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Hands on the future: facilitation of cortico-spinal hand-representation when reading the future tense of hand-related action verbs

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Abstract

Reading action-related verbs brings about sensorimotor neural activity, suggesting that the linguistic representation of actions impinges upon neural structures largely overlapping with those involved in actual action execution. While studies of direct action observation indicate that motor mirroring is inherently anticipatory, no information is currently available on whether deriving action-related knowledge from language also takes into account the temporal deployment of actions. Using transcranial magnetic stimulation, here we sought to determine whether reading action verbs conjugated in the future induced higher cortico-spinal activity with respect to when the same verbs were conjugated in the past tense. We recorded motor-evoked potentials (MEPs) from relaxed hand and leg muscles of healthy subjects who were reading silently hand- or leg-related action, sensorial (non-somatic) and abstract verbs conjugated either in future or past tense. The amplitude of MEPs recorded from the hand was higher during reading hand-related action verbs conjugated in the future than in the past. No future-related modulation of leg muscles activity was found during reading leg-related action verbs. In a similar vein, no future-related change of hand or leg muscles reactivity was found for abstract or sensorial verbs. These results indicate that the anticipatory mirroring of hand actions may be triggered by linguistic representations and not only by direct action observation.

Introduction

The discovery of monkeys' premotor and parietal 'mirror' neurons activated by both action execution and observation (di Pellegrino *et al.*, 1992; Gallese *et al.*, 1996; Fogassi *et al.*, 2005) inspired human research demonstrating the involvement of motor regions in action perception (Schütz-Bosbach & Prinz, 2007a). Transcranial magnetic stimulation (TMS) studies, for example, show that observing actions induces a selective facilitation of the muscles that would be involved in the actual execution of the same actions (Fadiga *et al.*, 1995; Urgesi *et al.*, 2006a), supporting the proposal that simulation may allow one to understand the actions performed by other individuals (Gallese & Goldman, 1998).

Crucially, the functional role of motor activation during action perception (motor mirroring) may be fundamental for anticipating others' intentions and predicting others' behaviours (Kilner *et al.*, 2007). Indeed, anticipatory mechanisms are at play during action execution (Wolpert *et al.*, 1995) as well as during action observation (Kilner *et al.*, 2004; Van Schie *et al.*, 2004; Aglioti *et al.*, 2008), and may provide an internal model of the ongoing action that generates top-down expectations and predictions on its deployment in time (Wilson & Knoblich, 2005; Prinz, 2006; Schütz-Bosbach & Prinz, 2007b), allowing onlookers to understand early the goal of actions (Blakemore & Frith, 2005; Kilner *et al.*, 2007). The anticipatory nature of mirror simulation has been demonstrated in both monkeys (Umiltà *et al.*, 2001) and humans (Gangitano *et al.*, 2004; Urgesi *et al.*, 2006b, 2010). In particular, we have demonstrated that observation of static images of hand (Urgesi *et al.*, 2006b, 2010) and leg postures (Candidi *et al.*, 2010), which imply a given action, selectively facilitates the cortico-spinal representations of the 'in-motion' muscles. This result suggests that the motor system is preferentially activated by the inner anticipatory simulation of the deployment of future actions (Urgesi *et al.*, 2006b, 2010).

Simulation of actions is not only triggered by direct observation, but may also be evoked by their linguistic retrieval. Reading action verbs, for example, brings about an increase of neural activity in motor brain regions (Pulvermüller *et al.*, 2001; Hauk *et al.*, 2004; Buccino *et al.*, 2005; Tettamanti *et al.*, 2005; Aziz-Zadeh *et al.*, 2006), thus suggesting a link between action execution and higher order action-related linguistic representations (Pulvermüller, 2005; Barsalou, 2008). What remains unknown is whether the simulation process induced by the linguistic derivation of action features is based on anticipatory coding.

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To test specifically the hypothesis that the human motor system may be more sensitive to action verbs indicating a future than a past action, we asked participants to silently read different types of verbs conjugated in future and past tenses. The verbs could refer to hand- or leg-related actions (e.g. grasp, walk), to sensory (e.g. hear) or to abstract (e.g. know) processes. As an index of cortico-spinal excitability, we recorded motor-evoked potential (MEP) amplitudes evoked by single-pulse TMS (s-p TMS) delivered over the cortical representation of hand and leg muscles.

