connectivity that may facilitate communication between brain regions responsible for analytical and intuitive processing. In contrast, males' brain showed increased within-hemispheric cortical connectivity along the posterior–anterior dimension that may improve the action–perception link (e.g., Ingalhalikar et al. 2014). However, some believe the neuroscience literature on gender difference is plagued by "innumeracy, misinterpretation, publication bias, weak statistical power, inadequate control and worse" (Eliot 2019), and the reported anatomical/functional differences (e.g., Sommer et al. 2008) may be a consequence of distinctive education of males and female still present in our society.

Regardless of the nature–nurture question, which is outside the scope of the present study, we believe that a deeper understanding of gender differences at the neural level may provide interesting information about brain plasticity. In particular, looking for differences in elementary cognitive tasks using abstract stimuli, such as tones (Fozard et al. 1994) or geometric configurations (Steffensen et al. 2008) rather than human voices or faces eliciting social or emotional feelings, may allow an evaluation of the pervasiveness of the "gender effect" on basic brain mechanisms that support complex behavior.

In the present study, we focused on behavioral and neurophysiological differences between males and females in simple and discriminative visuo-motor tasks of abstract stimuli by means of the event-related potential (ERP) technique, a suitable tool to unveil motor and cognitive cortical activities associated with behavioral performance. ERP literature on this topic is contradictory and fails to address directly brain correlates of the speed/accuracy trade-off associated with gender. A number of studies have found evidence of sex differences in the amplitudes and/or latencies of post-stimulus visual ERP components (Hoffman and Polich 1999; Mitchell et al. 1987; Vaquero et al. 2004), while others have found no evidence of such differences (Sangal and Sangal 1996; Steffensen et al. 2008; Yuan et al. 2008; Wirth et al. 2006). These contrasting results may be due to differences between experimental tasks; however, an important role is certainly played by the relatively small sample size of those studies (12–30 participants per group). Indeed, as suggested by many studies (e.g., Chu 1987; Boles 2005; Ruigrok et al. 2014), large samples are necessary to consistently detect gender effects on ERP components, due to the wide variability inside each gender category. Following these considerations, in the present study we considered a large sample (60 participants per gender).

Most ERP studies on gender differences focused on "reactive" brain functions occurring in response to specific events, neglecting the "proactive" brain functions associated with motor and cognitive preparation to an upcoming event. Only few studies (Duregger et al. 2007; Howard et al. 1992) investigated gender differences in proactive brain functions using a contingent negative variation paradigm (CNV; Walter et al. 1964). Duregger et al. (2007) used an acoustic Go/No-Go task and observed larger frontal CNV amplitudes in females and larger temporal–parietal amplitudes in males. The authors interpreted their data proposing higher level of cognitive preparation in females, and higher sensory processing in males; however, the small sample and the unexpected differences between the CNV preceding the Go and the No-go stimuli (that were randomly displayed) limited the above-mentioned conclusions. In a visual CNV paradigm, Howard et al. (1992) found left hemispheric dominance for verbal tasks and right dominance for spatial tasks in males, whereas females showed left dominance in both tasks. However, the small sample size and the use of only three recording channels limited the authors' conclusions. One aim of the present study was to investigate the effect of gender on proactive cortical activity. We accomplished this goal using two visuo-motor tasks in which we could record the effect of spontaneous trait disposition (such as to be fast or accurate) of participants while minimizing expectancy and conflict effects on ERP measures. Motor and cognitive preparations were detected through the analysis of the Bereitschaftspotential (BP) and the prefrontal negativity (pN), respectively. The BP is a slow negative wave whose source is in the supplementary motor area (SMA), indicating motor readiness (e.g., Shibasaki and Hallett 2006). The pN is a prefrontal distributed component (Berchicci et al. 2012), localized in the inferior frontal gyrus (iFg) (e.g., Di Russo et al. 2016), and associated with top-down cognitive control (Perri et al. 2015), including proactive inhibition (Bianco et al. 2017b). In addition to these components, a preparatory activity at occipital cortex level was recently described, labeled as visual negativity (vN) component (Di Russo et al. 2019). The vN was observed in active and, especially, in passive visual tasks, presumably reflecting a form of pre-stimulus sensory readiness (Bianco et al. 2019). Previous studies employing the same DRT paradigm of the present study showed that a larger BP amplitude has been associated with faster RT and larger pN amplitude to increased accuracy (e.g., Bianco et al. 2017a, c; Di Russo et al. 2019). Indeed, we propose that the BP and the pN might reflect a sort of proactive accelerator/brake system that, based on predictive internal models, plans and anticipates future actions (Di Russo et al. 2016; Bianco et al. 2017b). In this context, the increase in amplitudes of the component might reflect the involvement of augmented neural resources to guarantee efficiency or the accuracy of the response, respectively, in favor of an enhanced need to accelerate (higher BP, faster RT) or to inhibit (higher pN, higher accuracy rates).

Regarding the reactive ERP components, beyond the contradictory results reported above for many well-known components, to the best of our knowledge, no data are available concerning the effect of gender on the anterior novel components labeled as the prefrontal N1, P1 and P2 (pN1, pP1 and pP2) associated with anterior insular cortex activity (Di Russo et al. 2016; Perri et al. 2018a, b; Sulpizio et al. 2017; Ragazzoni et al. 2019). The pN1, peaking at 110–120 ms, was associated with perceptual awareness (Perri et al. 2018a, b; Gonçalves et al. 2018; Sanchez-Lopez et al. 2017). The pP1, peaking at 150–180 ms, was associated with the conscious experience of the sensory–motor coupling (Perri et al. 2018b; Gonçalves et al. 2018); the pP2, peaking at around 300 ms, was associated with processes of accumulation of sensory evidence and stimulus–response (S–R) mapping (Perri et al. 2015; Ragazzoni et al. 2019), an interpretation which is in line with studies referring to the same component under different labels (e.g., P2a: Potts et al. 1996; P3f: Makeig et al. 1999).

Overall, in the present study, we used a large sample of participants to evaluate gender differences in both simple (SRT) and complex (DRT) response tasks. In particular, the study aimed: (1) to confirm the existence of a different speed/accuracy trade-off tendency between males and females; (2) to test whether gender differences were already detectable in the preparation stage modulating motor (BP component), cognitive (pN component) and sensory (VN component) preparation activities; (3) to evaluate the presence and direction of gender differences in the post-stimulus early and late ERPs, with a pivotal attention for the insular components (not yet investigated); (4) to evaluate whether task complexity (simple vs. complex) has different effects in males and females.

Based on previous findings (Silverman 2006; Fozard et al. 1994), we expected to observe faster responses in males than females in both simple (SRT) and discriminative (DRT) response tasks; further, in the complex task, we expected that females were more accurate. Our hypothesis is that the gender-related speed/accuracy trade-off disposition might be associated with specific cortical activities in the proactive stage of processing. In particular, longer RTs in females might be associated with larger amplitude of the pN and/or decreased BP amplitude compared to males. A larger pN in females would be in line with Duregger et al.'s (2007) proposal of a higher cognitive preparation in females. The higher temporal–parietal activity observed in males by Duregger et al. (2007) using acoustic stimuli and explained in terms of higher sensory processing might have its visual counterpart in a larger occipital activity (the vN component) in the present study using visual modality.

Regarding post-stimulus components, given the contradictory findings from previous studies, we did not have clear predictions. However, based on previous studies reporting larger gray matter volume in the anterior insula in females (for a meta-analysis see Ruigrok et al. 2014), we expected larger insular activities in females.

