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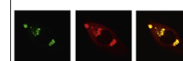
Research Report

How are the motor system activity and functional connectivity between the cognitive and sensorimotor systems modulated by athletic expertise?

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ABSTRACT

Expertise offers a unique insight into how our brain functions. The purpose of this experiment was to determine if motor system activity and functional connectivity between the cognitive system and sensorimotor system is differentially modulated by an individual's level of expertise. This goal was achieved through the acquisition of functional neuroimaging data in 10 expert volleyball players and 10 novice individuals who were presented with a series of sentences describing possible technical volleyball-specific motor acts and acts that cannot be performed as positive ("Do …!") or negative ("Don't …") commands, while they were silently reading them and deciding whether the actions were technically feasible or not. Compared with novices, experts' activity in the left primary motor cortex hand area (M1) and in the left premotor cortex (Pm) was decreased by impossible actions presented as positive commands. Sensorimotor activation in response to action-related stimuli is not that automatic as held since we found that these areas were deactivated during the task, and their functional connectivity to the primary visual cortex was strengthened for possible actions presented as positive commands, reflecting the neural processes underlying the interaction between motor and visual imagery. These results suggest that the neural activity within the key areas implicitly triggered by motor simulation is a function of the expertise, action feasibility, and context.

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1. Introduction

Studies that compare groups with different levels of experience on specific actions are instrumental for testing how motor expertise shapes our sensorimotor representations. Expertise-dependent differences in cognitive and neural operations during overt action production in sports have already been observed in studies involving participants with different

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levels of highly skilled motor experience (see Supplementary Table S1). (Calvo-Merino et al., 2005), for example, compared experts in classical ballet, in capoeira and novice dancers who viewed videos of ballet or capoeira actions and found that, compared to untrained movements, trained movements led to greater bilateral activations in premotor cortex and intraparietal sulcus, right superior parietal lobe and left posterior superior temporal sulcus of the expert dancers' brain (Calvo-Merino et al., 2005). This approach has been successfully applied to the processing of sentences describing actions. In Beilock et al.'s (2008) study, the left dorsal premotor cortex was found to be activated as a function of the expert ice hockey players' experience (vs. fans and novices), when they passively listened to sentences describing ice-\hockey actions (vs. everyday actions). The authors argued that, when processing sentences describing sport-specific actions, participants were able to associate the described action scenarios with motor plans (Abreu et al., 2012; Beilock et al., 2008; Pezzulo et al., 2010) by triggering automatic *implicit* motor simulation (Jeannerod and Frak, 1999) thanks to their extensive motor experience. *Implicit* motor simulation occurs when individuals, imagine the corresponding actions even when not instructed to do so (Parsons et al., 1995). Sentences describing ice hockey-related actions (Beilock et al., 2008) were all motorically possible and, as such, they *implicitly* activated the corresponding sensorimotor representations. However, what it still needs to be explained is whether experts apply motor simulation only when the sentences describe actions that can be physically experienced (Buccino et al., 2004; Calvo-Merino et al., 2005; Costantini et al., 2005; Stevens et al., 2000). One way to explore *implicit* motor representations, is to ask expert volleyball players and novices to process sentences referring (or not) to a possible action, presented either within a positive (e.g., "Do …") or a negative (e.g., "Don't …") *context*. It is known that processing words describing actions activates the premotor and motor cortex, e.g., (Hauk et al., 2004; van Elk et al., 2010; Willems et al., 2010b), while negative ("Don't" run!) commands cause a reduction of activation in left fronto-parietal regions (Tettamanti et al., 2008) as well as in the hand region of the primary motor and premotor cortices (Tomasino et al., 2010b), see also (Liuzza et al., 2011) for a TMS study on negations. In addition, positive and negative action-related imperatives cause a modulation of participants' RTs, namely a positive faster than negative context (Tomasino et al., 2010b). This effect may reflect motor simulation/suppression mechanisms. Exposure to commands and contexts can therefore be used as a measure of *implicit* motor simulation (Jeannerod and Frak, 1999).

In the present fMRI study, 10 expert volleyball players and 10 novice individuals were presented with a series of sentences describing possible technical volleyball-specific motor acts and acts that cannot be performed as positive ("Do …!") or negative ("Don't …") commands, and they silently read them and decided whether the actions were technically feasible or not. We investigated whether activity in sensorimotor areas and functional connectivity between cognitive and sensorimotor systems are differentially modulated by an individual's level of expertise. In particular,

impossible stimuli described semantically and syntactically correct sentences that did not correspond to any significant motor act (e.g., "Bagher run-up!"). Nevertheless, in this sentence, the verb "run-up" is contained and might have triggered the simulation of the corresponding "running-up" action. No fMRI study has to date investigated how possible–impossible action sentences can modulate their simulation, and the neural activations accordingly. Thus, we expected that volleyball experts, as compared to novices, should be able to discriminate possible vs. impossible actions and to implicitly simulate feasible actions presented as positive contexts. By contrast, no simulation should occur for impossible actions (e.g., "Do … an impossible action"). Based on a previous behavioral study (Tomasino et al., 2010b, 2012) we know that experts' reaction times, as compared to novices', are shorter for the possible (vs. impossible) actions presented as positive (vs. negative) commands. Accordingly, in the present study, we expected that sensorimotor activation should be modulated for the positive action-related commands depending on whether possible–impossible actions are processed, and no modulation is expected for negative commands, since negations transiently reduce the access to sensorimotor representations (Tettamanti et al., 2008). We also know that novices do not distinguish possible vs. impossible actions and try to perform simulation every time they encountered a description of action, independently of its motor feasibility (Tomasino et al., 2010b, 2012). Novices showed a nonspecific effect of context for all types of stimuli, which is not linked to the degree of motor knowledge. Accordingly, in the present study, we expected that sensorimotor activation should be not modulated by possible–impossible actions.

By using action-related sentences as stimuli, results derived from the present motor imagery fMRI study will also add further information with respect to debate on the role of the sensorimotor areas in language processing, e.g. (Kemmerer and Gonzalez-Castillo, 2010; Willems and Hagoort, 2007). Theories of embodied cognition promote the idea that conceptual representations are modality-dependent and built from sensory and motor experiences. They also hold that recognition of objects, actions and words is necessarily accomplished via simulation—that is, by re-enacting sensorimotor memories acquired through experience (Barsalou, 1999, 2008; Gallese and Lakoff, 2005). According to the predictions of the embodied cognition, independent of whether the verb stimuli were presented as positive or negative imperatives, we should find similar activations for action-related sentences because is the meaning of an action word per se that is represented in overlapping networks (Pulvermuller, 2005). On the contrary, showing that positive or negative imperatives exert a different effect on action verbs would rather support the view that the involvement of sensorimotor areas depends on the context (van Dam et al., 2010, 2012a, 2012b) in which conceptual features are retrieved, see also (Tomasino and Rumiati, 2013).

The embodied view implies also an increased functional connectivity between language- and motor-related areas. Processing action sentences should trigger a stronger functional integration between the perisylvian regions and M1. There is a limited number of studies addressing this issue

Table 1 – Results from the ANOVAs performed on the mean accuracy and mean response times.

Factors	Accuracy		Response times	
	Effects	Direction	Effects	Direction
Group	$F(1,18)=$ 38.61, $p<.001$	Athletes: 92.38±6.59>novices: 78.33±13.22	$F(1,18)=.021$, $p>.05$	–
Stimuli	$F(1,18)=.193$	PWs: 99.83±.51>IMPs: 72.33±26.13 and >Ps ($p<.001$, 83.91±12.30), n.s. for IMPs vs. Ps ($p=.140$)	$F(2,36)=98.23$, $p<.001$	PWs (1298.02±432.22)>IMPs ($p<.001$, 2064.19±370.95) and >Ps (2092.73±333.22), n.s. IMPs vs. Ps ($p=.93$)
Context	$F(1,18)=.193$	–	$F(1,18)=20.68$, $p<.001$	Neg>Pos (1770.48±358.83 vs. 1866.14±399.65)
Group × Stimuli	$F(1,18)=.24$	IMPs in athletes>novices, ($p<.001$, 89±8.71 vs. 55.66±26.82) Ps: $p=.070$, 88.5±10.35 vs. 79.33±12.84; PWs: $p=.15$, n.s., 99.66±.71 vs. 100±0.	$F(2,36)=.56$	–
Group × Context	$F(1,18)=.24$	–	$F(1,18)=1.39$	–
Stimuli × Context	$F(2,36)=4.0$, $p<.05$	Ps+>Ps− ($p<.05$, Ps, 87.33±8.48 vs. 80.5±8.48; IMPs, $p=.37$, n.s. 70.16±28.08 vs. 74.5±24.18; PWs, $p=.15$, n.s., 100±0 vs. 99.66±1.02).	$F(2,36)=17.84$, $p<.001$	Ps−>Ps+ ($p<.001$, 2214.5±339.2 vs. 1970.96±327.24), n.s. for IMPs− vs. IMPs+ ($p=.184$, 2096.8±423.5 vs. 2031.57±318.39) n.s. for PWs ($p=.180$, 1287.13±436.26 vs. 1308.9±430.86).
Group × Stimuli × Context	$F(2,36)=.185$	–	$F(2,36)=5.6$, $p<.01$	athletes: Ps−>Ps+ ($p<.001$, 2233.83 ±367.41 vs. 1949.62±344.64), n.s. IMPs− and IMPs+ (1993.44±483.21 vs. 2036.09±386.55, $p=.53$, n.s) and n.s. PWs (1300.21±439.16 vs. 1329.3±437.02, $p=.204$, n.s.). Novices: Ps−>Ps+ ($p<.001$, 2195.16±327.22 vs. 1992.30±326.01) and IMPs−>IMPs+($p<.05$, 2200.17±348.44 vs. 2027.06±254.04), n.s. between − and +PWs (1274.05±456.67 vs. 1288.51±447.21, $p=.18$, n.s)

(Ghio and Tettamanti, 2010; Tettamanti et al., 2008; van Dam et al., 2012a). In one of those studies, authors used dynamic causal modeling (DCM) to analyze fMRI data during a listening task involving action- and non-action related stimuli presented first as affirmative and then negative sentences (Tettamanti et al., 2008). They found that the degree of functional integration between the left inferior frontal gyrus and the left fronto-parieto-temporal system, including the dorsal premotor cortex, the supra-marginal gyrus, and the left posterior inferior temporal gyrus, was more positive for processing action-related vs. abstract sentences (Tettamanti et al., 2008). We performed PPI analyses on the left M1 and Pm (as revealed by the motor localizer task) as seed to assess the areas with increased connectivity with the left M1 and Pm during action sentences processing. PPI analysis is used to explain the neural responses in one brain area in terms of the interaction between influences of another brain region and a cognitive process (here: action sentences processing). According to the embodied view, we should expect that the functional connectivity between the language-related areas and M1 is increased for action related sentences independent of the context. On the contrary, a lack of functional connectivity changes between motor and cognitive systems would support the view that sensory-motor activity is context dependent (Mahon and Caramazza, 2008; Papeo et al., 2012; Postle et al., 2013; Tomasino et al., 2010b; van Dam et al., 2010, 2012b). Furthermore, if athletes' and novices' sensorimotor activity differs as a function of their motor experience, their functional connectivity should change accordingly.

