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The disembodiment effect of negation: negating action-related sentences attenuates their interference on congruent upper limb movements

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Bartoli E, Tettamanti A, Farronato P, Caporizzo A, Moro A, Gatti R, Perani D, Tettamanti M. The disembodiment effect of negation: negating action-related sentences attenuates their interference on congruent upper limb movements. *J Neurophysiol* 109: 1782–1792, 2013. First published January 9, 2013; doi:10.1152/jn.00894.2012.—Human languages can express opposite propositions by means of the negative operator "not," which turns affirmative sentences into negative ones. Psycholinguistic research has indicated that negative meanings are formed by transiently reducing the access to mental representations of negated conceptual information. Neuroimaging studies have corroborated these findings, showing reduced activation of concept-specific embodied neural systems by negative versus affirmative sentences. This "disembodiment effect" of sentential negation should have two distinct consequences: first, the embodied systems should be computationally more free to support concurrent tasks when processing negative than affirmative sentences; second, the computational interference should only be reduced when there is a strict semantic congruency between the negated concept and the referent targeted by concurrent tasks. We tested these two predictions in two complementary experiments involving the comprehension of action-related sentences and kinematic measurements of its effects on concurrent, congruent actions. Sentences referred to actions involving either proximal or distal arm musculature. In *experiment 1*, requiring a proximal arm movement, we found interference reduction for negative proximal sentences. In *experiment 2*, requiring a distal arm movement, we found interference reduction for negative distal sentences. This dissociation provides the first conclusive evidence in support of a disembodiment theory of negation. We conclude that the computational cost resulting from the insertion of an additional lexical item ("not") in negative sentences is compensated by solely storing a concept in affirmative form in semantic memory, since its negative counterpart can be produced by transiently reducing the access to such stored semantic information.

negation; concept; semantic memory; embodied systems; disembodiment

HUMAN LANGUAGES have the essential capacity to express opposite propositions by inverting truth value conditions and by affirming or denying any given state of affairs. These oppositions can be expressed by distinct lexical items (e.g., "affirm/deny"). A more parsimonious alternative, with respect to the lexicon size, is provided by sentential negation constructions, i.e., by the negative operator "not," which can reverse virtually any affirmative utterance into a negative one (Horn 1989; Moro 2008; Tettamanti and Moro 2012; Zanuttini 1997). Little is known about the neural mechanisms underlying the reversal of semantic polarities through sentential negation. A fundamental open question is whether this lexical parsimony corresponds to an equivalent parsimony of the underlying neural resources.

Early psycholinguistic studies evidenced how negated information is more difficult to elaborate than its affirmative counterpart (Carpenter and Just 1975; Trabasso et al. 1971). Increased difficulty, however, does not appear to be a constitutive property of sentential negation, as the difficulty effect may disappear when sufficient semantic or pragmatic contextual information is provided (Dale and Duran 2011; Glenberg et al. 1999; Nieuwland and Kuperberg 2008). Experiments investigating the timing of sentential negation processing have shown that the semantic representation of the factual state of affairs conveyed by negative propositions occurs with a time delay of several hundred milliseconds compared with affirmative proportions (Anderson et al. 2010; Kaup et al. 2006; Lüdtke et al. 2008). The representation of the factual state of affairs of negative propositions may occur after the representation of the counterfactual negated state of affairs (Kaup et al. 2006). These findings have led to the so-called two-step simulation hypothesis of negation processing (Kaup et al. 2007). However, whether negated propositions are semantically represented in the same or different format than corresponding affirmative propositions is still not clear. One possibility is that the presence of sentential negation leads to a, possibly transient, reduced accessibility of the negated lexical-semantic information (Kaup 2001; Kaup and Zwaan 2003; MacDonald and Just 1989). In this view, sentential negation blocks the mental representation of the information it denies, engendering a subjective experience of absence (Kaup et al. 2007). This hypothesis follows the principle of lexical parsimony, by requiring that only the affirmative concept be represented in semantic memory. However, it leaves unspecified what neural mechanisms instantiate the block of conceptual representations to produce negative counterparts.