Experimental procedures

Participants

120 participants were selected from a large database containing EEG data of more than 300 healthy subjects. The inclusion criteria were: 18–40 years old and EEG containing less than 10% of artifact-contaminated trials (differential amplitude exceeding 150 μV). Based on gender, participants were divided into two groups matched for age and education level (60 females, mean age 30.8 years, SD = 9.1, education level 16.7 years, SD = 2.0; 60 males, mean age 30.1 years, SD = 9.1, education level 15.9 years, SD = 1.8). They had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders; all were righthanded (Edinburgh Handedness Inventory; Oldfield 1971). After explaining the procedure to the participants, they provided written informed consent, approved by the Ethical Committee of the Santa Lucia Foundation.

Procedure

Participants were tested in a sound-attenuated, dimly lit room. During the experiment, participants sat comfortably in front of a 24'' CRT screen at a distance of 114 cm, and a board was fixed on the armchair allowing them to push a button with their right index finger. The fixation point was a yellow circle (diameter 0.15° × 0.15° of visual angle) constantly displayed on the monitor center. One of four different visual stimuli made by vertical and horizontal bars subtending 4° × 4° of visual angle was displayed for 250 ms on a dark gray background (Fig. 1) in central vision. The configurations were randomly selected with equal probability ($p = 0.25$); equiprobability was selected to reduce the conflict in the Go/No-go paradigm (e.g., Barry and De Blasio 2015). Inter-stimulus interval (ISI) varied randomly from 1 to 2 s continuously to avoid time prediction effects on the RTs and entrainment of EEG activity. In separate runs, the participants performed two tasks: a simple response task (SRT) and a discriminative response task (DRT). In the SRT, the participants had to press a button with their right index finger as quickly as possible when any of the four configurations appeared on the screen ($p = 1.0$). In the DRT, two

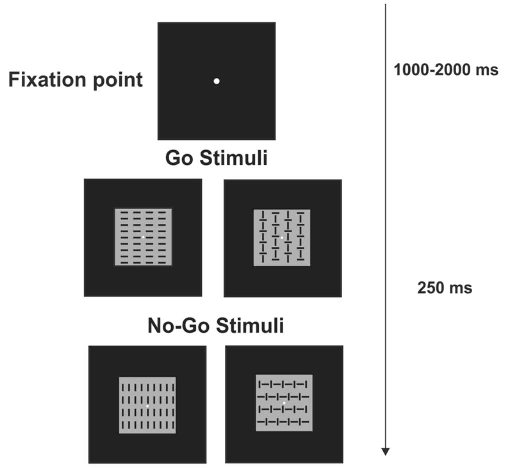

Fig. 1 Stimuli. Schematic representation of the tasks considered in the study. In the simple response task (SRT), all stimuli were targets and required a motor response. In the discriminative response task (DRT), 50% of the stimuli were targets requiring a motor response (Go Stimuli) and 50% were non-targets (No-Go Stimuli)

configurations were defined as target, and two configurations were defined as non-target. The participants had to press a button with their right hand when a target appeared on the screen ($p = 0.5$) and withhold the response when a non-target appeared ($p = 0.5$). The order of presentation was randomized within runs. The duration of each run was 2 min and consisted of 80 trials. Five runs of the SRT (Session 1) and ten runs of the DRT (Session 2) were performed with pauses interleaved, for a total duration of about 40 min. We obtained 400 trials for the SRT and 800 for the DRT (400 target and 400 non-target trials).

Behavioral analysis

To confirm the gender-related speed/accuracy trade-off described in literature (Silverman 2006; Fozard et al. 1994), response speed was assessed using the individual median RT for correct responses both in SRT and in DRT. The accuracy was assessed considering the percentage of omission errors (OE, i.e., missed responses to Target) in SRT and in DRT and the percentage of commission errors (CE, i.e., responses to Non-target) in DRT only. In addition, to test possible effect in response consistency, the intra-individual coefficient of variation (ICV) was calculated for each participant as follows: ICV = standard deviation (SD) of RT/mean RT, for SRT and DRT; the range of ICV is between 0 and 1 corresponding to minimum and maximum of RT variability, respectively. RT and ICV were submitted to a 2 × 2 ANOVA with Group (males vs. females) and Task (SRT vs. DRT) as factors. OE and CE were submitted to *t* tests with Group as independent variable. Pearson's correlational analysis was performed between individual RT and accuracy (OE and CE).

EEG recording and ERP analysis

EEG data were recorded using a 64-channel EEG system (Brainamp™ amplifiers) with active electrodes (Acticap™) and software (Recorder 1.2 and Analyzer 2.1) all by Brain Products GmbH (Munich, Germany). The electrodes were mounted according to the 10–10 International System and initially referenced to the M1 electrode, and then re-referenced to M1 + M2. Electrode impedances were kept below 5 KΩ. Horizontal and vertical electrooculogram (EOG) were monitored by bipolar recordings. The EEG was amplified, digitized at 250 Hz and filtered (bandpass of 0.01–80 Hz including a 50 Hz notch filter) and stored for offline averaging. The correction of eye movement artifacts was performed using the independent component analysis (ICA). This method, introduced by Jung et al. (2000), has been shown to produce better results than other ocular correction methods (e.g., Hoffmann and Falkenstein 2008). To reduce high-frequency noise, the EOG-corrected EEG signal was low pass filtered at 30 Hz (slope 24 dB/octave). To investigate both pre- and post-stimulus activities, the signal was segmented in epochs starting 1100 ms prior the stimulus onset and lasting for 2000 ms. Semi-automatic artifact rejection was performed prior to signal averaging to discard epochs contaminated by signals exceeding the amplitude threshold of ± 60 μV. On average, 4% of trials were rejected. Artifact-free trials were averaged into Target for SRT and into target and non-target for DRT. For pre-stimulus ERPs analysis, a 200 ms baseline (− 1100/− 900 ms) was used; for DRT, since the stimuli were presented randomly with equal probability, we did not expect to find differences between target and non-target at this stage, thus each pre-stimulus component was calculated by averaging target and non-target trials. Following this procedure, the SRT included 400 trials and the DRT 800 trials. This difference is not a problem because the noise in the ERP waveforms is reduced by a factor given by the square root of the trials number. Therefore, 400 trials reduce the noise by a factor of 20 and 800 trials by a factor of 28. Consequently, the noise level in the two conditions was not very different. For post-stimulus ERP, a − 200/0 ms baseline was used.

To select the region of interest (ROI) and the time window to use in the statistical analysis, the collapsed localizers method was used (e.g., Luck and Gaspelin 2017). Following this method aimed to detect different topographies during the tasks, regardless of gender, the pre- and post-stimulus ERP were initially inspected looking at the global field power, at scalp mapping and at recent normative data (Di Russo et al. 2019) on the present ERP paradigms.

For the pre-stimulus ERP, in the DRT, the time window from −800 to −600 ms showed a dominance of bilateral prefrontal activity (the pN). From −600 ms to stimulus onset, a dominance of medial central and parietal activity (the BP and the vN) was present. The SRT did not show notable differences, with a steady central–parietal distribution. In addition, to evaluate possible interactions between gender and task difficulty during the early and late phases of the pre-stimulus ERP, ANOVAs were performed using Group (males vs females), Task (SRT vs DRT) and Interval (early vs late) as factors. To limit multiple comparisons, the analysis was performed using the following ROIs constituted by electrode pools best representing the detected components based on their topographical features: for the pN, the AF7/8, F7/8 and F5/6 pool was adopted; for the BP, the Cz-CPz pool; for the vN, the PO7/8 pool.