Materials and methods

Subjects

Nineteen native Italian-speaking subjects (nine males, mean age 21 ± SD 2 years) participated in this experiment. Data from one subject were excluded from the analysis due to muscular pre-activation in more than 30% of trials during leg muscle stimulation. All subjects were right-handed according to the Standard Handedness Inventory (Briggs & Nebes, 1975), and had normal or corrected-to-normal visual acuity. All subjects gave their written informed consent prior to their inclusion in the study. Subjects were naïve as to the purpose of the study and were compensated for their participation. Specific information concerning the aim of the study was provided only after the subject had completed all experimental sessions. The experimental procedures were approved by the Fondazione Santa Lucia ethics committee, and were carried out in accordance with the principles of the 1964 Helsinki Declaration. None of the participants had a history of neurological, psychiatric or other medical problems, or any contraindication to TMS (Wasserman, 1998). No discomfort or adverse effects during TMS were noticed or reported.

Stimuli

The experimental visual stimuli consisted of the future and past tense of 16 different verbs belonging to one out of four possible types (motor hand-related, motor leg-related, sensorial non-somatic, abstract verbs). Sensory and abstract verbs allowed us to control for any possible cortico-spinal modulation when reading non-motor (sensory) or non-body-related verbs (abstract). Each stimulus subtended a visual angle of about 0.6 degrees and was perceived effortlessly by the participants. The full set of experimental stimuli is provided as Data S1 in Supporting Information.

To control for verb imageability effects that may affect the speed of word processing and the motor reactivity *per se* (Paivio, 1971; Tomasino *et al.*, 2007), and in the absence of Italian verb databases providing such information, we selected the 16 verbs used in the experiment from a set of 172 verbs preliminarily rated by 10 subjects according to their easiness in triggering visual and sensorial mental images. The ratings were provided by means of Likert scales where zero corresponded to 'impossible to associate a mental image to the verb' and 7 indicated 'no effort in associating a mental image to the verb'. Imageability ratings of the 16 chosen verbs (four for each category) were entered in a mixed-model two-way ANOVA, with Type of verb as between-factor and Tense as within-factor (4 × 2). No main effects or interactions turned out to be significant (all $P > 0.39$), thus ruling out that any purported cortico-spinal modulation observed for stimuli of different verb Type or Tense could be due to the different imageability of the different stimulus categories. Stimuli set consisted of Italian verbs whose lexical frequency ranged between 0 and 19.42 times per million words according to the averaged values of ColFIS (Laudanna *et al.*, 1995) and Wikipedia (http://it.wikipedia.org/wiki/Corpus#Dimensione) database. We checked for lexical frequency, length and orthographic neighbourhood differences between stimuli of the different experimental conditions by means of three mixed-model 4 (verb Type as between-factor: motor hand- or leg- related, sensorial non-somatic, abstract) × 2 (verb Tense as within-factor: future, past) ANOVAs. No difference in lexical frequency was found (all $P > 0.16$). The ANOVA on verbs' length showed a significant main effect of the Tense ($F_{1,60} = 183.54$, $P = 0.00$), which was accounted for by the higher length of future (8.20 ± SD 1.63 letters) than past tense (7.17 ± SD 1.61 letters). Neither the Type of verb nor its interaction with Tense reached significance ($P > 0.22$). Orthographic neighbourhood of future verbs (1.22 ± SD 1.21 words) resulted lower than past tenses (1.94 ± SD 3.28 words; $F_{1,60} = 4.46$, $P = 0.04$). No other main factor or interaction reached significance (all $P > 0.39$). It has been suggested that the length of verbs and their orthographic neighbourhood can strongly affect word-evoked electrocortical responses (Pulvermüller *et al.*, 1999). In view of this, it is crucial that no interaction between verb Type and verb Tense was found in the analysis on verb length and orthographic neighbourhood. Indeed, such a result rules out that these variables *per se* influenced the modulation of cortico-spinal excitability of the first dorsal interosseous (FDI) and tibialis anterior (TA) during reading the future and past Tense of different verb Types. The mean (cm ± SD) of all the subjective Likert judgements on imageability, lexical frequency, length and orthographic typicality of Past and Future tenses of each verb Type are reported in Table 1.