A first hint toward the clarification of such neural mechanisms came from an fMRI study (Tettamanti et al. 2008) showing a reduction of both blood oxygenation level-dependent activation and effective connectivity for negative versus affirmative sentences. These reductions were observed in different neural systems according to the specific conceptual-semantic contents, namely, in left fronto-parietal regions for negative sentences with an action-related content and in the retrosplenial cingulate cortex for negative sentences with an abstract content. The involvement of these concept-specific neural systems (see Aziz-Zadeh et al. 2006; Ghio and Tetta-

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manti 2010; Hauk et al. 2004; Tettamanti et al. 2005) is consistent with their proposed role in embodied modal representations. Theories on the grounding of conceptual knowledge in embodied modality-specific systems claim that the retrieval and elaboration of concepts rely on the specific reactivation of the neural systems involved in the experience, e.g., sensory-motor or affective, with the concepts' referents (Barsalou 1999, 2008; Gallese and Lakoff 2005; Glenberg and Kaschak 2002). These theories have received support from a growing body of behavioral and neurobiological evidence (Binder and Desai 2011; Kiefer and Pulvermüller 2012; Meteyard et al. 2012). Thus sentential negation appears to reduce the embodied neural representations elicited by the concepts expressed within its scope.

Two independent studies more recently confirmed these results. Tomasino et al. (2010) showed that fMRI activations in the hand region of the primary motor and premotor cortices were reduced for negative hand action-related imperatives, such as "Don't grasp!" compared with "Grasp!". By means of transcranial magnetic stimulation (TMS) of the hand motor cortex and a concurrent reading task, Liuzza et al. (2011) showed that the suppression of motor evoked potentials from hand muscles observed for affirmative hand action-related sentences was reduced for negative sentences.

On the basis of this evidence and the lexical parsimony principle, we hypothesized a disembodiment effect, by which the blocking of conceptual representations operated by sentential negation leads to a computational load reduction in concept-specific embodied systems, yielding a reduced interference on concurrent tasks (Fig. 1*A*). By inducing a simultaneous engagement of common neural resources between linguistic processing and motor execution (see Boulenger et al. 2006), we defined a paradigm to elicit interference effects between language and action. In this framework, we tested the disembodiment effect and its semantic specificity. We manipulated sentence polarity (affirmative vs. negative) and concreteness of the sentence's semantic content [abstract vs. actions involving mainly proximal arm musculature (i.e., shoulder and arm muscles) or actions involving mainly distal arm musculature (i.e., hand and finger muscles)] and measured the Polarity × Concreteness interference effects on upper limb kinematic parameters (reaction time and time to peak of the grip aperture) in two distinct experiments. We expected an interference reduction on upper limb movements, in the form of more optimal kinematic parameters that are associated with a more precise motor performance (Castiello 2005), namely, faster reaction times and delayed time to peak of hand grip aperture [i.e., the automatic adaptation of the distance between the thumb and the index finger, which, in the case of a precisely planned grasping movement, reaches its maximum amplitude during the reaching trajectory closer to the target object (Gage et al. 2007; Lin et al. 2007)]. More specifically, in *experiment*