Pearson's correlations were also computed between the three pre-stimulus ERPs components (pN, BP and vN) and RT adopting the same electrode pools used for the ANOVA as mean amplitude in the −800/0 ms window. Further, Pearson' correlations were computed between each of the pre-stimulus components and the OE and CE for the DRT task. However, the pN pool was split into left and right electrodes to test possible hemispherical difference. In fact, a right prefrontal cortex dominance in the inhibitory control has been reported (e.g., Aron et al. 2004). A univariate linear model was used to evaluate the interaction between correlations of the two genders.

Similarly, for post-stimulus ERP components, mean amplitudes were analyzed in predefined time windows, ROI and conditions as shown in Table 1. Most components were analyzed using factorial 2 × 3 ANOVAs including as factors Group and Task (SRT, DRT Target and DRT Non-Target). However, the pP2, present in the DRT only, was analyzed using a 2 × 2 ANOVA with Group and Task (DRT Target vs DRT Non-Target) as factors. The P2, present in the SRT only, was compared between groups using an unpaired *t* test. Finally, the dpP2, obtained from the DRT Target minus DRT Non-Target subtraction, was also analyzed using an unpaired *t* test with Group as independent variable.

All statistical analyses were performed using the Statistica 13.1 software. For both the behavioral and ERP data, the Levene's test for equality of variance was performed for data to be submitted to *t* tests, while for all the ANOVAs the Mauchly's test of sphericity was adopted. Both tests showed non-significant results ($p > 0.5$) for all considered comparisons indicating that the assumption of equality of variances and sphericity has not been violated. For post hoc comparisons, the conservative Bonferroni test of the Statistica software was used, and this test returned adjusted *p* values that are divided for the number of comparisons. To evaluate the effect size, the partial eta squared (${}_{p}\eta^2$) has been reported for ANOVA and the Cohen's *d* (*d*) for *t* tests. The alpha level for ANOVAs was set at 0.05. For the *t* tests, the alpha level was set at 0.01 to control the multiple comparisons. We used all these statistical cautions to avoid that the large number of subjects studied, and the multiple comparison performed may render the resulting *p* values less meaningful due to higher likelihood of Type 1 errors.

Table 1 Post-stimulus ERP components definition, time windows and region of interest (ROI) used in the analysis

Components	Time windows (ms)	ROI	Task
P1	80–120	PO7–PO8	SRT, DRT-T, DRT-NT
pN1	80–120	AFz-Fz	SRT, DRT-T, DRT-NT
N1	140–200	PO7–PO8	SRT, DRT-T, DRT-NT
pP1	140–200	AFz-Fz	SRT, DRT-T, DRT-NT
P2	200–300	PO7–PO8	SRT
pP2	300–400	AFz-Fz	DRT-T, DRT-NT
dpP2	250–350	AFz-Fz	DRT-T − DRT-NT
P3	200–400 SRT 400–600 DRT	Cz-CPz	SRT, DRT-T, DRT-NT

The tasks considered were the SRT, the DRT Target (DRT-T) and the DRT Non-Target (DRT-NT)

Results

Behavioral results

As shown in Fig. 2a, a significant main effect of Group on RTs was observed ($F_{1,118} = 11.1$, $p = 0.0011$, ${}_{p}\eta^2 = 0.086$), indicating shorter RTs in males (322 ± 3.8 ms) than females (341 ± 4.2 ms); also, the effect of Task was significant ($F_{1,118} = 3051.7$, $p < 0.0001$, ${}_{p}\eta^2 = 0.851$), with shorter RTs for SRT (221 ± 2.2 ms) than DRT (442 ± 4.5 ms). For ICV (Fig. 2b), a significant main effect of Task was found ($F_{1,118} = 6.3$, $p = 0.0134$, ${}_{p}\eta^2 = 0.051$), with less variable RTs in SRT (ICV 0.171 ± 0.003) than DRT (ICV 0.184 ± 0.004). The Group × Task interaction was also significant ($F_{1,118} = 4.3$, $p = 0.0403$, ${}_{p}\eta^2 = 0.035$); post hoc tests indicated a significant difference between tasks in males only (SRT 0.167 ± 0.004; DRT 0.192 ± 0.005; $p = 0.0127$), while females' variability in response time was comparable between tasks (SRT 0.173 ± 0.004; DRT 0.176 ± 0.005; ns); further, females had less variable RTs than males in DRT ($p < 0.05$). Regarding the accuracy, no gender differences were found in the SRT for OEs (that were rare; < 1%). However, in the DRT males were less accurate than females (Fig. 2c), in both CEs (males 11.1 ± 7.2%; females 7.2 ± 4.6%; $t_{118} = 3.7$, $p = 0.0003$, $d = 0.65$) and OEs

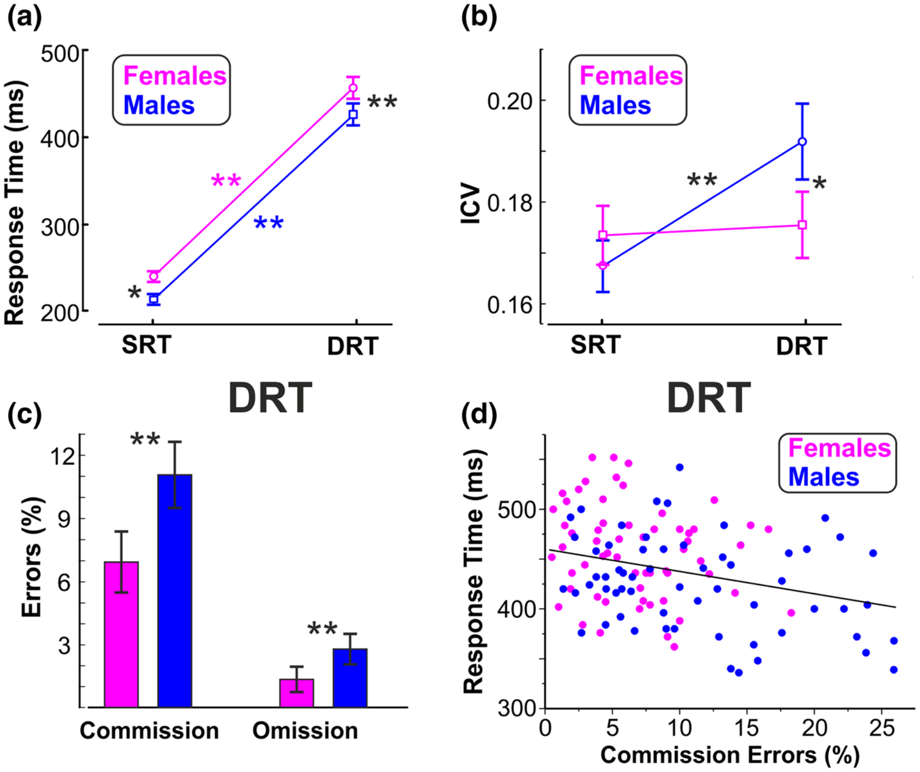

Fig. 2 Behavioral data. Male and female data are reported by blue and pink color, respectively. **a** Main effect of Gender on RTs, i.e., males were faster than females and main effect of Task, i.e., RTs were faster in SRT than DRT). **b** RTs in SRT were less variable than DRT. The difference between SRT and DRT was significant only in males; females had less variable RTs than males in DRT. **c** Accuracy, i.e., the error rates in DRT (both CE and OM) were higher in males than females. **d** Correlation between individual commission errors and RTs in DRT

(males 3.2 ± 3.0%; females 1.0 ± 1.8%; $t_{118} = 3.5$, $p < 0.0005$, $d = 0.89$). For completeness of information, the hits in the SRT were 99.2% for both groups. The hits for targets in the DRT were 88.9% and 92,7% for males and females, respectively. The correct non-responses for non-targets in the DRT were 96.8% and 99.0% for males and females, respectively.