2. Results

2.1. Behavioral results

2.1.1. Accuracy
Mean correct responses were significantly higher for athletes than novices, for pseudo words (PWs) than impossible sentences (which are semantically correct but could not be performed IMPs) and possible sport-specific action sentences (Ps) action sentences (n.s. for IMPs vs. Ps). The significant *group × stimulus* interaction revealed a higher accuracy for IMPs in athletes, whereas for Ps there was a trend towards significance. The *stimulus × context* interaction revealed higher %
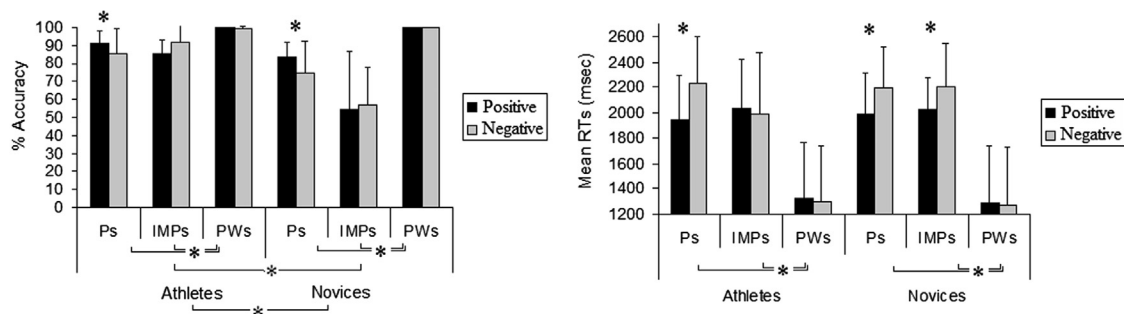
Fig. 1 – Mean accuracy (a) and mean response times, (b) of athletes and novices during the categorization task of impossible sentences (which are semantically correct but could not be performed IMPs), possible sport-specific action sentences (Ps) action sentences and pseudo words (PWs) presented in positive and negative contexts. Error bars indicate the standard error (SEM). Asterisks denote significant differences between conditions.

of correct responses for positive (+) vs. negative (−) Ps. All the other interactions did not reach significance (see Table 1 and Fig. 1).

2.1.2. Response times

Mean RTs were significantly higher for PWs than IMPs and Ps (n.s. for IMPs vs. Ps), and for negative vs. positive sentences. The significant *stimulus × context* interaction revealed slower negative than positive Ps (n.s. for IMPs and PWs). The *group-× stimulus × context* interaction showed that this effect was driven by athletes, who were significantly slower for negative than positive Ps (n.s. for IMPs and PWs), while for novices the context was significant both for Ps and IMPs (n.s. for PWs). All the other interactions did not reach significance (see Table 1 and Fig. 1).[1] Behavioral data replicated the previously-described pattern of results (Tomasino et al., 2012).

2.2. fMRI results

2.2.1. Common activations for both tasks: conjunction analysis of categorization and motor localizer

To test a prerequisite of theories supporting a necessary interaction between motor and the language systems (embodied view) that the regions involved in processing action-related sentences overlap with those underlying motor processing we performed a conjunction analysis. The conjunction analysis ([task>baseline]∩[motor localizer>baseline]) showed that the common activations for the task and the hand motor localizer consisted of activation clusters including: (i) the SMA bilaterally extending to the left precentral gyrus (Areas 4a and 6), (ii) the right postcentral gyrus (Areas 1 and 2), extending to areas 3b and 4p, (iii) the left supramarginal gyrus extending to the postcentral gyrus (Areas 2 and 1) and to the rolandic operculum, (iv) the bilateral inferior frontal gyrus (Pars Opercularis) extending to the rolandic operculum, (v) the

right precentral gyrus (Area 6); (vi) the cerebellum bilaterally extending to the inferior occipital gyrus (See Table 2 and Fig. 2).[2]

2.2.2. Region of interest (ROI) analysis

The activation of the left and right M1 and Pm cortex, as revealed by the above conjunction analysis, was further addressed by performing a ROI analysis. We assessed whether the sensorimotor area is more active in participants presented with positive sentences describing actions for which they had real physical experience. The ANOVA performed on the beta values extracted from the individual anatomically-constrained functional ROIs comprising the hand area of the left and right primary motor cortex (M1), as well as that of the left and right premotor cortex (Pm), as defined for each of the right-handed subjects (for the mean coordinates see Supplementary Table S1) revealed the following pattern of results. We found a significant three-way group × stimuli × context interaction (see Table 3 and Fig. 3) for the mean parameter estimates extracted from the left and the right M1, and premotor cortex. While athletes (vs. novices) showed impossible<possible actions when are presented as positive context (i.e., "Do…") in the left M1 and left Pm, for novices, no modulation was found, neither in the left M1 nor in the Pm cortex. By contrast, novices (vs. athletes) showed impossible>possible actions when presented as positive context (i.e., "Do…") in the right M1 and possible<impossible when presented as positive context (i.e., "Do…") in the right Pm.[3] For all the other interactions and main effects see Table 3.

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[1] The pattern of RT was not due to the speed-accuracy trade-off. For each condition, we failed to find any significant negative correlation between error-rates and response-times (across subjects in that group, IMPs positive $r = .68$ $r = .217$; IMPs negative $r = .23$, $r = −.030$; P positive $r = −.013$, $r = .108$; P negative $r = .427$, and $r = −.80$ and all $p > .05$, for athletes and for novices respectively).

[2] To ensure that any reported difference in neural activity between the conditions was not due to the hand used to respond, an additional regressor coding for hand used to respond was included in the statistical parametric mapping (SPM) analysis. Results of this analysis remained unchanged.

[3] This pattern of results was confirmed by a further analysis we run by re-coding items closely following the participant's categorization, e.g., an impossible action related sentence, interpreted by a subject as a possible action, was recorded as such. The ANOVA performed on the parameter estimates ruled out the possibility that impossible action related sentences could have biased the result.

Table 2 – Whole brain analysis: brain regions showing significant relative increases of BOLD response associated with the task.

Region	Side	MNI			Z	Cluster size
		x	y	z		Voxel
Task-related network: $(Ps_+ + Ps_- + IMPs_+ + IMPs_-) >$ Rest						
Cerebellum	L	−46	−70	−20	6.25	8343
Inferior occipital gyrus	L	−44	−82	−10	6.13	
Precentral gyrus (Area 44)	L	−54	12	30	6.04	10976
Inferior frontal gyrus (pars operculais)	L	−60	12	6	5.81	
Supplementary motor area (SMA)	L	−2	16	56	5.78	6036
Precentral gyrus (Area 6)	L	−30	−8	62	5.57	
Temporal pole	R	46	22	−20	5.63	3408
Angular gyrus	R	34	−58	40	5.52	
Precentral gyrus	R	56	12	38	5.44	
Insula	R	38	0	14	5.12	252
Rolandic operculum	R	46	4	10	4.67	
Putamen	R	24	16	−2	4.96	901
Calcarine gyrus (Area 17)	R	10	−70	10	4.41	261
Thalamus	R	10	−14	6	4.28	426
Middle temporal gyrus	L	−60	−40	−6	4.24	316
Superior temporal gyrus	L	−60	−42	20	3.64	
Task > Rest ∩ Motor Localizer > Rest						
Cerebellum	L	−26	−68	−28	5.79	3484
Cerebellum	R	36	−62	−30	5.58	
SupraMarginal gyrus (Area 2)	L	−50	−24	42	5.12	1602
Postcentral gyrus	L	−56	−22	30	4.84	
Rolandic operculum	L	−48	−24	16	4.82	
Supplementary motor area (SMA)	L	−2	0	58	5.00	1802
Precentral gyrus (Areas 6, 4a)	L	−44	−12	60	4.56	
Inferior frontal gyrus (pars opercularis (Area 44)	L	−58	10	24	4.82	696
Rolandic operculum	L	−60	10	4	4.39	
Postcentral gyrus (Area 2)	R	48	−28	44	4.49	526
Postcentral gyrus (Area 1)	R	56	−18	40	4.11	
Postcentral gyrus (Areas 3b, 4p)	R	36	−34	54	4.04	
Inferior occipital gyrus	R	42	−84	−2	4.43	339
Inferior frontal gyrus (pars opercularis, Area 44)	R	58	14	28	4.17	184
Precentral gyrus (Area 6)	R	58	6	38	4.05	
Precentral gyrus (Area 6)	R	38	−10	64	4.08	116
Putamen	R	22	12	−4	4.00	88
Insula	R	42	26	−4	3.76	131

For each region of activation, the coordinates in MNI space are given in reference to the maximally activated voxel within an area of activation, as indicated by the highest Z-value ($p < .05$, corrected for multiple comparisons at the cluster level, height threshold $p < .001$, uncorrected). L/R = left/right hemisphere

To date, the three-way group × stimulus × context interaction did not reach significance in the other regions included the network commonly activated by the task and the motor localizer suggesting that regions other than M1 and the Pm cortex were not modulated by expertise. For instance, in the left post-central gyrus (Areas 1 and 2) we found a significant context × type of stimulus interaction ($F(1,9) = 5.57$, $p < .05$), with a significant decrease of the beta values for positive IMPs vs. Ps ($p < .05$), with n.s. for negative IMPs and Ps ($p > .05$). All the other factors were not significant (Group, $F(1,10) = 2.37$; type of stimulus, $F(1,9) = 1.31$; Context, $F(1,9) = .10$; Group × type of stimulus, $F(9,9) = 1.3$; Group × Context, $F(9,9) = 1.25$; 3-way interaction, $F(9,9) = .81$, all Ps > .05, n.s.). The parameter estimates extracted from the left (Group, $F(1,10) = 1.87$; Stimulus, $F(19,9) = 2.28$; Context, $F(1,9) = 1.87$; context × type