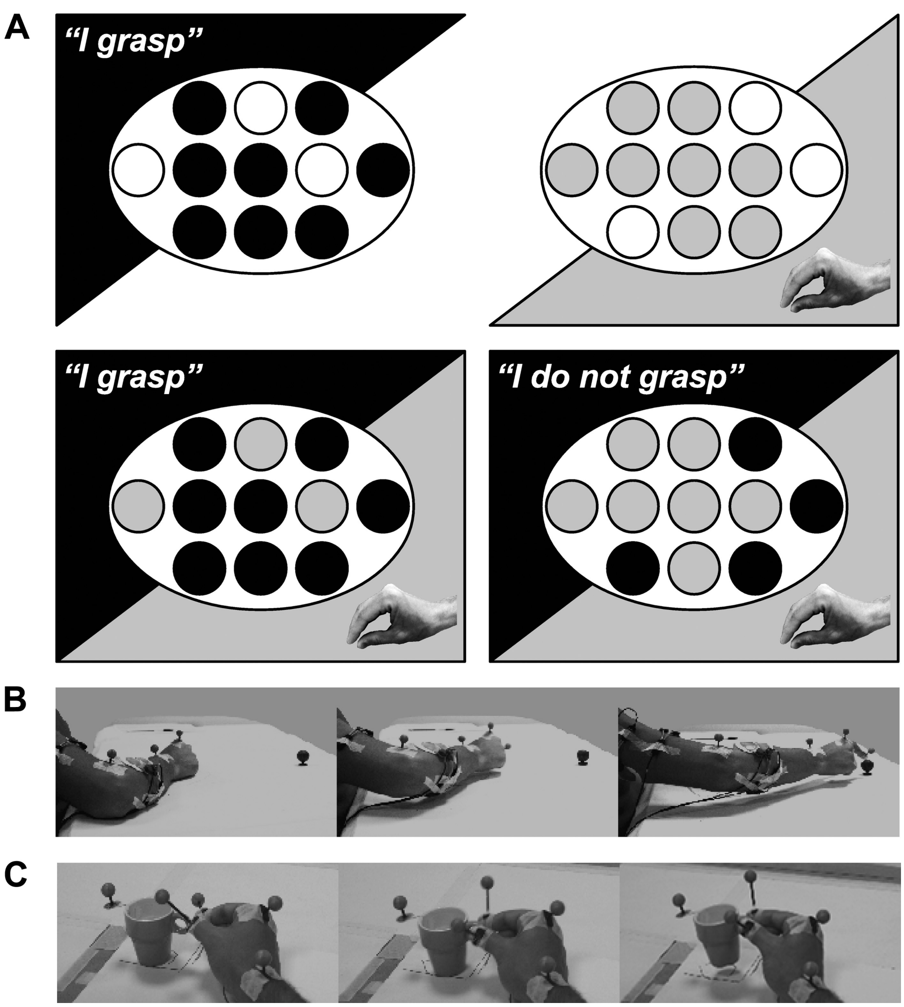

Fig. 1. Experimental hypothesis of a disembodiment effect of sentential negation and setup for kinematic recordings in *experiments 1* and *2*. *A*: previous evidence showed that the processing of action-related sentences, such as "I grasp" (*top left*, black triangle in background), activates cell populations (*top left*, black circles) largely overlapping with those activated (*top right*, gray circles) by the execution of a congruent movement (*top right*, gray triangle in background). This embodied conceptual processing leaves insufficient computational resources available and thus interferes with concurrent movement execution (*bottom left*). The present study tested the hypothesis that sentential negation reduces the access to embodied conceptual representations, and that such a disembodiment effect reduces the inference with concurrent movement execution (*bottom right*). *B*: in *experiment 1*, participants reached to grasp a sphere and we expected reduced interference for negative sentences related to proximal arm musculature. *C*: in *experiment 2*, participants grasped an object without reaching and we expected reduced interference for negative sentences related to distal arm musculature.

1, requiring a reach-to-grasp movement (Fig. 1*B*), we expected a more pronounced polarity effect of faster reaction times and delayed grip aperture for negative versus affirmative proximal sentences, compared with abstract and distal sentences. In *experiment 2*, requiring grasping without reaching (Fig. 1*C*), we expected a more pronounced polarity effect of faster reaction times and delayed grip aperture for negative versus affirmative distal sentences, compared with abstract and proximal sentences. The two experiments should therefore lead to complementary results, with a more pronounced interference reduction induced by negative proximal sentences in *experiment 1* involving proximal arm musculature and more pronounced interference reduction induced by negative distal sentences in *experiment 2* involving distal arm musculature. This prediction of complementary results was specifically tested by a three-way Experiment × Polarity × Concreteness interaction.

In *experiment 1*, we also introduced a latency factor (visual go-signal for the reach-to-grasp movement presented at either 0 ms or 500 ms after the end of the sentence), in order to account for the possible temporal delay required to mentally simulate the factual state of affairs in the presence of sentential negation, as predicted by the two-step simulation hypothesis of negation processing. Accordingly, the interference reduction by negative proximal sentences on the reach-to-grasp movement should be more pronounced in the 500 ms than in the 0 ms latency condition.