In the overall population, the RTs correlated with the percentage of commission error ($r = -0.27$, $p = 0.0054$). Inspection of Fig. 2d shows a clear speed–accuracy trade-off, with a good amount of data points of females and males contributing to the extreme left and right portions of the curve, respectively. This result indicates that the individual disposition to be very fast and inaccurate or slow and accurate is more common in males and females, respectively. Correlations limited to each group separately were not significant.

Pre-stimulus ERPs

Figure 3a shows pre-stimulus ERP activities for the two groups and tasks at the most representative sites; inspection of the figure shows clear effects of gender in some preparatory components. In SRT, the BP started at − 800 ms and reached its maximum amplitude after stimulus onset, showing larger amplitude in males than females throughout the time window. Concomitantly, the visual negativity (vN) emerged on parietal–occipital leads with comparable amplitudes between groups. The pN component was nearly absent in this task, as observed in previous studies (Di Russo et al. 2016). In DRT, a slow-rising negativity was evident on prefrontal sites (pN) starting at − 850 ms; this component had larger amplitude in females than males. At central leads, the BP started at − 700 ms and its amplitude was comparable between groups. At parietal–occipital sites, the vN started earlier in females (− 850 ms) than males (− 650 ms) and, after a steep slope increase, the vN became flat, reaching its maximum at about stimulus onset; in the − 300/0 ms interval, the vN amplitude was comparable between groups. Figure 3b shows voltage scalp topography for the two groups in the − 800/− 600 and − 600/0 time windows, separately for SRT and DRT. In SRT, the scalp topography was quite similar for the two groups, but, in the − 600/0 interval, the BP activity (at medial central and central–parietal electrodes) was significantly larger in males than females. In DRT, in the − 800/− 600 ms interval females showed a tendency to have more bilateral negative activity (source of the pN component).

ANOVA on the pN showed significant main effects of Group, Task and Interval ($F_{1,118} > 8.1$, $p < 0.005$, ${}_{p}\eta^2 > 0.064$). The pN was larger in females than in males, in the DRT than in the SRT and in the later than in the earlier interval. Moreover, the Group × Task × Interval interaction was also significant ($F_{1,118} > 10.1$, $p = 0.0019$, ${}_{p}\eta^2 = 0.079$). Post hoc comparison on the three-level interaction indicated that the females had larger pN in the later interval of the DRT ($p < 0.005$). ANOVA on the BP showed significant main effects of Group and Interval ($F_{1,118} > 7.7$, $p = 0.0064$,

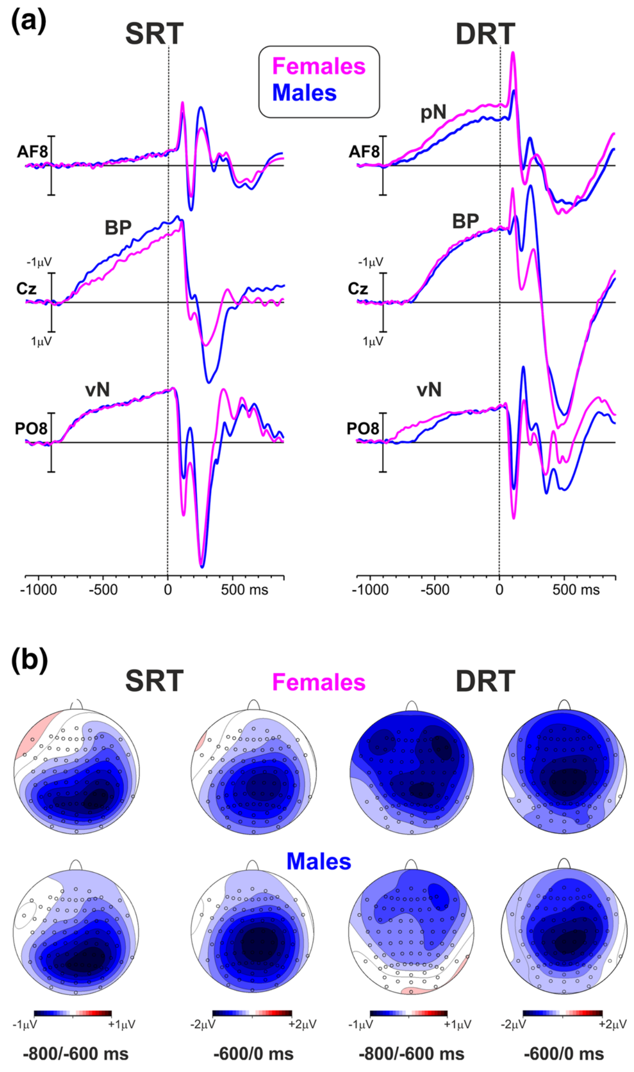

Fig. 3 Pre-stimulus ERP data**: a** averaged ERP waveforms at prefrontal, central and parietal–occipital electrodes in the two tasks superimposed for males (blue) and females (pink). The considered ERP components, i.e., the BP, the pN and the vN, are indicated. **b** Topographical distribution of the pre-stimulus ERP activities depicted separately for tasks and genders

$_p\eta^2 = 0.061$). The BP was larger in males than females and in the later than the earlier interval. Moreover, the Group × Task × Interval interaction was also significant ($F_{1,118} = 13.9$, $p = 0.0003$, $_p\eta^2 = 0.105$). Post hoc comparison on the three-level interaction indicated that the males had larger BP in the later interval of the SRT ($p < 0.001$). ANOVA on the vN showed significant main effects of Group, Task, and Interval ($F_{1,118} > 6.9$, $p < 0.0098$, $_p\eta^2 > 0.057$). The vN was larger in females than males, in the SRT than the DRT and in the later than in the earlier interval ($p < 0.0071$). Moreover, the Group × Task × Interval interaction was also significant ($F_{1,118} = 12.5$, $p < 0.0006$, $_p\eta^2 = 0.096$). Post hoc comparison on the three-level interaction indicated that females had larger vN in the early interval of the DRT ($p < 0.0034$). Figure 4 show the mean amplitudes and the standard errors of the three pre-stimulus components submitted to statistical analysis.

Figure 5 shows the correlation between pre-stimulus ERPs (in the whole interval, from − 800 to 0 ms) and behavioral performance. For SRT, only response times were considered (Fig. 5a) because the omissions were nearly absent; for DRT, both RTs (Fig. 5b) and accuracy (Fig. 5c, d) were reported. Distinct colors show data of females and males. For both SRT and DRT, medial central and central–parietal activities (the BP ROI) correlated with the RTs (the more negative the amplitude, the faster the response). As for accuracy (in DRT), the right prefrontal and frontal electrode activities (the pN ROIs, Fig. 5d) correlated with the commission errors (the more negative the amplitude, the lower the CE percentage) in both males and females; in contrast, for the left hemisphere, the correlation was significant only in females (see Fig. 5c). Inspection of Fig. 5c, d also shows that the commission error percentage was never higher than 17% in females, while a consistent proportion of males (about 20%) made 18–26% of errors. Figure 6 reports the correlation between the activity at bilateral parietal–occipital electrodes (the vN ROIs) and RTs in both SRT and DRT. The correlation was significant in both cases, and for both groups. No significant interactions between the correlation of the two groups were found, except for the correlation between the left pN and the CEs ($F_{(1.118)} = 5.4$, $p < 0.0218$) reported in Fig. 5c.