of stimulus, $F(1,9) = 1.01$; Group × type of stimulus, $F(9,9) = 1.39$; Group × Context, $F(9,9) = 1.25$; 3-way interaction, $F(9,9) = .33$ and all Ps > .05, n.s.) and the right (Group, $F(1,10) = 1.53$; stimulus, $F(19,9) = .15$; context, $F(1,9) = .42$; context × type of stimulus, $F(1,9) = .55$; Group × type of stimulus, $F(9,9) = 1.41$; Group × Context, $F(9,9) = 1.21$; 3-way interaction, $F(9,9) = 1.37$, all Ps > .05, n.s.) IFG (pars opercularis) were not modulated by the experimental factors. Lastly, the parameter estimates extracted from the cerebellum were significantly modulated by the type of stimulus ($F(1,9) = 6.03$, $p < .05$) with higher mean parameter estimates for possible as compared to impossible items. All the other factors were not significant (Group, $F(1,10) = .3$; context, $F(1,9) = 2.09$; context × type of stimulus, $F(1,9) = 4.08$; Group × type of stimulus, $F(9,9) = .78$; Group × Context, $F(9,9) = 1.16$; 3-way interaction, $F(9,9) = .73$, all Ps > .05,
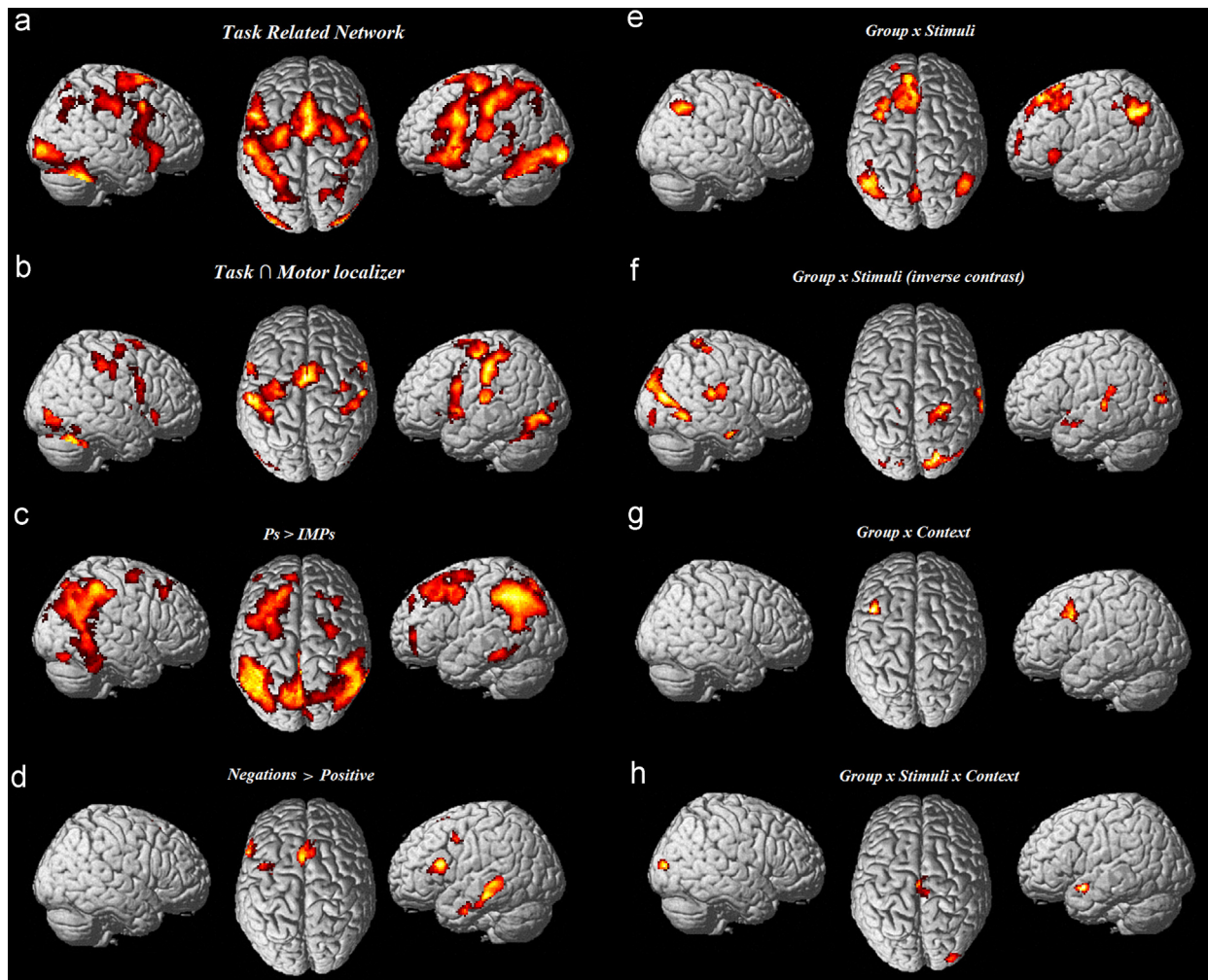
Fig. 2 – (a) Task-related network as revealed by the whole brain analysis; (b) common network for the task and the hand localizer as evidenced by the conjunction analysis; (c) relative increases in neural activity underlying possible, as compared to impossible items; (d) differential activation related to negations as compared to positive sentences; (e) group by stimuli interaction: relative increases in neural activity associated with the processing of possible (Ps) as compared to impossible (IMPs) sentences, by athletes, as compared to novices; (f) context by stimuli interaction. Relative increases in neural activity associated with the processing of possible (Ps) as compared to impossible (IMPs) sentences, presented as positive as compared to negatives; (g) the 3 group × stimuli × context way interaction. Relative increases in neural activity associated with the contrasts (P < .05, FWE corrected at the cluster level) are displayed on a rendered template brain provided by spm5.

n.s.). Next we will report how the other brain regions were differentially modulated by the main factors and interactions, as revealed by the whole brain analysis.

2.2.3. Whole brain analysis

The task-related network that reflected language processing and imagery and was predominantly lateralized in the left hemisphere (see Fig. 2 and Table 2). The main effect of stimuli showed that Ps trials (relative to IMPs) differentially activated the superior/inferior parietal lobe, the precentral gyrus (Area 6) bilaterally, the left pars orbitalis of the IFG, the superior/middle frontal gyrus and the anterior cingulate cortex, the middle/inferior temporal gyri bilaterally, and the left fusiform gyrus. No differential activation was found at the predefined statistical threshold for the IMPs vs. Ps (see Fig. 2, Table 4).

The main effect of context showed that negative context (relative to positive) differentially activated in the left

hemisphere the precentral gyrus, the inferior frontal gyrus (Area 44), and the middle temporal gyrus, in addition to the supplementary motor area (SMA) bilaterally and the middle cingulate cortex. No differential activation was found at the predefined statistical threshold for the reverse comparison (see Fig. 2, Table 4).

The Context × Stimuli interaction showed that positive Ps vs. IMPs (as compared to negative) led to a significant increase in the left postcentral gyrus ($p < .001$ and $p = .07$, n.s. for Ps_positive vs. IMPs_positive and for Ps_negative vs. IMPs_negative respectively), the left ($p < .01$ and $p = .78$, n.s.) and the right ($p < .001$ and $p = .10$, n.s.) middle occipital gyrus, the left ($p < .01$ and $p = .76$, n.s.) and the right ($p < .001$ and $p = .06$, n.s.) STS. Positive IMPs vs. Ps (as compared to negative) led to a significant decrease in the left insula ($p < .05$ and $p = .27$, n.s.) and in the right postcentral gyrus ($p = .75$, n.s. and $p > .05$). Positive Ps vs. IMPs and negative IMPs vs. Ps led to a

Table 3 – Results from the three-way ANOVAs performed on the mean parameter estimates extracted from the four regions of interest.

ROIs	Factors	Effects	Direction
LH M1	Group	$F(1,18)=5.64$, $p<.05$	Nov$<$Ath
	Stimuli	$F(1,18)=22.37$, $p<.001$	Imp$<$p
	Context	$F(1,18)=82.71$, $p<.001$	pos$<$neg
	Group × Stimuli	$F(1,18)=17.99$, $p<.001$	Ath: imp$<$p, $p<.001$
			Nov: imp vs. p, n.s.
	Group × Context	$F(1,18)=7.75$, $p<.05$	Athl: pos$<$neg, $p<.01$
			Nov: neg$<$pos, $p<.01$
	Stimuli × Context	$F(1,18)=22.37$, $p<.001$	Pos: imp vs. p, $p<.001$
			Neg: imp vs. p, n.s.
	Group × Stimuli × Context	$F(1,18)=17.99$, $p<.001$	Ath, Pos: imp vs. p, $p<.001$
			Ath, neg: imp vs. p, n.s.
			Nov, Pos: imp vs. p, n.s.
			Nov, neg: imp vs. p, n.s.
LH Pm	Group	$F(1,18)=.09$, $p>.05$, n.s.	–
	Stimuli	$F(1,18)=9.76$, $p<.01$	Imp$<$p
	Context	$F(1,18)=44.34$, $p<.001$	pos$<$neg
	Group × Stimuli	$F(1,18)=35.78$, $p<.001$	Ath: imp$<$p, $p<.001$
			Nov: imp vs. p, n.s.
	Group × Context	$F(1,18)=1.56$, $p>.05$, n.s.	–
	Stimuli × Context	$F(1,18)=9.76$, $p<.01$	Pos: imp vs. p, $p<.01$
			Neg: imp$>$p, n.s.
	Group × Stimuli × Context	$F(1,18)=35.78$, $p<.001$	Ath, Pos: imp vs. p, $p<.001$
			Ath, neg: imp vs. p, n.s.
			Nov, Pos: imp vs. p, n.s.
			Nov, neg: imp vs. p, n.s.
RH M1	Group	$F(1,18)=8.57$, $p<.01$	Ath$<$nov
	Stimuli	$F(1,18)=23.48$, $p<.001$	Imp$>$p
	Context	$F(1,18)=2.13$, $p>.05$, n.s.	–
	Group × Stimuli	$F(1,18)=14.9$, $p<.001$	Ath: imp vs. p, n.s.
			Nov: p$<$imp, $p<.001$
	Group × Context	$F(1,18)=1.13$, $p>.05$, n.s.	–
	Stimuli × Context	$F(1,18)=23.48$, $p<.001$	Pos: imp vs. p, $p<.001$
			Neg: imp vs. p, n.s.
	Group × Stimuli × Context	$F(1,18)=8.57$, $p<.01$	Ath, Pos: imp vs. p, n.s.
			Ath, neg: imp vs. p, n.s.
			Nov, Pos: imp vs. p, $p<.001$
			Nov, neg: imp vs. p, n.s.
RH Pm	Group	$F(1,18)=.036$, $p>.05$, n.s.	–
	Stimuli	$F(1,18)=4.07$, $p>.05$, n.s.	–
	Context	$F(1,18)=15.40$, $p<.001$	pos$<$neg
	Group × Stimuli	$F(1,18)=9.75$, $p<.01$	Ath: imp vs. p, n.s.
			Nov: imp$<$p, $p<.005$
	Group × Context	$F(1,18)=12.29$, $p<.005$	Ath: pos vs. neg, n.s.
			Nov: pos$<$neg, $p<.001$
	Stimuli × Context	$F(1,18)=4.07$, $p>.05$, n.s.	–
	Group × Stimuli × Context	$F(1,18)=9.75$, $p<.01$	Ath, Pos: imp vs. p, n.s.
			Ath, neg: imp vs. p, n.s.
			Nov, Pos: imp vs. p, $p<.005$
			Nov, neg: imp vs. p, n.s.

significant increase in the right MTG ($p<.05$ and $p<.05$). The reverse interaction led to a significant increase in the BOLD response in the left middle frontal gyrus (pars triangularis), where activity increased significantly for IMPs_negative vs. Ps_negative (vs. positive, $p<.05$ and p=.28, see Fig. 2, Table 4 and Supplementary Fig. S1).