MATERIALS AND METHODS

Participants

Eighteen volunteer subjects [9 women, 9 men; mean age 24.83 yr, standard deviation (SD) 5.65] took part in *experiment 1*. All subjects were right-handed (mean score 0.87, SD 0.13) according to the Edinburgh Inventory (Oldfield 1971).

Experiment 2 comprised 24 right-handed (mean score 0.82, SD 0.18) volunteer subjects (15 women, 9 men; mean age 21.58 yr, SD 1.41).

No subjects participated in both experiments. All participants of both experiments were native Italian speakers, with comparable educational level (high school certificate). They had normal or corrected to normal visual acuity and had no history of neurological or psychiatric disorders.

All volunteer subjects gave written informed consent to participate after receiving an explanation of the procedures, according to the Declaration of Helsinki, while remaining naive as to the purpose of the study. The study was approved by the Ethics Committee of the San Raffaele Hospital, Milan.

Linguistic Stimuli

In both *experiment 1* and *experiment 2*, we used the same set of linguistic stimuli, which consisted of declarative sentences created following a basic 2 × 3 factorial combination, with factors Polarity (2 levels: affirmative vs. negative syntactic polarity) and Concreteness (3 levels: semantic content of verbal predicates referring to abstract entities, movements performed with a higher load on the proximal musculature, or movements performed with a higher load on the distal musculature). Twenty affirmative sentences for each of the three levels of Concreteness were formed by combining first person singular, present simple tense transitive verbs with the first person pronoun "io" (English: "I"). The corresponding negative sentences were derived by inserting the monomorphemic negative operator "non" (roughly corresponding to English "not"), yielding the complete set of 120 experimental stimuli. This resulted in 20 sentences for each of the following 6 experimental conditions (see Table 1 for the full list of stimuli): abstract affirmative sentences {AA; e.g., "Io auspico," "I wish" [first person singular (1ps)]}; abstract negative sentences [AN;

Table 1. *Complete list of experimental sentences*

Condition	Sentence	English Translation
Abstract	Io (non) allieto	I (do not) gladden
	Io (non) auspico	I (do not) wish
	Io (non) consolo	I (do not) cheer up
	Io (non) deduco	I (do not) deduce
	Io (non) dissimulo	I (do not) conceal
	Io (non) esaudisco	I (do not) grant
	Io (non) inganno	I (do not) cheat
	Io (non) insinuo	I (do not) insinuate
	Io (non) invidio	I (do not) envy
	Io (non) lodo	I (do not) praise
	Io (non) medito	I (do not) meditate
	Io (non) presumo	I (do not) presume
	Io (non) rievoco	I (do not) recall
	Io (non) rimpiango	I (do not) regret
	Io (non) stimo	I (do not) esteem
	Io (non) suppongo	I (do not) suppose
	Io (non) teorizzo	I (do not) theorize
	Io (non) tollero	I (do not) tolerate
	Io (non) vagheggio	I (do not) fancy
	Io (non) venero	I (do not) venerate
Proximal	Io (non) accarezzo	I (do not) stroke
	Io (non) acchiappo	I (do not) catch
	Io (non) accoltello	I (do not) stab
	Io (non) afferro	I (do not) grasp
	Io (non) aggancio	I (do not) hook
	Io (non) agguanto	I (do not) grab
	Io (non) bastono	I (do not) thrash
	Io (non) imbuco	I (do not) post
	Io (non) impasto	I (do not) knead
	Io (non) levigo	I (do not) rub down
	Io (non) martello	I (do not) hammer
	Io (non) massaggio	I (do not) massage
	Io (non) raccatto	I (do not) pick up
	Io (non) rastrello	I (do not) rake
	Io (non) scavo	I (do not) dig
	Io (non) spazzo	I (do not) sweep
	Io (non) stiro	I (do not) iron
	Io (non) strofino	I (do not) rub
	Io (non) sventolo	I (do not) wave
	Io (non) zappo	I (do not) hoe
Distal	Io (non) abbottono	I (do not) button up
	Io (non) allaccio	I (do not) fasten
	Io (non) annodo	I (do not) tie
	Io (non) avvito	I (do not) screw
	Io (non) cucio	I (do not) sew
	Io (non) digito	I (do not) key in
	Io (non) disegno	I (do not) draw
	Io (non) gratto	I (do not) scratch
	Io (non) impugno	I (do not) clasp
	Io (non) infilo	I (do not) thread
	Io (non) inietto	I (do not) inject
	Io (non) manipolo	I (do not) handle
	Io (non) pennello	I (do not) paint
	Io (non) pizzico	I (do not) pinch
	Io (non) rammendo	I (do not) darn
	Io (non) ricamo	I (do not) embroider
	Io (non) ritaglio	I (do not) cut out
	Io (non) sbuccio	I (do not) peel
	Io (non) sfoglio	I (do not) leaf through
	Io (non) sminuzzo	I (do not) chop up