Post-stimulus ERPs

Figure 7 shows post-stimulus ERP components at relevant electrodes. In both SRT and DRT (Target and Non-Target), the earliest prefrontal component (the pN1) peaked at about 105 ms, followed by the pP1 at about 170 ms (see top row). At bilateral parietal–occipital sites (bottom row), the P1 and the N1 peaked at 110 and at 160 ms, respectively. Inspection of the figure suggests that the P1 amplitude was larger in females than males (in both SRT and DRT). The N1 amplitude, much larger in DRT than SRT (as reported in other studies, see Di Russo et al. 2010), also suggests a gender effect in DRT, but in the opposite direction with respect to the P1. The P2, present in the SRT only, peaked at 250 ms, with larger amplitude in males than females. In the SRT, the P3 peaked over medial central–parietal site at 300 ms; its amplitude was larger in males than females (see central row, left). In the DRT, the pP2 (top row, Target and Non-Target) peaked over medial prefrontal site at about 350 ms, and the P3 (central row) peaked over medial central–parietal sites at about 500 ms, showing differences between groups.

The ANOVA on the P1 showed significant main effect of Group ($F_{1,118} = 17.8$, $p < 0.0001$, $_p\eta^2 = 0.131$) with larger

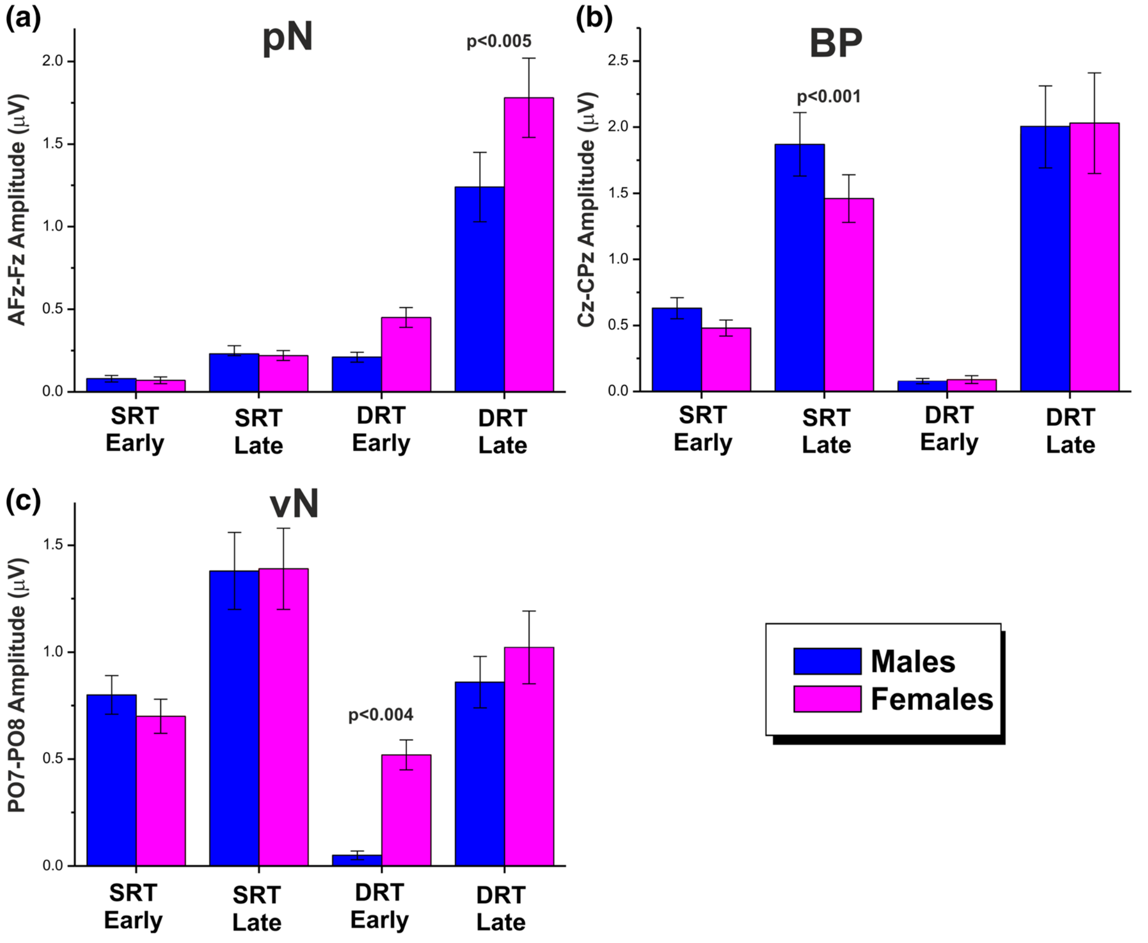

Fig. 4 Statistical comparisons: early (– 800/– 600 ms) and late (– 600/0 ms) pre-stimulus ERP amplitude compared between groups. Vertical bars represent the standard errors and the significant difference between groups is marked by the relative *p* value. **a** pN component measured at the AFz-Fz pool. **b** BP component measured at the Cz-CPz pool. **c** vN component measured at the PO7–PO8 pool

amplitude in females. The effect of Task and the interactions were not significant ($F_{2,236} < 2.3$, $p > 0.1025$). The ANOVA on the pN1 showed significant main effects of Group ($F_{1,118} = 8.5$, $p = 0.0025$, ${}_{p}\eta^2 = 0.067$) and Task ($F_{2,236} = 6.6$, $p = 0.0114$, ${}_{p}\eta^2 = 0.053$). The pN1 was larger in females than males, and larger in the DRT than in the SRT (Target and Non-target trials did not differ). Moreover, the interaction was also significant ($F_{2,236} = 12.7$, $p < 0.0001$, ${}_{p}\eta^2 = 0.097$). Post hoc comparisons indicated that the group difference was present only in the DRT ($p = 0.0012$). The ANOVA on the N1 showed significant main effects of Group ($F_{1,118} = 7.1$, $p = 0.0088$, ${}_{p}\eta^2 = 0.057$) and Task ($F_{2,236} = 10.4$, $p < 0.0001$, ${}_{p}\eta^2 = 0.081$). The N1 was larger in males than females and larger in the DRT than in the SRT (Target and Non-Target trials did not differ). Moreover, the interaction was also significant ($F_{2,236} = 11.7$, $p < 0.0001$, ${}_{p}\eta^2 = 0.090$). Post hoc comparisons indicated that the group difference was only present in the DRT ($p = 0.0008$). The ANOVA on the pP1 showed no significant effect of Group ($F_{1,118} = 3.0$, $p = 0.0859$) and Task ($F_{2,236} = 1.4$, $p = 0.2486$). However, the interaction was significant ($F_{2,236} = 7.2$, $p = 0.0009$, ${}_{p}\eta^2 = 0.058$). Post hoc comparisons indicated that males had larger pP1 than females in SRT only ($p = 0.0015$). In the SRT, the effect of Group on the P2 component was significant ($t_{118} = 8.89$, $p = 0.0003$, $d = -0.60$), indicating larger P2 in males. In the DRT, the ANOVA on the pP2 showed a significant effect of Group ($F_{1,118} = 15.2$, $p = 0.0002$, ${}_{p}\eta^2 = 0.114$) and Task ($F_{1,118} = 17.4$, $p < 0.0001$, ${}_{p}\eta^2 = 0.128$) with larger amplitude in males than females, and in Target than Non-Target trials. The interaction was not significant ($F_{1,118} = 2.7$, $p = 0.1030$). The ANOVA on the P3 showed no significant main effect of Group ($F_{1,118} = 2.1$, $p = 0.1499$) and a significant effect of Task ($F_{2,236} = 23.5$, $p < 0.0001$, ${}_{p}\eta^2 = 0.166$) with largest amplitude in the DRT Target trials, intermediate in the DRT Non-Target trials and lowest in the SRT. The interaction Group × Task was significant ($F_{2,236} = 14.4$, $p < 0.0001$, ${}_{p}\eta^2 = 0.109$). Post hoc comparisons indicated that males had larger P3 than females in the SRT