The Group × Stimuli interaction showed that many of the activation clusters found in the main effect of stimuli, i.e., for

Ps relative to IMPs, was driven by the athletes group: angular gyrus/inferior parietal lobe/precuneus bilaterally ($p<.005$, p=38, n.s., $p<.001$, p=.15, n.s., Ps vs. IMPs for athletes and novices for the right and the left hemisphere respectively), the left superior frontal gyrus ($p<.001$, and p=.89, n.s., for athletes and novices), the left superior medial gyrus ($p<.001$, and p=.06, n.s.), the cingulate cortex medially ($p<.001$ and p=.33, n.s), and the left inferior frontal gyrus ($p<.005$ and
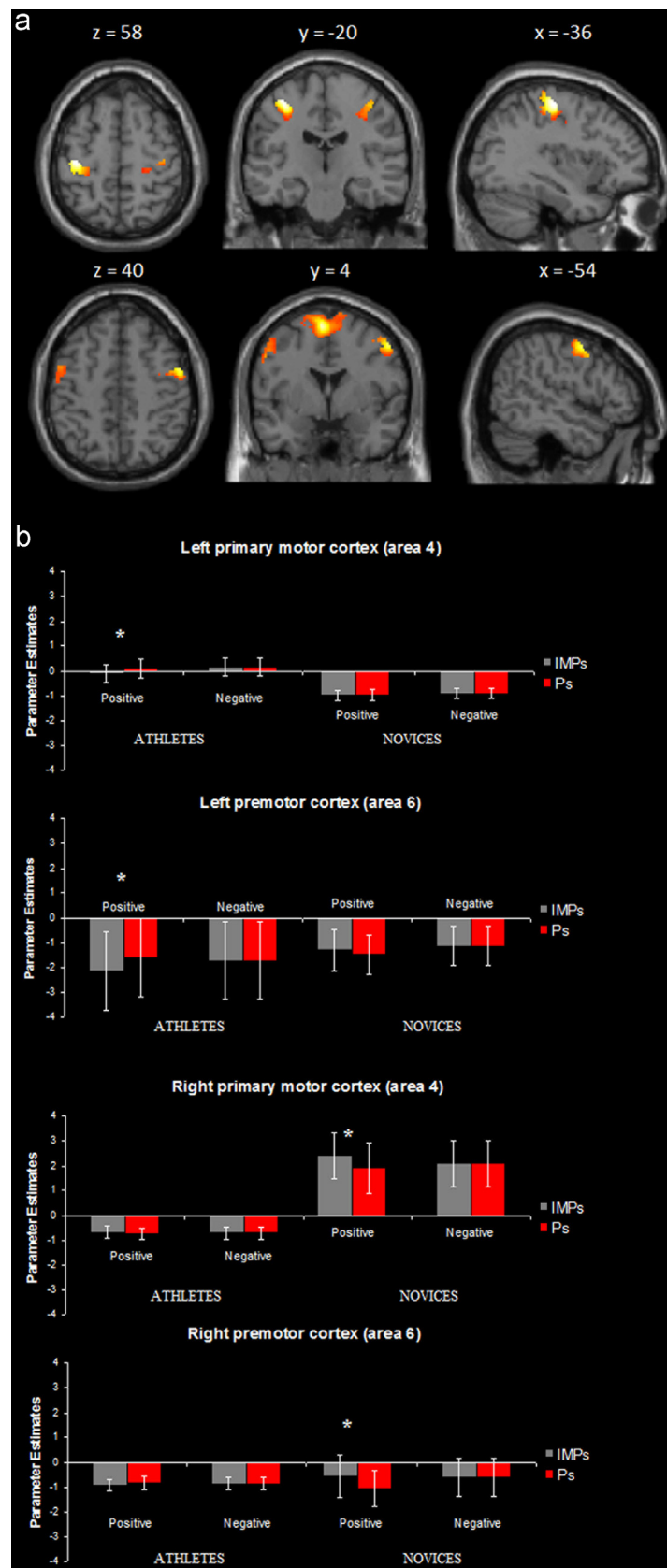
Fig. 3 – (A) An individual left hand M1-ROI (maximally activated voxel at −36, −20, +58) and left premotor cortex-ROI (maximally activated voxel at −54, 4, +40) is superimposed on an axial, coronal, and sagittal slice of the spatially normalized single subject brain (subject #1). (B) Group mean beta values extracted from the individual anatomically-constrained functional ROIs comprising the hand representation within the left primary motor and premotor cortex (two upper rows) as well as the right primary motor and premotor cortex (two lower rows) for possible (Ps) and impossible (IMPs) actions presented in a positive or negative linguistic context are plotted for athletes (left panel) and for novices (right panel). Error bars indicate standard error (SEM).

Table 4 – Whole brain analysis: brain regions showing significant relative increases of BOLD response associated with each experimental condition.

Region	Side	MNI			Z	Cluster size
		x	y	z		Voxel
Main effect of Stimuli: Ps > IMPs						
Inferior parietal lobule	L	−44	−58	46	6.14	18058
Angular gyrus	L	−44	−68	42	6.14	
Precuneus	L	−8	−66	44	5.71	
Superior parietal lobule	R	44	−40	48	5.46	
Middle frontal gyrus	L	−34	26	46	5.38	2436
Superior frontal gyrus	L	−18	36	52	5.07	
Precentral gyrus (Area 6)	L	−54	6	40	5.03	
Superior frontal gyrus	R	32	−4	62	4.18	311
Precentral gyrus (Area 6)	R	26	−6	52	3.93	
Middle frontal gyrus	R	36	26	44	4.04	197
Superior medial gyrus	L	−10	50	32	3.97	184
Inferior frontal gyrus (pars orbitalis)	L	−44	48	−14	4.06	165
Anterior cingulate cortex	L	−4	32	−2	4.18	161
Inferior temporal gyrus	L	−62	−38	−18	4.81	297
Middle temporal gyrus	L	−64	−54	−8	3.94	
Fusiform gyrus	L	−28	−42	−12	4.57	492
Lingual gyrus	L	−20	−54	−4	4.13	
Main effect of context: Negative > Positive						
Inferior frontal gyrus (Area 44)	L	−56	18	18	5.23	301
Middle temporal gyrus	L	−52	−40	0	4.88	708
Supplementary motor area	L	−4	14	60	4.59	473
Supplementary motor area	R	6	14	60	4.49	
Middle cingulate cortex	R	8	30	34	4.35	
Precentral gyrus	L	−32	−4	42	3.92	140
Stimuli × Context: (Ps: Positive > Negative) > (IMPs: Positive > Negative)						
Middle occipital gyrus	R	42	−74	10	4.70	1023
Inferior temporal gyrus	R	46	−56	−6	4.53	
Superior temporal gyrus	R	68	−34	16	4.30	346
Supramarginal gyrus	R	62	−20	22	4.08	
Calcarine gyrus (Area 17)	R	16	−88	−2	4.25	197
Lingual gyrus (Area 18)	R	24	−90	−4	4.09	
Postcentral gyrus (Area 3a)	L	−18	−42	50	4.23	151
Middle cingulate cortex	L	−12	−36	52	3.42	
Postcentral gyrus (Areas 3b, 4p)	R	26	−34	58	4.17	333
Postcentral gyrus (Areas 3b, SPL)	R	20	−40	66	4.13	
Middle occipital gyrus	L	−20	−82	16	4.04	340
Superior occipital gyrus	L	−12	−84	22	3.74	
Superior temporal gyrus	L	−52	−38	22	4.00	196
Middle temporal gyrus	L	−60	−30	2	3.51	
Insula	L	−38	12	−12	3.84	126
Superior temporal gyrus	L	−44	0	−14	3.55	
Middle temporal gyrus	R	44	−10	−24	3.76	136
Middle temporal gyrus	R	54	−12	−24	3.72	
Insula	R	42	−6	−16	3.58	
Stimuli × Context: (IMPs: Positive > Negative) > (Ps: Positive > Negative)						
Middle Frontal gyrus	L	−36	12	36	4.50	299
[(Ps: Positive > Negative) > (IMPs: Positive > Negative)]_ATHLETHES > [(Ps: Positive > Negative) > (IMPs: Positive > Negative)]_NOVICES						
Superior temporal gyrus	L	−44	2	−14	4.10	169
Temporal pole	L	−54	10	−14	3.97	
Middle occipital gyrus	R	32	−94	10	3.90	137
Paracentral lobule	R	8	−26	62	3.79	127
Supplementary motor area	L	−4	−18	56	3.58	
Paracentral lobule	L	−2	−26	64	3.54	
Stimuli × Group: (Ps > IMPs)_ATHLETHES > (Ps > IMPs)_NOVICES						
Angular gyrus	L	−46	−70	44	5.41	923
Inferior parietal lobe	L	−52	−62	42	4.89	
Angular gyrus	R	46	−70	46	4.64	424
Inferior parietal lobe	R	58	−56	46	3.75	

Table 4 (continued)

Region	Side	MNI			Z	Cluster size
		x	y	z		Voxel
Superior medial gyrus	L	−8	30	48	4.62	2010
Superior frontal gyrus	L	−24	58	14	4.35	168
Middle cingulate cortex	R	2	−42	32	4.23	1086
Precuneus	L	−6	−64	42	4.04	
Inferior Frontal gyrus (pars triangularis)	L	−52	24	−8	4.02	157

For each region of activation, the coordinates in MNI space are given in reference to the maximally activated voxel within an area of activation, as indicated by the highest Z-value ($p < .05$, corrected for multiple comparisons at the cluster level, height threshold $p < .001$, uncorrected). L/R=left/right hemisphere

Table 5 – Brain regions in athletes showing significant increases of connectivity to the left M1 hand area and to the left premotor area respectively, as revealed by psycho–physiological interaction (PPI) analysis.

Side	Region	MNI coordinates			Z	Size (k_E)
		x	y	z		
ATHLETES						
Seed × Stimulus × Context: significant increases of connectivity to the left M1 hand area						
L	Linual gyrus	−8	−42	−2	4.30	40
R	Calcarine gyrus	18	−48	0	4.02	91
Seed × Stimulus × Context: significant increases of connectivity to the left premotor area						
L	Fusiform gyrus	−32	−64	−16	4.67	42
R	Middle Temporal gyrus	50	−62	8	4.10	38
NOVICES						
Seed × Stimulus × Context: significant increases of connectivity to the left M1 hand area						
–	–	–	–	–	–	–
Seed × Stimulus × Context: significant increases of connectivity to the left premotor area						
R	Fusiform gyrus	24	−78	2	4.35	40

For each region of activation, the coordinates in MNI space are given referring to the maximally activated voxel within an area of activation as indicated by the highest Z-value. All the activations are significant at $p < .05$ (corrected for multiple comparisons at the cluster level using a height threshold of $p < .001$, uncorrected). L/R=left/right hemisphere, Size (k_E)=number of voxels in a cluster.