Sentences are listed in the affirmative form (conditions AA, PA, DA) and in the negative form (conditions AN, PN, DN) by adding the negation operator "non" (English: "do not").

e.g., “Io non auspico,” “I (do) not wish” (1ps)]; proximal affirmative sentences [PA; e.g., “Io afferro,” “I grasp” (1ps)]; proximal negative sentences [PN; e.g., “Io non afferro,” “I (do) not grasp” (1ps)]; distal affirmative sentences [DA; e.g., “Io pizzico,” “I pinch” (1ps)]; distal negative sentences [DN; e.g., “Io non pizzico,” I (do) not pinch (1ps)].

Proximal and distal verbs were selected based on a normative rating on 10 normal adults (5 women, 5 men; mean age 22.10 yr, SD 0.99), who assigned each verb to a value on a 7-point Likert scale [1 = only distal musculature (i.e., hand and finger muscles) involved; 7 = only proximal musculature (i.e., only shoulder and arm muscles) involved]. The final sets of proximal versus distal verbs were neatly separated with only minimal overlap in terms of such scores [Kruskal-Wallis χ^2 (df = 1) = 148.78, $P < 2.2 \times 10^{-16}$]: distal verbs averaged a 2.5 score (range 1.2–3.8), whereas proximal verbs averaged 4.9 (range 3.1–6.9).

The lexical frequency of all verbs was balanced across the three affirmative experimental conditions, using the Italian Corpus of Lexical Frequency (Laudanna et al. 1995). The number of syllables in the affirmative sentences was also balanced across conditions.

Sentences were digitally recorded by a female Italian native speaker. Pitch and intensity of the vocal waveforms were assessed with Praat 4.6.09 (**www.praat.org**), and their means were balanced across conditions. Average sentence duration was 907 ms (SD 111). Sentence duration differed between the two levels of the Polarity factor [ANOVA, $F(1,114) = 61.24$, $P = 2.8 \times 10^{-12}$], because of the additional presence of the negative operator “non” in negative sentences with respect to affirmative ones. Nevertheless, the main effect of Concreteness and, most importantly, the Polarity × Concreteness interaction were not significant [AA: mean 844 ms, standard error (SE) 117; AN: mean 955 ms, SE 102; PA: mean 837 ms, SE 70; PN: mean 970 ms, SE 77; DA: mean 844 ms, SE 69; DN: mean 990 ms, SE 100]. Thus the crucial Polarity × Concreteness comparisons testing our main experimental hypotheses were not biased by sentence duration.

Experiment 1: Reach-to-Grasp Movement (Load on Proximal Arm Musculature)

Procedure. Participants were asked to carefully listen to each sentence presented through an earphone set and to perform a reach-to-grasp movement with their thumb and index finger toward a sphere, in response to a visual go-signal presented at either 0 ms or 500 ms after the end of the sentence. Thus for *experiment 1*, the basic 2 × 3 factorial (Polarity × Concreteness) design was expanded to a 2 × 3 × 2 design by addition of a Latency factor (2 levels: go-signal at 0 ms vs. 500 ms).