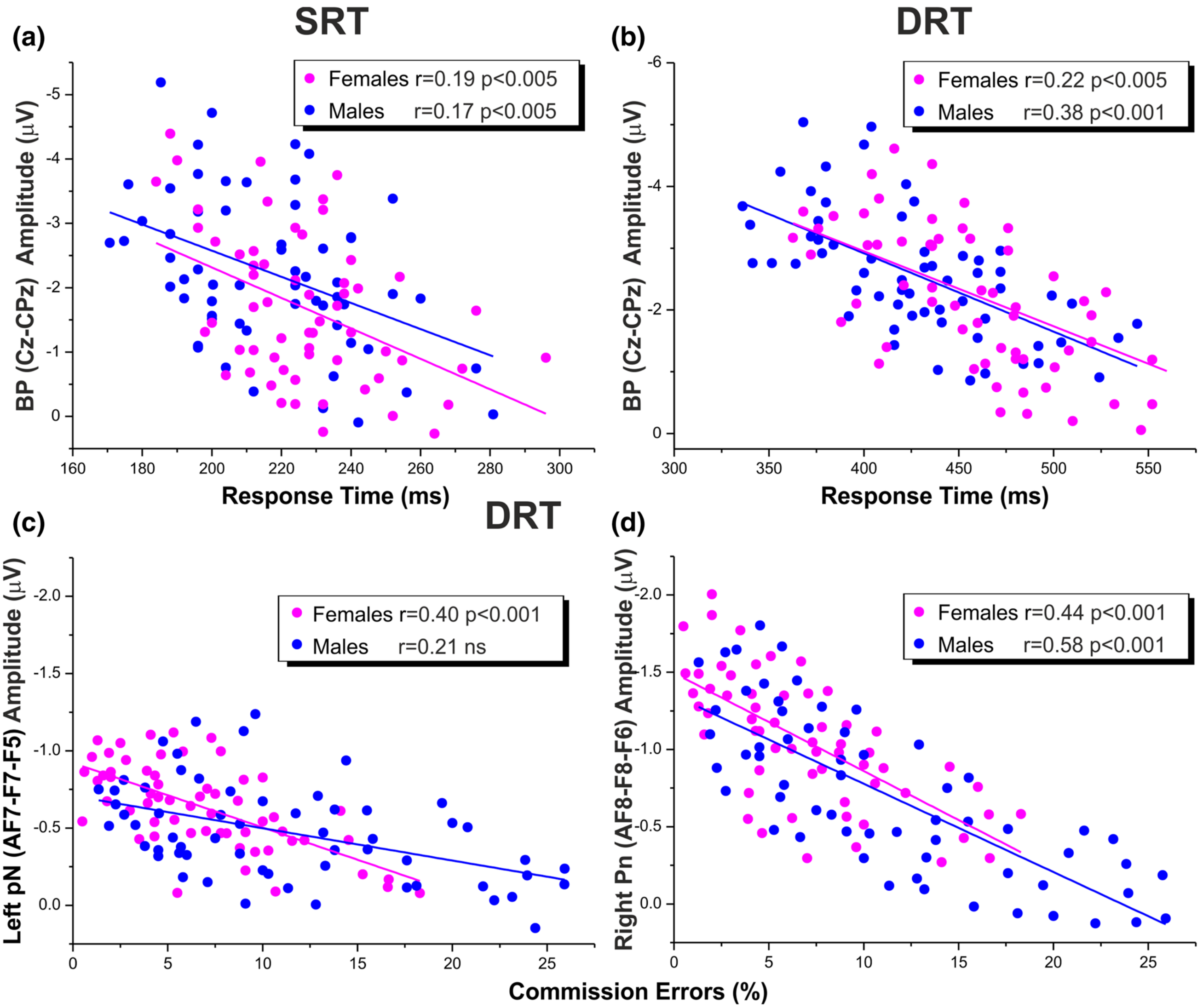

Fig. 5 Correlational analyses between ERP components and behavior. **a** SRT, correlations between the BP (Cz-CPz pool) and RTs. **b** DRT, correlations between the BP (Cz-CPz pool) and the RT. **c** DRT, correlation between the left pN (AF7–F7–F5 pool) and commission errors (CE). **d** DRT, correlation between the right pN (AF8–F8–F6 pool) and CE. ERP were measured in the −800/0 ms interval and correlations were plotted for the two genders separately

($p = 0.0005$), while females had larger P3 in DRT (in both Target and Non-Target trials, $p < 0.0017$).

Figure 8a shows the differential waves (DRT Target minus DRT Non-Target) for the two groups at anterior (AFz) sites, where the differential pP2 (dpP2) was maximal. Figure 8b shows the topographic distributions of these two differential waves separately for females and males. The unpaired t test on the dpP2 was significant ($t_{118} = 6.17$, $p = 0.0003$, $d = -1.53$), indicating larger dpP2 in females.

Considering that one criticism of sex differences literature is that such differences might be observed if one simply compares two distinct groups of individuals independently of sex, we conduct additional analyses spitting each gender group into two age-matched subgroups of 30 subjects each. Then, the same statistical analyses were repeated with these subgroups and results were confirmed. In addition, the two subgroups of each gender were statistically compared yielding null results. The results of this control analysis confirmed the data reliability also showing the results invariability with smaller samples that reduce the likelihood of Type 1 errors.

Discussion

The main purpose of the present study was to explain, using EEG recordings, the different behaviors of males and females in two sensory–motor tasks of different complexities

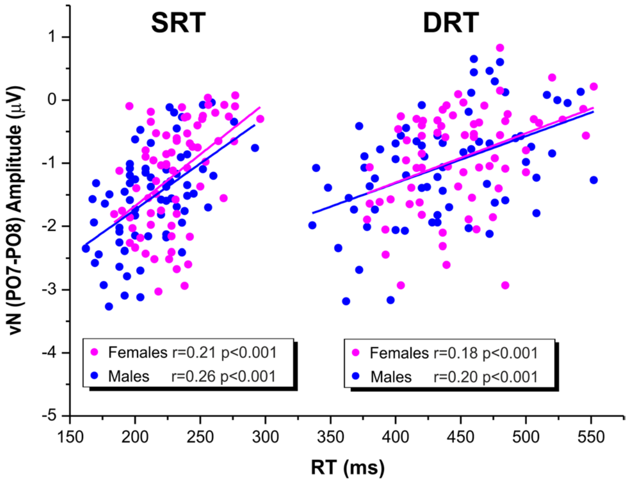

Fig. 6 Correlational analysis for the vN component. Correlations between the vN and the RT. The vN is measured at the PO7–PO8 pool in the – 800/0 ms interval. Correlations are reported separately for SRT and DRT and for the two groups

(the SRT and the DRT) as function of different proactive and reactive neurocognitive mechanisms.