$p = .08$, n.s) (see Fig. 2, Table 4 and Supplementary Fig. S2). The Group × Context interaction showed that there were no significant activations at the predefined statistical threshold.

Lastly, the three way interaction showed that for athletes (as compared to novices) the BOLD response in the right M1/foot area significantly decreased for positive IMPs vs. Ps ($p < .05$ for athletes and $p = .79$ for novices) and did not differed between negative Ps vs. IMPs ($p = .21$ for athletes and $p = .08$ for novices), and the BOLD response in the left M1/foot area significantly increased for negative Ps vs. IMPs ($p < .05$ for athletes and $p = .14$ for novices) and did not differed between positive Ps vs. IMPs ($p = .07$ for athletes and $p = .76$ for novices). In addition, the BOLD response in the left STG for athletes (as compared to novices) significantly decreased for positive IMPs vs. Ps ($p < .01$ for athletes and $p = .95$ for novices) and for negative Ps vs. IMPs ($p < .002$ for athletes and $p = .69$ for novices). Lastly, the BOLD response in the right middle occipital gyrus for athletes (as compared to novices) significantly

decreased for positive IMPs vs. Ps ($p < .01$ for athletes and $p = .41$ for novices) and did not differed between negative Ps vs. IMPs ($p = .141$ for athletes and $p = .488$ for novices) (see Fig. 2, Table 4 and Supplementary Fig. S3).

2.2.4. Psycho–physiological interactions (PPI)

Psycho–physiological interaction (PPI) analyses were performed with left M1 hand area and the left Pm cortex as seeds to assess the areas with increased connectivity with left M1 hand area and the left Pm cortex. PPI analysis aims at explaining the neural responses in one brain area in terms of the interaction between influences of another brain region and a cognitive process (here: implicit simulation of possible and impossible items in positive or negated context). In athletes, for Ps presented in positive context as compared to IMPs (controlled for negative), we found increased connectivity between the left M1 and the left lingual gyrus and the right calcarine gyrus (Table 5 and Fig. 4). The mean
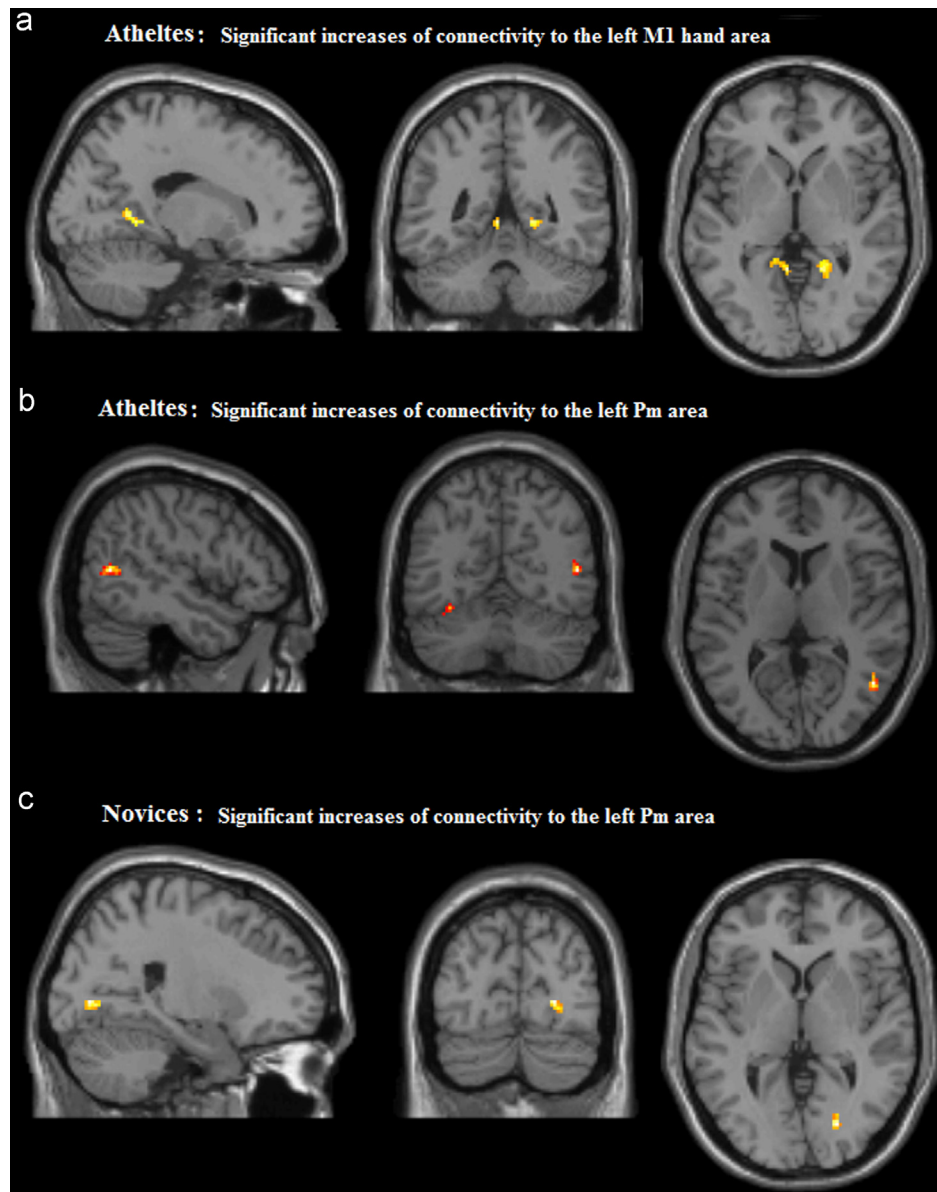
Fig. 4 – Psycho–physiological interactions (PPI) showing the brain regions whose functional connectivity with the left M1 and Pm cortex increased significantly during Ps items presented in positive context as compared to IMPs (controlled for negative) are displayed on sections of the single subject template brain provided by spm5.

parameter estimates extracted from these two areas were significantly modulated by the type of stimulus (left lingual gyrus stimulus, $F(1,9)=7.5$, $p<.05$; context $F(1,9)=.605$, $p>.05$, n.s.; stimulus $\times$ context $F(1,9)=1.75$, $p>.05$, n.s.; right calcarine gyrus: stimulus, $F(1,9)=8.174$, $p<.05$; context $F(1,9)=.004$, $p>.05$,n.s.; stimulus $\times$ context $F(1,9)=2.02$, $p>.05$, n.s.). In addition, we found increased connectivity between the left Pm area and the left fusiform gyrus and the right occipito-temporal cortex. The mean parameter estimates extracted from these two areas were significantly modulated by the type of stimulus $\times$ context interaction (left fusiform gyrus: stimulus, $F(1,9)=3.4$, $p>.05$, n.s.; context $F(1,9)=.08$, $p>.05$, n.s.; stimulus $\times$ context $F(1,9)=20.7$, $p<.005$; right middle temporal gyrus: stimulus, $F(1,9)=2.2$, $p>.05$, n.s.; context $F(1,9)=1.29$,

$p>.05$, n.s.; stimulus $\times$ context $F(1,9)=5.69$, $p<.05$). For both regions parameter estimates significantly increased for IMPs_negative compared with Ps_positive ($p<.01$ and $p<.05$ respectively). In contrast, the difference between Ps_negative and IMPs_negative was not significant ($p>.05$, n.s). No significant changes in the functional coupling between the left M1 or the left premotor cortex and other brain areas were observed during the inverse interaction. In novices, for Ps items presented in the positive context as compared to IMPs (controlled for negative) there were no significant changes in the functional coupling between the left M1 and other brain areas, whereas there was an increased connectivity between the left premotor area and the right fusiform gyrus. No significant modulation was found for the mean parameter

estimates extracted from the right fusiform gyrus (stimulus, $F_{(1,9)} = 2.34$, $p > .05$, n.s.; context $F_{(1,9)} = .103$, $p > .05$, n.s.; stimulus × context $F_{(1,9)} = .63$, $p > .05$). [4]

3. Discussion

Exposure to commands and contexts (e.g., positive "Do …" or a negative "Don't …") can be used as a measure of *implicit* motor simulation *context*. Positive and negative action-related imperatives cause a modulation of the activation in left fronto-parietal regions (Tettamanti et al., 2008) as well as in the hand region of the primary motor and premotor cortices (Tomasino et al., 2010b) and a modulation of participants' RTs, namely a positive faster than negative context (Tomasino et al., 2010b). This effect was found also in the present study: experts were significantly faster for positive than negative only when they processed possible actions, while for novices the context was significant for both possible and impossible actions. The novices' pattern of performance suggests that they tried to simulate all actions, whether they were possible and impossible. All sentences were semantically correct and included a common familiar verb, which had a motor reference (e.g., in Jump roll, the verb "jump" might trigger the simulation of the corresponding "jumping" action). Accordingly, novices were not fully able to distinguish possible from impossible volleyball actions, and they tended to attribute motor feasibility to non feasible actions, thus their implicit strategy could have been trying to perform simulation every time they encountered a description of action, independently of its motor feasibility. Novices showed a nonspecific effect of context for all types of stimuli, which is not linked to the degree of motor knowledge.

3.1. Investigating the effects of action feasibility and contextual factors

Investigating positive/negative imperatives and possible/impossible linguistic cues has its ecological validity. For example, while hearing imperatives, which are commonly used as commands (e.g., "Don't move/shoot/hit!"), we refrain ourselves from performing the corresponding action. An imperative such as "Don't move!" shouted to a person who is crossing a road could, for instance, be of vital importance if suddenly a car is darting at high speed. Another example is the overuse of imperatives with kids. Thus, while processing a negative imperative, for instance, "Don't grasp" an action needs to be withheld. By contrast, ecological validity is null for possible/impossible linguistic cues. Including possible and impossible movement descriptions is nonetheless essential for testing theories about how our cognitive system and about how our brain works. Obviously, we never perform, or

listen to the description of, or observe, impossible actions such as walking upside down. However, the key question is whether it is possible to imagine movements that could never be performed, e.g., (Costantini et al., 2005; Romani et al., 2005; Stevens et al., 2000).

3.2. Interaction between group, action feasibility and context in M1 and the Pm cortex

The conjunction analysis (Friston et al., 1999) evidenced which regions involved in processing action sentences overlap with those involved in motor processing. The activation of the left and right M1 and Pm cortex was further addressed by performing a ROI analysis. We demonstrated that the BOLD signal in the M1 and Pm cortex was differentially modulated by the context in which stimuli were presented (i.e., positive or negative commands) and type of stimuli (i.e., possible or impossible actions), depending on the group, as revealed by the significant groups × stimuli × context interaction. For athletes, as compared to novices, the activity of left M1 hand area and of the left Pm cortex significantly decreased when participants processed impossible action sentences which were presented as positive commands ("Do…[an impossible action]"). This result suggests that athletes differentiated between possible and impossible actions when the items were presented as positive commands and the BOLD signal in the left M1 hand area and premotor cortex changes accordingly The positive context "do" has been shown to trigger motor preparation or imaginary processes (Tettamanti et al., 2008, 2010b), compatible with the imperative form of a verb serving as an instruction (e.g., "sit!") (Postle et al., 2008) or motor planning (Boulenger et al., 2006) and with significantly faster RTs for positive than negative Ps (as compared to impossible items). Accordingly, for novices, when the positive context is associated to an impossible action, the activation of the left M1 and Pm significantly decreased.