TABLE 1. Mean (cm ± SD) of subjective Likert judgements on imageability, lexical frequency, length and orthographic typicality of Past and Future tenses of each verb Type

Verb type	Verb tense	Imageability	Lexical frequency	Length	Orthographic typicality
Sensorial	Fut	5.18 ± 0.83	1.63 ± 4.24	8.38 ± 1.67	0.31 ± 0.60
	Pas	5.31 ± 0.53	2.15 ± 5.14	7.44 ± 1.63	1.06 ± 3.23
Abstract	Fut	4.95 ± 0.76	0.73 ± 1.58	7.88 ± 1.50	1.50 ± 1.15
	Pas	4.92 ± 0.69	1.58 ± 2.72	6.69 ± 1.35	2.38 ± 3.69
Leg	Fut	4.99 ± 0.72	0.20 ± 0.39	8.69 ± 1.82	0.88 ± 1.09
	Pas	5.29 ± 0.72	0.15 ± 0.30	7.50 ± 1.83	1.38 ± 1.96
Hand	Fut	5.31 ± 0.79	0.90 ± 2.34	7.88 ± 1.54	1.69 ± 1.45
	Pas	5.22 ± 0.83	0.32 ± 0.46	7.06 ± 1.61	2.56 ± 3.97

Electromyographic (EMG) and TMS recording

Pairs of Ag/AgCl surface electrodes (1 cm diameter) were placed over the muscle belly (active electrode) and over the associated joint or tendon (reference electrode) in a classical belly–tendon montage. The ground electrode was placed over the ventral part of the wrist for FDI and over the knee for TA recordings. Leg and hand muscle activity was recorded in different experimental blocks. EMG recording was performed with a Viking IV (Nicolet Biomedical, Madison, WI, USA) electromyograph. The EMG signal was band-filtered (20 Hz–2.5 kHz, sampling rate 10 kHz), digitalized and stored for off-line analysis.

TMS of FDI was performed using a 70-mm figure-of-eight coil, connected to a Magstim Super Rapid Transcranial Magnetic Stimulator (The Magstim Company, Carmarthenshire, Wales, UK), placed over the left motor cortex. The coil was held tangentially to the skull with the handle pointing 45° away from the nasion–inion line in a postero-lateral direction (Brasil-Neto *et al.*, 1992; Mills *et al.*, 1992). For the TA muscle, as its motor cortical representation is located deep along the interhemispheric sulcus and difficult to reach with the magnetic pulse, a double-cone coil was connected to the same Magstim Super Rapid Transcranial Magnetic device used for FDI stimulation (The Magstim Company, Carmarthenshire, Wales, UK). To find individual optimal scalp positions (OSP; i.e. the stimulation position that induces MEPs of maximal amplitude) for each muscle, the coil was moved in steps of 1 cm over the motor cortex and the OSP was marked on a bathing cap worn by the subjects. Once the OSP was found, the resting motor threshold (rMT) was defined as the lowest intensity of stimulation that produced five MEPs out of 10 consecutive magnetic pulses with an amplitude of at least 50 μV. The mean rMT was 49.22 ± SD 6.76% of maximum stimulator output for FDI and 55.89 ± SD 10.14% for TA. During the experimental sessions, s-p TMS with 120% intensity of individual rMT were delivered over the muscles' OSP. EMG recording started 100 ms before magnetic pulse delivery. It was thus possible to control for the absence of muscular pre-activation in each trial. Furthermore, to continuously verify on-line throughout the experimental block the absence of muscular contraction, the EMG signal was converted in white noise and transmitted via a loudspeaker. MEP peak-to-peak amplitudes (in mV) were collected and stored on a computer for off-line analysis. Single magnetic pulses were randomly delivered in a time window of 200 ms centred 600 ms after visual stimuli onset (600 ± 100 ms). This choice was inspired by electrophysiological studies showing modulation of the activity of the motor cortex during the processing of linguistic material (Pulvermüller *et al.*, 1999; Oliveri *et al.*, 2004).