Males were faster in both tasks and females were more accurate in the DRT. Further, although slower, females RTs in DRT were more consistent (i.e., the intra-individual variability of the RT was lower). As predicted by the speed–accuracy trade-off (Wickelgren 1977), correlational analysis suggests that in complex task males would sacrifice accuracy in favor of speed, while females would produce more slow and accurate responses. In SRT, the very low percentage of errors (less than 1%) did not allow to measure speed–accuracy trade-off. Overall, present findings agree with previous reports (Fozard et al. 1994; Silverman 2006), indicating a more conservative response style in females. Since commission errors are erroneous motor responses likely reflecting impulsivity (e.g., Krishnan-Sarin et al. 2007), present results suggest that, on average, males have reduced inhibitory control compared to females. Arguing whether this effect is a result of social education (less inhibition required to males)

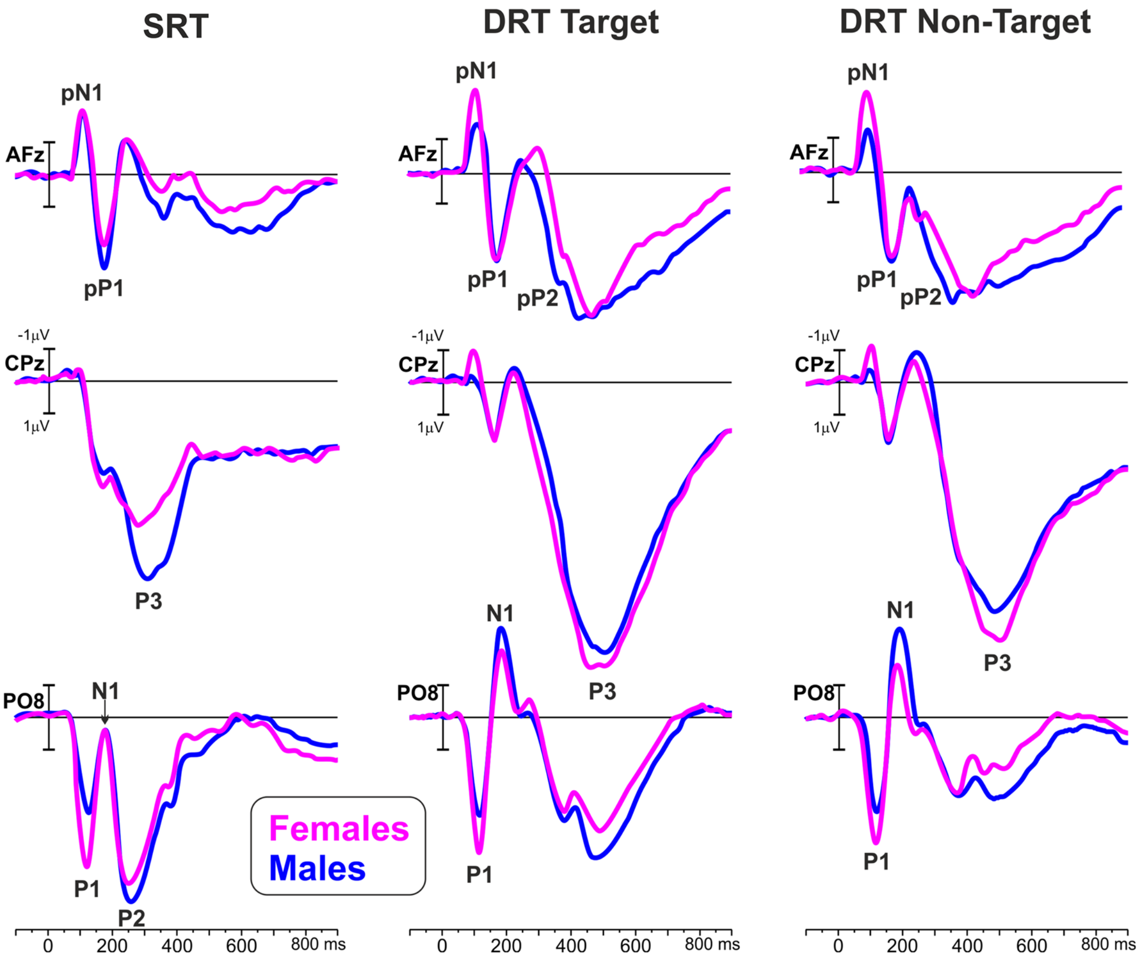

Fig. 7 Post-stimulus ERP. Grand-averaged waveforms at anterior–frontal, central–parietal, and parietal–occipital electrodes for the three task conditions. The waveforms for females and males' groups are superimposed to facilitate comparison. The considered ERP components are labeled

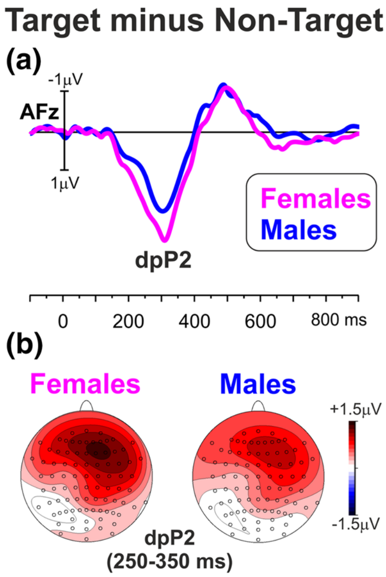

Fig. 8 Differential ERP (Target minus Non-Target) in the DRT**. a** ERP waveform for the two groups at AFz showing the dpP2 peak. **b** Topographical distribution of the dPp2 over 250–350 ms interval

or inherited (by evolution, as proposed by some authors; Yuan et al. 2008) is beyond the scope of the present study.

Males' responses in DRT were also more variable (higher ICV), partially in contrast with previous findings in SRT and CRT reporting opposite results (e.g., Deary and Der 2005; Der and Deary 2006). However, these latter data were collected in samples of participants older than those recruited for the present study, and age may play a role in modulating spontaneous (or early acquired) trait disposition. The lower response consistency observed in males in the present study might be explained by less efficient sustained attention (Bellgrove et al. 2004), which in turn may impair inhibitory ability; alternatively, the hypothesis of a specific inhibition weakening in males should be considered (see Bezdjian et al. 2009, for similar results in children).

Proactive ERPs

Behavioral results were associated with several gender effects of pre-stimulus cortical activities. First, the BP component was larger in males than females, and correlated with the RTs, as previously found in groups matched for gender (Perri et al. 2014; Bianco et al. 2017a, c; Di Russo et al. 2019). In both DRT and SRT, observation of the females' BP amplitude (see Fig. 5a, b) indicate a prevalence of small activity associated with slow RTs.

A gender difference was also found for the pN component, interpreted as a neural correlate of top-down attentional control (Perri et al. 2015), including proactive inhibition (Bianco et al. 2017b). In DRT, the right pN amplitude correlated with the commission error rate in both males and females, confirming the association between right prefrontal cortex (PFC) activity and inhibitory functions (Aron 2011). Regarding the left PFC activity, which was associated with implementation of control by actively maintaining the attentional demands of the task (e.g., MacDonald et al. 2000), a significant correlation with commission errors was found in females only, possibly reflecting a greater involvement of this region to maintain attentional control with respect to males. The larger pN in females is also in line with the Duregger et al. (2007) hypothesis of a higher cognitive preparation in females.