Second, we found that activity for possible actions did not differed from negative possible and even from impossible actions.[5] In a previous study investigating the effect of stimulus and context on M1 and Pm activation (Tomasino et al., 2010b), we found that, the BOLD signal in M1 during processing pseudo-words reached similar levels as action-related phrases. However, pseudo-words related activations in M1 and Pm cortex were not modulated by linguistic context (in contrast to action verbs for which the motor

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[4]For athletes, second order interactions were not significant. For novices, the seed activity × stimulus interaction revealed an increased connectivity between the left M1 area and the right calcarine/linual gyrus, the left middle occipital gyrus, and the right middle temporal gyrus and between the left premotor area and the right caudate nucleus and the middle cingulate cortex for Ps items as compared to IMPs. The seed activity × context interaction was not significant.

[5]We ruled out that the possibility that the possible/impossible distinction can be processed more in terms of one action vs. a sequence of two actions instead of possible vs. impossible specifying that although there were few items (see appendix in Tomasino et al. (2012)) that might have been processed as sequence of two actions, these were present both in the positive and in the negative conditions. Therefore, the sequence of actions was the same independent of whether the context was positive or negative. In the interaction term (stimuli × context), such 'confounding factor' is controlled for since the interaction term constitutes the difference of the differences ([possible_positive-possible_negative] > [impossible_positive-impossible_negative]). Thus, any differential modulation found for the interaction term cannot simply be explained in terms of differences in simulating two actions in sequence.

system activations are systematically modulated). Similarly, in the present study, although negative items and possible positive ones triggered a comparable M1 signal, processing the former was not really modulated by linguistic context. Note that unspecific activations of motor areas have been observed by (Postle et al., 2008) for imageable concrete words (unrelated to actions) and to "non-words" with regular phonology. In previous studies (Tomasino et al., 2010b), we argued that it is not the activation of motor areas per se that allows to differentiate the effects of action verbs from those of pseudo-verbs, but rather the *systematic modulation* of that motor system activity as expressed by the significant interaction of the type of stimulus (i.e., possible vs. impossible) and context (i.e., positive vs. negated). In our study, for negated sentences, motor activity was not sensitive to motor feasibility. To date, no fMRI investigation has demonstrated such a distinction for action-related sentences; in fact, previous studies on expert-novice differences in action word processing investigated only actions that could all be performed (Beilock et al., 2008).

Finally, we found that, although significantly modulated by context and action feasibility, the activity in the M1 and Pm tended to be at, or below, baseline in most conditions (negative betas). That activity in the M1 cortex can be suppressed during tasks tapping motor imagery is not surprising (Solodkin et al., 2004). It has been shown that inputs to M1 are suppressed during kinesthetic imagery, suggesting the existence of a physiological mechanism whereby the motor system prevents overt movements (Solodkin et al., 2004). Other authors argued that the lack of activation in M1 during motor imagery in their task was caused by the suppression exerted by the SMA emphasizing the role of this region in suppressing movements that are represented in the motor system but not to be performed (Kasess et al., 2008). However, we acknowledge that this view does not apply well to the premotor regions since their involvement in motor planning does not necessarily require inhibition. In addition, while in prior work on expert simulation of action sentences, a deactivation of the sensorimotor cortex was found (see in Beilock et al.'s (2008) study Fig. 4b), activity above baseline was found in the premotor area (at least for experts). First, this difference can be accounted for by the fact our and their study used different stimuli. In Beilock et al.'s (2008) study the sentences describing ice hockey-related actions were all motorically possible and, as such, they implicitly activated the corresponding sensorimotor representations. In the present study the premotor BOLD signal may have thus been influenced by using sentences describing actions that can be physically experienced, those that cannot be performed, even if they are semantically and syntactically correct, and negated ones. Second, the pattern of negative betas we found calls into question whether the premotor regions were involved in language processing at all. Given that the sentences were written and participants were asked to read them in order to perform action familiarity judgments, linguistic comprehension is mandatory to carry out the task. Even if subjects have perceived the task rather as a sensibility/familiarity judgment task (than a linguistic task), this might have triggered even deeper linguistic processing. Our finding thus challenges the view that any linguistic

processing of action-related words (which might be even deeper when our subjects perceived the current experimental task as a sensibility judgment) should result in an activity *increase* in the motor areas independent of the linguistic context (Pulvermuller, 2005) To sum up, the patterns of increased and decreased activations in motor related regions described above could be an expression of a non-automatic, flexible and context dependent modulation of the motor areas activation during processing of action-related sentences (van Dam et al., 2010, 2012b). Accordingly, our study included not only the context factor (positive and negative imperatives) but also the stimuli factor (possible, impossible), whereas previous studies included affirmatives and negatives and sentences describing possible actions only. Thus, our study indicates that sensorimotor activation is not automatically triggered by the type of stimulus and it is not necessary but, rather, accessory to linguistic processing (Mahon and Caramazza, 2005, 2008; Papeo et al., 2009; Postle et al., 2013; Raposo et al., 2009; Tomasino et al., 2010a, 2010b; Willems et al., 2010b). Several results indicate that the involvement of sensorimotor areas depends on the context (van Dam et al., 2010, 2012a, 2012b) in which conceptual features are retrieved. Flexibility is characterized by the relative presence or absence of activation in motor and perceptual brain areas. In addition, the involvement of sensorimotor areas may be subject to a top-down modulation which explicitly or automatically selects the type of strategy adopted while processing language (Tomasino and Rumiati, 2013).

The modulation of imperatives and stimuli was found for the M1/hand area only for the left hemisphere. This asymmetrical (left) brain modulations in motor areas as a function of motor feasibility might be related to a specialization of the left hemisphere for higher motor control of both left and right limbs (even in the case of mental rotation tasks (Tomasino et al., 2005)). This functional left–right asymmetry within M1 is consistent with previous neuroimaging results, e.g., (Kosslyn et al., 1998; Wraga et al., 2003), in which the right M1 hand area was not found activated during MR of hands, and with an fMRI study by Porro et al. (1996), in which an activation of the left and right M1 was found while subjects performed kinesthetic motor imagery involving the contralateral hand, with a greater activation in the left MI during left-hand movement and imagery. Consistently, ideomotor and ideational apraxia affect both limbs and it is typically caused by lesions of the left hemisphere (De Renzi et al., 1980, 1982). Similarly, studies on action words processing showed that right-handers preferentially activating the left premotor cortex during lexical decisions on manual-action verbs, while the right premotor areas were preferentially activated in left-handers (Willems et al., 2010a).

3.3. A different modulation for novices

The novices' pattern of performance showed a lack of significant modulation in the left M1 and the left Pm, which by contrast was found for athletes, and a significant modulation in the right Pm and M1, albeit in a different direction. Their lack of significant modulation in the left M1 and the left Pm suggest that as they did not distinguished between

possible and impossible actions no modulation of sensorimotor activity occurred. The inspection of novices' behavioral performance showed that they processed possible and impossible items in a similar fashion, suggesting that novices might have tried to simulate all actions, whether they were possible or impossible. Motorically-impossible actions are sensible sentences that do not correspond to any volleyball-specific motor act and, therefore, do not have a proper motor image. However given that all included a common familiar verb which has a motor reference it is likely that it might trigger the motor simulation of a part of the action. According to the predictive account of the motor system (Schubotz, 2007), movements that can and cannot be performed trigger qualitatively similar responses in the sensorimotor system, with quantitative differences evidenced as stronger activity for actions that can be performed. It is conceivable that, in our study, possible and impossible actions might have been processed in a quantitatively different way by novices and by athletes. It is also possible that no differential modulation of motor areas was found because only novices do not simulate actions kinesthetically. Previous studies have demonstrated that the visual experience of watching basketball actions modulates corticospinal excitability during action observation, even though only basketball players showed fine-tuned modulation of the motor evoked potentials (MEPs) related to prediction of the outcome of basket shots (Aglioti et al., 2008). This result is in line with the view whereby proper reproducibility is not a prerequisite for our ability to simulate. While the premotor areas code human actions regardless of whether they are biologically possible or impossible, sensorimotor parietal regions may be important in coding the plausibility of actions (Costantini et al., 2005). With respect to the further dissociation related to motor experience we found for novices (as compared to athletes) in the right Pm, activity decreased for stimuli presented as positive context for possible compared with impossible actions. Stimulation of the right vPMc in healthy participants selectively impairs RTs for discrimination of observing possible actions while leaving intact the discrimination of biomechanically impossible actions and of biomechanical plausibility (Candidi et al., 2008). Accordingly, we found a decrease of activation in this area for sentences describing possible actions. This pattern might indicate that novices' right Pm cortex is involved in processing feasibility of volleyball related actions. This view however is somehow at variance with a fMRI study in which the right premotor cortex was preferentially activated during lexical decisions of action words related to hand movements (compared to nonmanual action verbs) for left handed participants (Willems et al., 2010a), since it would suggest that novices would have preferentially used their left hand to implicitly simulating possible actions. Moreover, stimulation of the hand area in the left premotor cortex caused faster responses to manual-action verbs (but not to nonmanual-action verbs) than after stimulation of the hand area in right premotor cortex suggesting thus a preferential involvement of the left Pm area (Willems et al., 2011). Indeed, in a review of fMRI and PET studies it has been argued that the right PM is more frequently engaged by spatial tasks, whereas the left PM shows a preference for nonspatial tasks (Schubotz and von Cramon, 2003). A right PM activation was reported for spatial

working memory (Haxby et al., 1994; Jonides et al., 1993), spatial exploration (Gitelman et al., 1996), spatial body-centered judgment (Galati et al., 2001), and spatial attention (Gitelman et al., 1999). As a last point, selectively for novices, we found an increased activation in the right M1 for stimuli presented as positive context (i.e., "Do…") for impossible compared with possible actions. This pattern was reverse with respect to the pattern we found in athletes' left M1 cortex, suggesting that the right M1 cortex might detect incompatible motor situations like those presented as positive imperatives ("Do…") accompanying an impossible action. In a study in which a functional near-infrared imaging (fNIRS) was performed to examine whether a conflict at the level of the motor cortex could be detected in the incongruent relative to the congruent condition of a Stroop task (Szucs et al., 2012) authors found greater motor cortex activation in the hemisphere ipsilateral (the right one) to the response hand in the incongruent than in the congruent condition. Increased primary motor cortex excitability as a function of motor imagery of biomechanically impossible vs. possible movements was found in a TMS study (Bufalari et al., 2010). In that study authors argued that the plausibility of a movement is computed in regions upstream the primary motor cortex, and that motor imagery is a higher-order process not fully constrained by the rules that govern motor execution (Bufalari et al., 2010). By contrast our data show that it is not the increase of motor areas activation per se that allows to distinguish the effects of impossible from those of possible imperatives, but rather the significant interaction of the type of stimulus (i.e., impossible vs. possible) and context (i.e., positive vs. negated). These results suggest that for novices, while in the left M1 and left Pm no significant modulation was found, the fact that in the right M1 there was a significant modulation of the beta values suggest that the right M1 is involved in processing the incompatible or impossible motor situations.