Procedure

Participants were tested in two sessions (one for FDI and one for TA muscles) of approximately 90 min each. The stimulation order of the upper and lower limbs was counterbalanced across subjects. During the experimental blocks, the subjects were comfortably seated in a dimly lit room at a distance of 100 cm from a computer screen (SONY Trinitron CPD-E400P, 60 Hz refresh rate). Each session consisted of four experimental blocks of 32 trials (16 trials per condition in total). Before starting the experiment, subjects were instructed to pay attention to the visual stimuli presented on the screen. Moreover they were requested to report verbally the stimuli but only in the 9000-ms intertrial interval. This procedure ruled out that the verbal response could affect cortico-spinal excitability. During each experimental block participants were presented with stimuli randomized across all conditions (future or past tense of hand-, leg-, sensorial and abstract verbs). Each stimulus appeared at the centre of the screen for 1000 ms. During the stimulus presentation, a single pulse of TMS was delivered over the subjects' muscle OSP at 120% of rMT (an example of an event trial is shown in Fig. 1). The magnetic stimulation was delivered at random times ranging between 500 and 700 ms from stimulus onset to avoid any priming effects that could affect MEP amplitude. The frequency of TMS pulses was < 0.1 Hz to avoid that TMS *per se* would influence motor cortex excitability (Chen *et al.*, 1997).

Data analysis

MEP amplitudes that fell 3 SDs above or below each individual mean for each experimental condition, or single trials contaminated by muscular preactivation (EMG traces in which the 100-ms pre-TMS signal exceeded 50 μV of amplitude) were excluded as outliers and precontracted trials. On this basis we discarded 242 trials in total, 5.25% of total, < 1 MEP for each experimental condition per subject. The assumption of sphericity was tested through the Mauchley test. Raw MEP amplitudes were thus entered in a (4 × 2 × 2) within-subject repeated-measures ANOVA with verb Type (leg-action, hand-action, sensorial, abstract), Tense (future, past) and Muscle (FDI, TA) as main factors. *Post hoc* comparisons were performed with the Duncan test. A significance alpha level of 0.05 was used for testing main effects, interactions and *post hoc* comparisons. All statistical tests were performed with the software STATISTICA 8 (StatSoft, Tulsa, OK, USA).

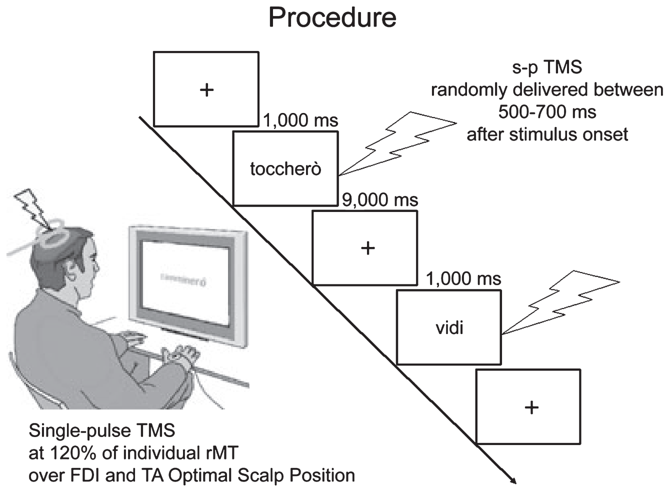

FIG. 1. Timeline and subjects' posture during the experimental procedure. Single-pulse transcranial magnetic stimulation (s-p TMS) was delivered on average 600 ms (± 100 ms) after verb appearance on the screen at intensities according to individual resting motor threshold (rMT) of first dorsal interosseous (FDI) and tibialis anterioris (TA), respectively, and in a counterbalanced order between subjects.

Results

Raw mean MEP amplitudes of all the experimental conditions are reported in Table 2. The factor Muscle reached statistical significance ($F_{1,17}$ = 6.32, P = 0.02). *Post hoc* testing revealed that the amplitude of MEPs was higher for FDI (1.24 ± SD 0.70 mV) than TA (0.83 ± SD 0.37 mV). This result simply reflects the differential reactivity of hand and leg cortico-spinal representations. Verb Type and verb Tense factors did not reach statistical significance (all P > 0.20).

Crucially, the only interaction that resulted significant was the triple interaction between Muscle, verb Type and verb Tense ($F_{3,51}$ = 2.92, P = 0.04; Fig. 2). Even if the Mauchley test showed that the sphericity assumption was not violated (all P > 0.09), we performed the Greenhouse–Geisser correction to verify the significance of the triple interaction with adjusted degrees of freedom. The crucial triple interaction survived the Greenhouse–Geisser correction, providing further evidence of its robustness (F = 2.92, P < 0.05, ε = 0.90, adjusted degrees of freedom 1 = 2.71, adjusted degrees of freedom 2 = 46.12).