Two blocks of 60 sentences were formed, each including 10 sentences per condition (AA, AN, DA, DN, PA, PN). In each block, five sentences per condition were associated with a 0 ms latency go-signal and the other five with a 500 ms latency go-signal. Sentence order in the two blocks was pseudorandomized to minimize the subsequent presentation of items belonging to the same combination of the three experimental factors. The presentation of the two blocks was counterbalanced across subjects.

The participants sat leaning on the back of a chair in front of a table. The height of the table was adjusted in approximate correspondence to the individual location of the xiphoid process. At the beginning of each trial, the right hand and forearm rested on the table, with the elbow forming a 90° flexion angle. Before the experimental trials, the silhouette of the right hand and forearm of the subject was drawn on the table and a marker was placed below the right thumb-index finger, for consistent repositioning before the start of each trial. The middle, ring, and little fingers were held blocked in flexion, while the left hand was kept still on the left leg to prevent any interference with movement.

A sphere (3-cm diameter) was positioned on the table in the sagittal plane passing by the midline of the body of the subject. The reference point for the sphere was tailored for each subject individually, taking into account interindividual differences in arm length. Prior to the experimental trials, subjects were asked to fully extend their elbow: the sphere reference point was defined by placing a marker below the subject’s distal metacarpus (mean distance from the right thumb-index finger start position to the sphere: 25.23 cm, SD 2.02, range 21–29 cm). Thus the distance covered by the reach-to-grasp movement was adjusted to the individual arm length.

Cogent 2000 (**www.vislab.ucl.ac.uk/cogent.php**), running in MATLAB 6.5 (MathWorks, Natick, MA), was used to present sentences auditorily, as well as visual fixation- and go-signals. Visual stimuli were presented on a VGA screen placed behind the experiment table. Each trial started with the presentation of a red fixation circle. The examiner then manually pressed a key, which triggered the presentation of one sentence, after a variable delay, randomly chosen between 1,800 and 2,400 ms, to avoid movement anticipation. After the end of sentence presentation (0 or 500 ms, according to the Latency factor), the red fixation circle was replaced by a green circle representing the go-signal, thus prompting the subject to perform the reach-to-grasp movement. The go-signal remained on the screen for 3 s and was then replaced by a black screen frame, which terminated the trial. During the interval from one trial to the next, subjects were given enough time to return to the arm-hand starting position. Furthermore, to promote a proper lexical-semantic decoding of the target sentences, in the interval subjects were required to rate each sentence with respect to a subjective estimate of the frequency with which the verb occurs in the Italian lexicon. Subjective verb frequency was rated according to a three-point Likert scale (rare, mean, frequent). It is important to note that, within each trial, the frequency rating task was temporally completely detached from the required movement at the go-signal, and it therefore did not have any direct influence on the measured kinematic parameters.

Acquisition of kinematic parameters. Kinematic parameters were calculated by recording the spatial position of the arm by hand with a three-dimensional (3D)-optoelectronic ELITE digital system (BTS Bioengineering, Milan, Italy), comprising six infrared cameras capable of registering the signal reflected by passive markers acquired at 100-Hz sample frequency. Markers were placed on seven points of interest on the right arm: nail of the thumb, nail of the index, radial side of the head of the second metacarpal bone (index knuckle), radial styloid (wrist), humerus epicondyle (elbow), acromion (shoulder), and C7 spinous process. Markers were directly placed on skin to minimize passive marker movements. Data were acquired with Biomech1.5 (BTS Bioengineering) software. A fourth-order Butterworth dual-pass filter (cutoff frequency 6 Hz) was applied to the raw signal. The calculated parameters were reaction time (defined as the time interval between the go-signal and the movement onset that was determined as the first value of a sequence of at least 5 increasing points on the basis of the wrist velocity profile) and normalized time to peak of the grip aperture (separation between the thumb and the index finger). The time to peak of grip aperture was normalized by movement duration values (time interval from onset to offset of wrist movement; the offset was determined as the last value of a sequence of at least 5 decreasing points on the basis of the wrist velocity profile), to account for the adjustment of the distance covered by the reach-to-grasp movement with respect to the individual arm length (see above).