Finally, the recently described vN component, possibly reflecting visual preparation for upcoming stimuli (Di Russo et al. 2019; Bianco et al. 2019), did not show gender differences in SRT; in contrast, the vN was more prominent in females than males in DRT, possibly suggesting that females' performance in visuo-motor complex tasks is mediated during the preparatory phase by more intense activities at two cortical levels: prefrontal (the pN activity) and parietal–occipital (the vN). If the interpretation of the vN as a sort of sensory anticipation holds true, we could propose that females, in the case of a cognitive demanding task (i.e., DRT) allocate more resources than males at this level. We may also note that this effect is in the opposite direction with Duregger et al. (2007) data, since they reported higher temporal–parietal activity in males in the preparation phase preceding acoustic stimuli and proposed that it might reflect brain processes related to auditory sensory processing. The view of different levels of sensory anticipation among genders is consistent with present data, but future studies are needed to address the gender difference between different sensory modalities.

Reactive ERPs

Males and females also showed several differences for the post-stimulus ERP components. At occipital sites, an effect of gender was observed on the P1 component amplitude, which was larger in females than in males in both tasks. Considering that the P1 mainly reflects early visual processing in the extrastriate visual areas (e.g., Di Russo et al. 2002) where early spatial attention effects can be detected (e.g., Di Russo et al. 2003; Hopfinger and West 2006), present findings indicate that, independently from task complexity, females allocate more sensory resources at this early stage of cortical visual processing. This result is partly in line (Chu 1987; Mitchell et al. 1987) or inconsistent (Vaquero et al. 2004; Steffensen et al. 2008) with previous literature. However, none of the above-mentioned studies used a large sample, and this is likely the most important reason for contrasting results. Present result suggests that early extrastriate activity in visuo-motor tasks is sensitive to gender.

The observation of larger N1 amplitude in the DRT compared to SRT supports the view that this component reflects, at least in part, larger selective attention for visual features to allow discriminative processes (e.g., Luck 1995). The finding that the N1 was larger in males than in females together with the males' smaller pN amplitudes suggests that males allocated more attentional resources at this reactive stage rather than during proactive stage. Larger N1 were reported in females (on temporal leads, Vaquero et al. 2004), and also no gender effect was reported (on parietal–occipital sites, Yuan et al. 2008; Steffensen et al. 2008). Trying to explain the contrasting result, one may note that in Vaquero et al. (2004) the N1 component was strongly modulated by spatial attention (not specifically modulated in the present study). Further, the lack of significant N1 differences in Yuan et al. (2008) might due to the use of natural scenes as standard and deviant stimuli and to the different tasks adopted (oddball). Again, the small size of the groups previously studied and the use of different tasks most probably account for contrasting results.

The P2 component (detectable only in the SRT) reflecting later activations of visual areas driven by a combination of feedforward and feedback activity in striate, extrastriate and posterior parietal areas (Di Russo et al. 2002; Lunghi et al. 2015) was larger in males. Considering that the P2, as the N1, is commonly enhanced by selective attention (Di Russo et al. 2003, 2011), this result is consistent with the reported N1 gender difference and suggests that males allocate more reactive (and less proactive) attentional resources in sensory–motor tasks. Although present results might appear in contrast with previous reports (e.g., Yuan et al. 2008), it must be noted that in those investigations the P2 enhancement in females was limited to the deviant stimuli and was interpreted as increased attentional resources to deviant features compared to males.

A significant effect of gender was found for the P3 amplitude, an index of categorization process and task closure (e.g., Mecklinger and Ullsperger 1993). Present DRT data show larger P3 amplitude in females than males, in line with results in a recent auditory equiprobable Go/No-go task (Melynyte et al. 2017), Stroop task (Shen 2005), oddball task (Yuan et al. 2008; Hoffman and Polich 1999) and an object recognition task (Steffensen et al. 2008). However, there are also studies reporting no gender differences in the amplitude of auditory (Polich 1986) or visual (Sangal and Sangal 1996; Shelton et al. 2002) P3. Likewise, few studies reported larger P3 amplitudes in males during a spatial attention task (Vaquero et al. 2004), consistent with present SRT results. A possible explanation for contradictory results could be methodological (such as different task, type of responses required, time windows used and so on). Indeed, the type of task seems a key feature for determining the direction of the gender P3 effect, as shown by present data, in which opposite results were observed in the same subjects according to task complexity (SRT: the P3 was larger in males; DRT: the P3 was larger in females). Possibly, higher resources allocated in the more complex task (DRT) in females may contribute to an optimal stimulus categorization ability, which, in turn, may lead to higher accuracy.

Regarding the prefrontal components, the pN1 was larger in females in DRT, suggesting higher perceptual awareness (Perri et al. 2018a, b) in complex tasks. Within this view, while females increased the level of perceptual awareness in the more complex task, males kept the same processing level independently from task complexity. The pP1 was larger in males in the SRT only, likely suggesting an enhanced visuo-motor awareness (Perri et al. 2018a, b) in simple tasks. The pP2 was larger in males for both target and non-target stimuli, suggesting a more intense processing for stimulus–response mapping (Perri et al. 2015); however, the larger differential pP2 (or dpP2) in females than males may suggest that the cortical activities associated to S–R mapping of targets on one hand, and non-targets on the other hand were better distinguishable in females with respect to males. Considering that commission errors were associated with inaccurate S–R mapping (Perri et al. 2015), it seems that clearly distinct neural signals might offer the basis for a better DRT accuracy in females. Future research is needed to evaluate this interpretation.

Some limitations of the present study must be acknowledged. First, at present, the number of studies on the vN component and insular components is limited. Additional investigations might better support the interpretation (and consequently also the meaning of gender differences) of these relatively novel components herein considered. Second, present results are limited to Caucasian adult subjects with a high level of instruction, and to the specific tasks investigated; indeed, the type of task seems a key feature for determining the direction of gender difference.

Conclusions

Present data suggest that in simple and complex visuo-motor tasks, males and females allocate their cortical resources in diverse ways, possibly leading to the well-documented gender-related speed/accuracy trade-off in visuo-motor performance. When the task is very simple, both preparatory (the BP) and reactive (the pP1, P2 and P3) cortical processing are enhanced in males with respect to females, leading to faster responses. When the task is more complex (implying stimulus discrimination and response selection), females' proactive allocation of more cortical resources at both prefrontal (pN) and sensory (vN) level, as well as several reactive stages after stimulus onset (the pN1, the P1, and the P3), leads to relatively slow and very accurate responses.

In contrast, males allocate a reduced level of pre-stimulus sustained attention to the task (smaller pN and vN), possibly compensating with enhanced reactive attention at visual level processing (larger N1 and P2). Even though the neural processing associated with S–R mapping (the pP2) is generally enhanced in males (for both target and non-target stimuli), signals associated to different stimulus categories are less distinguishable in males than females, as indicated by dpP2 effect, possibly facilitating female accuracy in a complex task.

Present research provides evidence that gender is an important variable to be considered in neurocognitive studies of perceptual decision making; this variable should be considered while planning experimental designs or interpreting the results because, per se, could explain the speed/accuracy trade-off in visuo-motor performance and relative differences in brain functions. In contrast, some studies excluded females from their samples or ignored gender as a factor in their findings (for review see Mendrek 2015), possibly jeopardizing their results' interpretation.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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