The analysis of *post hoc* comparisons demonstrates that while reading future and past tenses of any verb Type failed to modulate leg muscles' excitability, hand muscles' excitability was selectively enhanced during reading of future tense of hand-action's verbs with respect to their past (1.31 ± SD 0.71 mV, 1.23 ± SD 0.68 mV, P < 0.05). Reading hand-action-related verbs conjugated in the future tense facilitated FDI excitability also in comparison to reading leg-action verbs (P < 0.05) conjugated in the past, to sensorial verbs (P = 0.01) and, although marginally, also with respect to past tenses of

TABLE 2. Mean values (mV ± SD) of MEP amplitudes in all experimental conditions

	Leg-related		Hand-related		Abstract		Sensorial	
Muscle	Future	Past	Future	Past	Future	Past	Future	Past
FDI	1.28 ± 0.75	1.23 ± 0.75	1.31 ± 0.71	1.23 ± 0.68	1.21 ± 0.62	1.24 ± 0.72	1.21 ± 0.70	1.20 ± 0.74
TA	0.81 ± 0.40	0.86 ± 0.37	0.81 ± 0.33	0.85 ± 0.40	0.84 ± 0.42	0.81 ± 0.36	0.83 ± 0.40	0.81 ± 0.33

FDI, first dorsal interosseous; TA, tibialis anterioris.

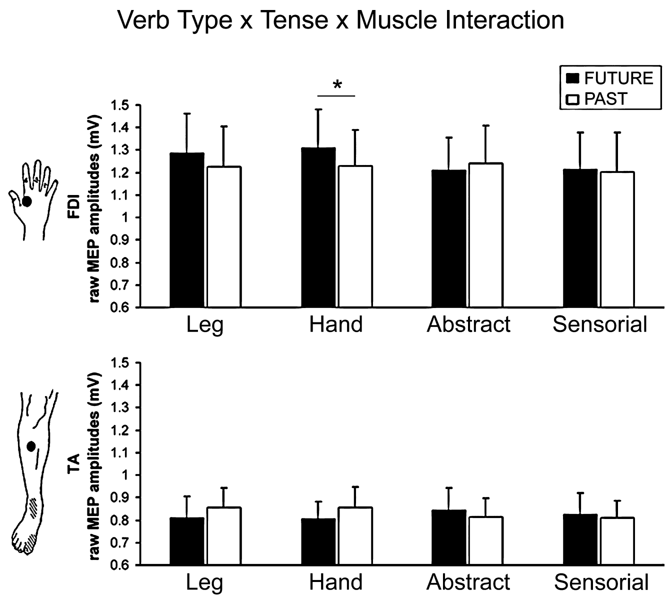

FIG. 2. Histograms show mean amplitude of motor-evoked potentials (MEPs) in mV plotted for each different experimental condition. The upper panel reports the amplitude of MEPs recorded from the first dorsal interosseous (FDI) hand muscle. The lower panel reports the amplitude of MEPs recorded from the tibialis anterioris (TA) leg muscle. The asterisk indicates the significant difference in the crucial comparison between future and past tense of hand action verb for FDI as indexed by the significant interaction between verb Type × Tense × Limb. Error bars represent SEM. *$P < 0.05$.

abstract verbs ($P = 0.07$). Furthermore, FDI excitability for hand-action-related verbs conjugated in the future was higher also with respect to abstract ($P = 0.02$) and sensorial ($P = 0.02$) verbs conjugated in the future.

Discussion

The present study demonstrates, for the first time, that reading hand-related action verbs conjugated in the future enhances the excitability of hand muscles with respect to reading the same verbs conjugated in the past tense. Moreover, reading future or past tenses of abstract, sensorial or leg-related action verbs does not affect either hand or leg muscles reactivity.

The future of action verbs in the human cortico-spinal system

Language has the unique capability to allow to place events back or forward in time and to unchain humans from time contingency. Within the motor domain, the signature of time is associated to movement memory and movement preparation. Both motor memory traces (Pascual-Leone *et al.*, 1995) and movement preparation (Sinclair & Hammond, 2008) lead to changes in local cortical movement representations and may be indexed by amplitude modulations of MEPs.