3.4. Psycho–physiological interactions (PPI) to assess areas with increased connectivity with left M1 hand area and the left Pm cortex

Functional connectivity analyses that we performed using psycho–physiological interactions (PPI) further revealed that the interaction of left M1 hand area with bilateral visual primary cortices selectively increased during the processing of positive (vs. negated) possible actions as compared with impossible actions. So did the interaction of the left premotor cortex hand representation with the left fusiform gyrus and the right occipito-temporal cortex. For novices PPI revealed an interaction of the left premotor cortex hand representation with the right fusiform gyrus. Primary visual areas are known to activate during visual mental imagery (Kosslyn et al., 2001), and the occipito-temporal cortex to be implicated not only in the visual processing of static body representations (Astafiev et al., 2004), but also in many other body-part related processes including motor imagery (Astafiev et al., 2004), goal-directed (Takahashi et al., 2008) movements (even when the limb is not visible (Astafiev et al., 2004)), as well as reaching to kinesthetically-defined targets (Darling et al., 2007). Interestingly the parameter estimates of the occipito-temporal cortex were significantly modulated by the type of

stimulus × context interaction. In the novices group, for Ps items presented in positive context as compared to IMPs (controlled for Neg) there were no significant changes in the functional coupling between the left M1 and other brain areas, whereas there was an increased connectivity between the left premotor area and the right fusiform gyrus. No significant modulation was found for the mean parameter estimates extracted from the right fusiform gyrus. The current PPI findings suggest that during implicit action simulation of positive (vs. negated) possible (vs. impossible) actions, the functional connectivity of left M1 and left Pm cortices along with the primary visual cortex and the occipito-temporal cortex are strengthened. Our PPI results strengthen the view that the role of motor areas during implicit imagery of the content of sentences describing actions could reflect the interaction between motor and visual imagery.

3.5. Main effect of action feasibility, of context and their interactions

Lastly we discuss, independent of the group factor, the neural network associated with the stimuli as well as those related to context, as revealed by the whole brain analysis. Irrespective of context, Ps trials (relative to IMPs) differentially activated the superior and inferior parietal lobe, mainly reflecting action observation (Caspers et al., 2010) and action words processing (Binder et al., 2009; Jirak et al., 2010). Interestingly, the parietal region distinguished whether described movements could actually be imagined or not. Bilaterally, the activation in the precentral gyrus (Area 6) is in keeping with action observation (Caspers et al., 2010) and with the literature on action word processing (Jirak et al., 2010). At variance with a previous study (Costantini et al., 2005), our results confirm that the premotor area was active only during the processing of actions that are part of the observer's motor repertoire (Stevens et al., 2000) whether actions are observed (Buccino et al., 2004) or linguistically processed. The bilateral activity in the middle and the inferior temporal gyri, confirms the role of this area in organizing concepts (Ruschemeyer et al., 2007) or categorization (Binder et al., 2009; Jirak et al., 2010). Relatively greater activation in the left pars orbitalis of the IFG is consistent with other fMRI studies on semantic processing (Bookheimer, 2002; Dapretto and Bookheimer, 1999) and may thus play an important role in possible action phrases comprehension. Lastly, activity in the superior and middle frontal gyrus and in the anterior cingulated cortex might reflect willed generation of virtual motor commands and analysis of virtual sensory signals (Hanakawa et al., 2008), which might implicitly be triggered by descriptions of possible as compared to impossible actions, or it might reflect cognitive demands of the task.

Irrespective of stimuli, trials presented as negative contexts (relative to positive), differentially activated the left precentral gyrus; this increase in activation is consistent with previous studies (Bahlmann et al., 2011; Carpenter et al., 1999; Christensen, 2011; Hasegawa et al., 2002), but in contrast with others (Tettamanti et al., 2008) in which the left BA 6 was found to be enhanced by affirmative (or, as they argue, negative showed decreased activation in BA 6 relative to affirmative), possibly reflecting increased syntactic and

semantic hierarchical structure processing (Christensen, 2011). Activity in the left inferior frontal gyrus (Area 44) is consistent with the role of this area in tasks involving computation of various types of syntactic complexity (Christensen, 2008; Grodzinsky, 2012; Moro et al., 2001; Stromswold et al., 1996) and with a previous study on negatives (Bahlmann et al., 2011). It was argued (Bahlmann et al., 2011) that it is surprising how all previous studies (Carpenter et al., 1999; Christensen, 2011; Hasegawa et al., 2002; Tettamanti et al., 2008) failed to report increased activity in Broca's area during comprehension of sentences presented as negations, in contrast with a frequently reported activation of this area for more demanding semantic or syntactic processing (Fiebach et al., 2005; Rodd et al., 2010). A possible reason of this discrepancy is that the tasks used in these studies were not sensitive enough (Bahlmann et al., 2011). Activity in the left middle temporal gyrus is consistent with previous studies (Carpenter et al., 1999; Hasegawa et al., 2002) possibly reflecting the added computational demand associated with understanding such sentences (Carpenter et al., 1999; Hasegawa et al., 2002; Just et al., 1996), while the bilateral activity in the supplementary motor area (SMA) could reflect the inhibitory suppression of movements that are represented in the motor system but are not performed (Kasess et al., 2008). Effective connectivity from SMA to M1 is enhanced during motor execution but is strongly suppressed during kinesthetic motor imagery (Solodkin et al., 2004). Of interest here is that the SMA has been found before to be activated during passive observation of movements (vs. active execution) that is when execution had to be suppressed (Dinomais et al., 2009), consistenlty with the view that SMA is involved in a task requiring proactive inhibition (Jaffard et al., 2008; Wardak, 2011).

The group × Stimuli interaction showed that many of the activation clusters found in the main effect of stimuli, i.e., for Ps relative to IMPs, was driven by the athletes group. In particular, greater activations in the premotor cortex and in the parietal lobe have been reported during action observation in athletes (Cross et al., 2006; Calvo-Merino et al., 2005). The experts also demonstrated increased activation in the prefrontal cortex reflecting higher-order aspects of the organization of behavior (Petrides, 1994), which may be relevant to action planning during motor imagery (Wei and Luo, 2010).

Lastly, the three-way interaction showed that activation in the M1 and Pm feet area was modulated by motor experience, stimuli and context. In the present study the sentences described actions that involve movements of the whole body and actions for which hands position/movement is determinant as much as the rest of the body, especially the legs. When investigating the signal changes in the feet representation, we found that the modulation of imperatives and stimuli was found bilaterally, while for the M1/hand area only for the left hemisphere. This asymmetrical (left) brain modulations in motor areas as a function of motor feasibility might be related to a specialization of the left hemisphere for higher motor control of both left and right limbs (even in the case of mental rotation tasks (Tomasino et al., 2005)). This functional left–right asymmetry within M1 is consistent with neuroimaging results, e.g., (Kosslyn et al., 1998; Wraga et al., 2003), in which the right M1 hand area was not found activated during MR of hands,

and with an fMRI study by Porro et al. (1996), in which an activation of the left and right M1 was found while subjects performed kinesthetic motor imagery involving the contralateral hand, with a greater activation in the left MI during left-hand movement and imagery. Consistently, ideomotor and ideational apraxia affect both limbs and it is typically caused by lesions of the left hemisphere (De Renzi et al., 1980, 1982). Similarly, studies on how we process action verbs showed that comparing premotor activity correlated with action verb understanding in right- and left-handers, with the former preferentially activating the left premotor cortex during lexical decisions on manual-action verbs, and the left-handers the right premotor areas (Willems et al., 2010a).

4. Conclusion

To conclude, our data suggest that implicit motor (and visual) simulation impacts the motor system activity depending on (i) the domain-relevant expertise, (ii) the feasibility of the actions and (iii) context. Our data show that it is not the activation of motor areas per se that distinguishes the effects of action verbs from those of impossible imperatives, but rather the significant interaction of the type of stimulus (i.e., possible vs. impossible) and context (i.e., positive vs. negated). Our view is consistent with the notion of flexibility whereby the degree to which a modality specific region contributes to a representation depends on the context (Hoenig et al., 2008; van Dam et al., 2010, 2012b) in which features are retrieved. Flexibility is characterized by the relative presence or absence of activation in motor and perceptual brain areas. The key idea is that words are associated with more than one experiential feature; accordingly word processing could be modified by encouraging participants to focus on one propriety vs. another (Tomasino and Rumiati, 2013).

We also add that this is similar to how the contextual effect of imperatives modulates sensorimotor activation, also supported by the increased functional connectivity between motor areas and occipito-temporal cortex, which may reflect the neural processes underlying the interaction between motor and visual imagery.

5. Experimental procedures

5.1. Participants

A total of 20 females (mean age±SD: 26.3±3.8 years) right-handed (mean±SD: 92.5±9.9, Edinburgh Inventory test) healthy subjects took part in the study. Half of the participants were expert volleyball players and the other half were novices (mean ages 25±4.07 and 27.8±3.5 respectively, $t(10)=-1.606$, $p=.139$, n.s.).[6] Athletes were recruited from the Regional Professional League. They trained three times

per week for 2 h each and had been playing volleyball on average for 15±2.1 years. Novices had no playing or watching experience and reported not having ever played a volleyball match. All subjects were native speakers of Italian with comparable levels of education, and all were monolinguals. All participants had normal or corrected-to-normal vision and reported no history of neurological illness, psychiatric disease, or drug abuse, and they all gave informed consent to participate in the study. The study was approved by the local ethics committee. The study has been carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans.

5.2. Stimuli

Stimuli ($N=120$) used in a previous behavioral study [for details on length, familiarity, naturalness, and uniqueness to volleyball of the selected sentences and for the action familiarity judgment task see Tomasino et al. (2012))] included 60 Italian sentences describing possible technical volleyball-specific motor acts, e.g., "Cut shot!", [i.e., possible, hereafter Ps], and 60 motor acts that cannot be performed and were meaningless both in the volleyball context and in the non sport specific domain, e.g., "Bagher run-up!" [i.e., impossible, hereafter IMPs]. Stimuli were presented in two contexts, half ($N=30$ Ps and 30 IMPs) in a negative one (e.g., "Don't do a reverse!"), and half ($N=30$ Ps and 30 IMPs) in a positive one (e.g., "Cut shot!"). Both positive and negative contexts included the infinitive form of the verb preceded by "Non" or "Devi" (i.e., "Don't" or "Do").