While several previous s-p TMS studies reported cortico-spinal modulations during language-related tasks but did not test any specific relation between words meaning and hand or leg cortico-spinal reactivity (Tokimura *et al.*, 1996; Seyal *et al.*, 1999; Terao *et al.*, 2001; Meister *et al.*, 2003; Watkins *et al.*, 2003; Liuzzi *et al.*, 2008), Buccino *et al.* (2005) have shown that passively listening to sentences with action verbs referring to the hand or the leg induced a selective inhibition of hand and leg motor excitability, respectively (Buccino *et al.*, 2005). Because no explicit information about specific movements was included in the test material, the suggestion was made that the inhibitory effect resulted from the need to inhibit the different possible actions associated to each action verb. Facilitatory effects of reading action-related sentences dependent on whether the reader took a first or a third person perspective have been reported (Glenberg *et al.*, 2008), and are reminiscent of studies in which action observation induces cortico-spinal facilitation when the observed action is attributed to others and not to the self (Schütz-Bosbach *et al.*, 2006, 2009).

No s-p TMS study has so far tested whether reading future and past tense of action verbs according to a first person perspective may modulate cortico-spinal excitability. One important result of the present study is that linguistic reference to the time in which an action may take place modulates cortico-spinal reactivity.

It can also be observed that cortico-spinal excitability is enhanced during actual movement preparation (Stinear *et al.*, 2009). However, because no overt movement was to be performed, the facilitation contingent upon reading the future of action verbs is more parsimoniously explained in terms of 'anticipatory' simulation. More specifically, we believe that our main result is reminiscent of what was found in our previous studies where the increase of MEPs amplitude to observation of pictures depicting the middle phase of grasping movements with respect to their final posture reflected the deployment of the action in the future rather than in the past (Urgesi *et al.*, 2006b, 2010; Candidi *et al.*, 2010). Our finding is also in keeping with studies showing electroencephalographic (readiness potential, Kilner *et al.*, 2004; lateralized readiness potential, Van Schie *et al.*, 2004) indices of anticipatory simulation even during mere action prediction in the absence of action execution.

Although the resonant coding of actual (Fadiga *et al.*, 1995; Gangitano *et al.*, 2004; Montagna *et al.*, 2005) or implied action (Urgesi *et al.*, 2006b, 2010; Proverbio *et al.*, 2009; Candidi *et al.*, 2010) may be linked to the activity of the premotor (Umilta *et al.*, 2001; Avenanti *et al.*, 2007) and the parietal cortex (Fogassi *et al.*, 2005; Avenanti *et al.*, 2007), s-p TMS of the primary motor cortex cannot provide any information about the source of such effects. It has been shown, however, that the premotor cortex does play a role in both action- and non-action-related anticipatory tasks (Schubotz & von Cramon, 2001a,b, 2003, 2004). Thus, the facilitation we observe during reading of future tense of hand's action verb may be an index of anticipatory mechanisms occurring either directly in the primary motor cortex (Dushanova & Donoghue, 2010) or elsewhere in the brain (premotor, Schubotz & von Cramon, 2003; Szpunar *et al.*, 2007).

It is also worth noting that s-p TMS studies cannot tell apart the exact meaning of the cortico-spinal motor facilitation during reading of future tense of hand-related action. In particular, we cannot make any claim on whether the above effect mediates language understanding (like strong embodied simulation proposals may imply; Hauk *et al.*, 2004; Gallese & Lakoff, 2005; Aziz-Zadeh *et al.*, 2006; Boulenger *et al.*, 2008a,b, 2009; Barsalou, 2008) or whether it represents a mere epiphenomenon of processes occurring elsewhere in the brain (cascade process, see Mahon & Caramazza, 2008). That reading the future of action verbs triggers the anticipatory simulation of hand-related action raises the question of whether such an effect may be observed also for languages that do not express time contingencies (e.g. Greenlandic that, according to some, seems to lack specific forms for referring to the future). While it is, in principle, possible that referring to future actions using very abstract means (e.g. colour cue) may induce anticipatory bias for fine represented movements, no studies have so far addressed this issue, which remains an outstanding question for future research.

Cortico-spinal representation of the temporal imminence of an action seems specific for hand-related action verbs

Finding that reading the future of hand-related action verbs facilitates hand representations and that reading leg-related verbs does not facilitate leg representations speaks against a classic somatotopic mapping. Indeed, strong embodied theories of language representation would predict similar modulations for both hand- and leg-action-related verbs. In a similar vein, an explanation based on differences in morphological load would imply no dissociation between upper and lower limb in mapping the future tense of hand- and leg-related action verbs.

Differences in the representation of motor skills associated to upper and lower limbs may provide an explanation of hand predominance in coding motor properties of action verbs according to an anticipatory framework. Typically, hands can perform much more sophisticated actions with respect to legs. Studies indicate that motor expertise parallels motor simulation abilities (Calvo-Merino *et al.*, 2006; Frey, 2008; Cross *et al.*, 2009). Importantly, a s-p TMS study in elite basketball players showed that higher motor expertise is linked to higher anticipatory mapping of observed hand actions (Aglioti *et al.*, 2008). Activation of finer and higher-order motor representations for extremely well-trained actions (resulting in asymmetries between trained and non-trained action neural representations) has recently been described also in the domain of language. Indeed, reading sentences that describe sport (ice-hockey) movements activates the dorsolateral premotor cortex of expert ice-hockey players with respect to non-athlete individuals (Beilock *et al.*, 2008). Beilock *et al.* (2008) report that the activity of the left premotor cortex, which is normally involved in higher-order action selection and implementation, positively correlates with individual's motor experience in the sport (Beilock *et al.*, 2008). Thus, the involvement of motor systems triggered by implicit simulation of linguistically presented actions is shaped by individuals' ability to perform the described action.

The possible influence of mental motor imagery on deriving information about pending actions from language deserves comments. It is now held that the network supporting overt motor behaviour largely overlaps with the regions involved in both explicit and implicit motor imagery, and that explicit action motor imagery and action verb reading are linked processes (Tomasino *et al.*, 2007, 2008; Willems *et al.*, 2009). In particular, reading action verbs would not automatically induce explicit motor imagery but only implicit action simulation (Willems *et al.*, 2009). At any rate, similar to action execution, the neural resources activated by explicit motor mental imagery (Fourkas *et al.*, 2008) as well as by implicit mental simulation are influenced by motor expertise (Beilock *et al.*, 2008). This would explain why the modulatory effect of hand-related action verbs is clearly present while no leg-related action verb modulation was found.

In view of this, we posit that the higher sensitivity of hand muscles to subtle information derived from language about an impending action may be a reflection of hand muscles higher skilfulness with respect to leg. In particular, we propose that reading action verbs draws on the motor resources available for movement execution, which are stronger or have lower activation thresholds for hand than for leg muscles. The functional organization of the motor cortex is affected by several overlapping action representations according to actions' ethological relevance, movement repertoire, object directedness, motor learning and memory (Sanes *et al.*, 1995; Fadiga *et al.*, 2000; Graziano & Aflalo, 2007). Action verbs may differently tap some of these factors (Fernandino & Iacoboni, 2010). We propose that time contingency may be a factor that, among others, modulates the cortico-spinal reactivity during abstract action representation.

Conclusions

The present study expands knowledge concerning the anticipatory nature of mirroring directly observed actions by showing that also deriving action-related features from linguistic material activates the motor system according to anticipatory rules. The specificity of this effect for hand and not for leg representations may suggest that anticipatory simulation is particularly important when skilled performances are involved. All in all, our results cannot be explained either in terms of morphological load effect (i.e. the facilitation of FDI excitability during future tense reading does not extend to all type of verbs) or in terms of association of pure somatotopic verbs to body parts (i.e. the modulation of cortico-spinal excitability of the leg muscle is not observed during the reading of future tense of leg-related verbs).

Supporting Information

Additional supporting information may be found in the online version of this article:

Data S1. Complete list of experimental verbs in future and past tense, and their translation.

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Abbreviations

EMG, electromyography; FDI, first dorsal interosseous; MEP, motor-evoked potential; OSP, optimal scalp position; rMT, resting motor threshold; s-p TMS, single-pulse transcranial magnetic stimulation; TA, tibialis anterioris; TMS, transcranial magnetic stimulation.

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