5.3. Experimental paradigm and task

The categorization task required participants to silently read the stimuli and make binary decisions as to whether an action described in a given sentence was technically feasible (a compatible relation between the used verb and its feasibility within the volleyball domain) or not (no relation between action description and its feasibility). To increase signal variability, pseudo-stimuli ($N=60$, 50% presented as positives and 50% as negatives) were generated by substituting or exchanging letters of the corresponding words, and were in agreement with the phonological and orthographic rules of Italian. Pseudo-stimuli required "no" as the correct response. If a participant answered that "bratupire una palla …", i.e., "bratupire [PW] a ball…" was feasible in the volleyball context this was scored as an error. All experimental trials lasted 3.5 s, in which a fixation cross (300 ms) was followed by stimulus presentation and then a variable inter-trial interval (range 1750–3250 ms), with incremental steps of 500 ms. In addition, 48 null events (i.e., blank screens), perceived as a prolongation of the inter-trial period, were randomly interspersed among the trials to increase the power of estimating the BOLD response.

Three pseudo-randomized stimulus sequences were alternated across participants, so that one participant would never hear "do bagher run up" and "don't bagher run up". To avoid any potential priming effect, we did not present the same verb in both the positive and negative contexts

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[6]In Beilock et al.'s (2008) study 12 experts, 8 fans and 9 novices were included; in Aglioti et al.'s (2008) paper 10 elite players, 10 expert watchers and ten novices took part in the study.

(Tomasino et al., 2010b) and the sequence of positive and negative imperatives was counterbalanced across participants. In addition, we included 29 randomly presented recognition trials, in which subjects were asked whether the last phrase started with "Devi" (i.e., "Do", in 15 of the recognition trials) or "Non" (i.e., "Don't", in 14 recognition trials). The rationale for these recognition trials was to ensure that subjects paid attention to the whole stimulus phrase, especially the "Devi" (i.e., "Dos") and "Non" (i.e., "Don'ts"), throughout the experiment (Tomasino et al., 2010b). Presentation of the stimuli and their synchronization with the MR scanner was realized by the software Presentation® (version 9.9, Neurobehavioral Systems Inc., CA, USA). Stimuli were projected through a VisuaStim Goggles system (Resonance Technology). Subjects responded by pressing one of two keys of an MRI-compatible response device (Lumitouch, Lightwave Medical Industries, Coldswitch Technologies, Richmond, CA) with the index and the middle fingers indicating yes/no answers. The hand of response was counterbalanced between subjects. Half of the subjects responded by using the right hand and the remaining subjects performed the reversed order. In this way, the level of activation in M1 related to motor responses per se should be controlled for. Prior to the experiment, subjects practiced the task outside the scanner ($N=20$ trials).

5.4. Statistical analyses of behavioral data

SPSS for Windows (version 12.0) was used for performing a repeated measure ANOVA with a between-subject factor "group" (athletes and novices) and within-subject factors type of "stimulus" (IMPs, Ps and PWs) and "context" (positive and negative) on the subjects' error rates and reaction time (RTs) data. All post hoc comparisons between single factors were carried out using LSD Fisher's test ($\alpha \leq .05$).

5.5. fMRI data acquisition

A 3-T Philips Achieva whole-body scanner was used to acquire T1-weighted anatomical images and functional images using a SENSE-Head-8 channel head coil and a custom-built head restrainer to minimize head movements. Functional images were obtained using a T2*-weighted echo-planar image (EPI) sequence of the whole brain. EPI volumes for the main experiment ($N=840$) contained 27 transverse axial slices (repetition time, TR=1500 ms; echo time, TE=35 ms, field of view, FOV=23 cm, acquisition matrix: 64×64, slice thickness: 4 mm with no gaps, 90° flip angle, voxel size: $3.59 \times 3.59 \times 4$ mm^3) and were preceded by 7 dummy images that allowed the MR scanner to reach a steady state. EPI volumes for the functional localizer ($N=265$ images) involving bilateral hand clenching movements, preceded by 5 dummy images, were acquired with the same sequence characteristics as in the main experiment except that each volume contained 21 transversal slices acquired with a TR of 1600 s. Both experiments were included in one single fMRI session. Each subject was scanned first for the main experiment and then again for the localizer task. After functional neuroimaging, high-resolution anatomical images were acquired using a T1-weighted 3-D magnetization-prepared, rapid acquisition gradient fast filed echo (T1W 3D TFE SENSE) pulse sequence (TR=8.2 ms, TE=3.76 ms, FOV=24 cm, 190 transverse axial slices of 1 mm thickness, 8° flip angle, voxel size: $1 \times 1 \times 1$ mm^3) lasting 8.8 min.

5.6. fMRI data processing and whole brain analysis

fMRI data pre-processing and statistical analysis were performed on UNIX workstations (Ubuntu 8.04 LTS, i386, http://www.ubuntu.com/) using MATLAB r2007b (The Mathworks Inc., Natick, MA/USA) and SPM5 (Statistical Parametric Mapping software, SPM; Wellcome Department of Imaging Neuroscience, London, UK). Dummy images were discharged before further image processing. Preprocessing included spatial realignment of the images to the reference volume of the time series, segmentation producing the parameter file used for normalization of functional data to a standard EPI template of the Montreal Neurological Institute template provided by SPM5, re-sampling to a voxel size of $2 \times 2 \times 2$ mm^3, and spatial smoothing with a 6-mm FWHM Gaussian kernel to meet the statistical requirements of the General Linear Model and to compensate for residual macro-anatomical variations across subjects. To delineate the network involved in the main action familiarity judgments task per se, we performed a whole brain random effects analysis. Low-frequency signal drifts were filtered using a cut-off period of 128 s. To correct for motion artifacts, subject-specific realignment parameters were modeled as covariates of no interest. The presentation of stimuli as positive and negative imperatives (Ps_positive, Ps_negative, IMPs_positive, IMPs_negative) were modeled as the regressors of main interest. Separate regressors modeled the presentation of the pseudoverbs (PWs_positive, PWs_negative). To ensure that any reported difference in neural activity between the conditions was not due to stimulus length differences per se, an additional regressor coding for word lengths was included in the statistical parametric mapping (SPM) analysis (Tomasino et al., 2010b). At the single subject level, specific effects were assessed by applying appropriate linear contrasts to the parameter estimates of the experimental conditions resulting in t-statistics for each voxel. For the second-level random effects analyses, contrast images obtained from individual participants were divided into two groups (athletes and novices) and entered into a flexible factorial analysis as implemented in SPM5 with subjects and conditions as factors. For subjects in Group 1, the scans as belonging to condition 1–4 were specified, and for subjects in Group 2 as belonging to conditions 5–9. In the ensuing design (with 8 cells corresponding to the four conditions in the two groups) all main effects and interactions were tested. We used a threshold of $p < .05$, corrected for multiple comparisons at the cluster level (using family-wise error (FWE)), with a height threshold at the voxel level of $p < .001$, uncorrected. At the second level we performed a conjunction null analysis (Friston et al., 1999), that showeding the common activated network for both tasks ([task > baseline] ∩ [motor localizer > baseline]) using a threshold of $p < .05$, FEW corrected at the voxel level.

5.7.   Hand area localizer and region of interest (ROI) analysis

Following our hypothesis about the role of the left M1 and the Pm cortex in the interaction between group and context in processing possible and impossible action sentences, we performed a ROI-analysis on M1. To determine the individual anatomically-constrained functional ROIs comprising the hand representations within the primary motor cortex (M1) and the premotor cortex (Pm) of both hemispheres in all subjects, we used the same functional localizer approach used in a previous study (Tomasino et al., 2010b). The localizer always followed the main experiment to avoid biasing the subjects' attention toward the hand action-related aspect of the stimuli. The localizer scan details and fMRI analysis were described elsewhere (Tomasino et al., 2010b). Using Marsbar written by Matthew Brett (http://www.marsbar.sourceforge.net/), ROIs comprising the hand repre sentations within the left and right hemispheres were defined for each subject of the athletes and novices group as the set of all contiguous voxels that were significantly more active for performing clenching hand movements vs. baseline at a threshold of $p < .05$, FWE corrected. Thereafter, we considered only these voxels of the functional ROIs that were located within the cytoarchitectonicallydefined MPMs of the primary motor cortex (Brodmann area 4) or the premotor cortex (Brodmann area 6) provided by the SPM Anatomy toolbox (http://www.fil.ion.ucl.ac.uk/spm/ext/) to derive the anatomically-constrained functional ROIs of the primary motor or the premotor cortex. This procedure was performed for both hemispheres separately resulting in four anatomically-constrained functional ROIs of the left and right primary motor cortex and the left and right premotor cortex. This combined anatomical and functional approach was necessary because the (anatomical) cytoarchitectonically defined probability maps do not specify the (functional) hand representations within the motor areas. Using functionally and anatomically defined ROIs of premotor and primary motor cortex ensured that the reported data are functionally relevant (only those voxels were included which were sig nificantly more active for hand movements during the locali zer task) and anatomically specific (only those voxels were included that were located with the MPM of either the premotor cortex or the primary motor cortex). This procedure constitutes an important methodological advance in compar ison with previous studies (Postle et al., 2008; Tomasino et al., 2010b). Subsequently, the beta values associated with each experimental condition (i.e., IMPs_positive, IMPs_negative, Ps_positive, and Ps_negative) were extracted from all voxels within the individually defined anatomically-constrained functional ROIs. Then, these beta values were entered into an ANOVA with group (athletes, novices) as between-factor and stimulus (IMPs vs. Ps) and context (positive vs. negative) as within-subjects factors.

5.8.   Psycho–physiological interactions (PPIs)

Psycho–physiological interactions (PPIs) (Friston et al., 1997) were calculated for the motor areas which revealed a high selectivity of responses to the modulation exerted by context and type of stimuli, i.e., a decreased activity when the stimuli are presented as positive context (i.e., "Do…") for impossible compared with possible actions, tuned to people's motor repertoire (see Section 2 above). Based on the individual coordinates for left M1 hand area and the left premotor area, the closest individual local maximum was determined at the single-subject level for the same interaction contrast ([IMPs_positive > IMPs_negative] > [Ps_positive > Ps_negative]) computed following (Friston et al., 1997). A sphere of 6 mm radius was centered at this individual local maximum of each single subject. Note that all participants could be included into the PPI-analyses as all of them exhibited significant individual local maxima close to the activation clusters. The mean-corrected blood oxygen level-dependent signal time course from this sphere was then used as the physiological factor. The psychological factor was a vector coding for the stimulus by context interaction term (1 for [IMPs_positive, −1 for IMPs_negative, −1 for Ps_positive and 1 for Ps_negative]) convolved with the hemodynamic response function. The PPI was then computed as the element-by-element product of the physiological and the psychological vectors. For each subject, a new statistical model containing the PPI and the psychological and the physiological vectors as regressors was created. Subjects' specific contrast images were then entered into random-effects group analysis. The statistical threshold was again set at $p < .05$, corrected for multiple comparisons at the cluster level with a height threshold at the voxel level of $p < .001$, uncorrected.

Acknowledgments

Appendix A.   Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.brainres.2013.09.048.

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