In addition, the temporal sequence of movement onsets was evaluated by extracting the onset of the grip aperture (angular distance calculated with respect to the markers on the index and thumb nails and on index knuckle), the onset of the elbow flexion-extension movement in the sagittal plane (defined as the projection on the horizontal plane, with respect to the markers on the acromion, on the humerus epicondyle and on the radial styloid), and the onset of the shoulder flexion-extension movement in the sagittal plane (defined as the projection on the horizontal plane, with respect to the markers on the C7 spinous process, on the acromion, and on the humerus epicondyle). The onsets of these three movements were compared to the wrist movement onset (i.e., the reaction time). With respect to the temporal sequence of these movement onsets, the data of five subjects had to be discarded because of the unreliable detection of the marker on the nail of the thumb at movement onset.

Experiment 2: Grasping Movement (Load on Distal Arm Musculature)

Procedure. No Latency factor was included in *experiment 2*, which therefore conformed to the basic 2 × 3 factorial (Polarity × Concreteness) design, as the results of *experiment 1* indicated the possibility of investigating the Polarity × Concreteness modulation in the 0 ms latency condition alone (see RESULTS and DISCUSSION), thus reducing the factorial model complexity. The visual go-signal was always presented at 0 ms after the end of the sentence. Participants were asked to carefully listen to each sentence presented through an earphone set and to perform a grasp movement with their thumb and index finger toward one of two possible target objects (a coffee cup or a screw). We introduced two different objects instead of the sphere used in *experiment 1* in order to elicit a more naturalistic and precise grip and to obtain kinematic parameters not biased by the shape of a particular object. Moreover, introducing objects with overlearned associated movements was an heuristic to reduce uncertainty in movement execution, thus allowing the kinematic parameters to be sensitive to the experimental manipulations rather than to other sources of confounding variability. It is also important to note that the obvious meaningfulness of the coffee cup and screw did not introduce a major source of discontinuity compared with *experiment 1*, since the sphere used in *experiment 1* also constitutes a meaningful object that can be used, e.g., as a bouncing toy.

The same two blocks of 60 sentences as in *experiment 1* were used. In each block, five sentences per condition were associated with the coffee cup and the other five with the screw. Sentence order in the two blocks was pseudorandomized to minimize the subsequent presentation of items belonging to the same combination of the two experimental factors and target objects. The presentation of the two blocks was counterbalanced across subjects.

The participants sat leaning on the back of a chair in front of a table. At the beginning of each trial, the right hand and forearm rested on the table, with the elbow forming a 60° flexion angle. The right hand was tilted to the side, with the lateral side resting on the table, the thumb and index finger joined and slightly retracted, and the other three fingers in a relaxed position. The target objects (coffee cup or screw) were also positioned on the table (the screw was inserted in a bolt attached to the table and stood in vertical position) and were put in contact with the tip of the joined thumb and index finger. In this manner, the participants could grasp the objects by simply opening and extending the thumb and index finger, without moving the wrist or the other upper limb joints. Before the experimental trials, the silhouettes of the right hand and forearm of the subject, as well as of the target objects, were drawn on the table for consistent repositioning before the start of each trial. The left hand was kept still on the left leg to prevent any interference with movement.

Cogent 2000, running in MATLAB 7.0, was used to present sentences auditorily, as well as visual fixation- and go-signals. Timing and structure of the trials, including subjective rating of verb frequency during the interval, were the same as in *experiment 1*. Participants were required to grasp the object and either slightly lift it (coffee cup) or rotate it in the horizontal plane (screw).

Acquisition of kinematic parameters. The equipment, software, and filtering used for the acquisition of kinematic parameters were the same as in *experiment 1*. Markers were placed on two points of interest on the right arm: nail of the thumb and nail of the index. To prevent the markers from being hidden during movements, we fixed them on 2-cm-long sticks, placed perpendicular to the fingernail planes. Three further markers placed on the radial side of the head of the second metacarpal bone (index knuckle), radial styloid (wrist), and humerus epicondyle (elbow) served as a control that the wrist and other upper limb joints remained still during the grasp movement (this was also always checked online before the start of each trial). Markers were directly placed on skin to minimize passive marker movements.

The calculated parameters were reaction time (defined as the time interval between the go-signal and the movement onset that was determined as the first value of a sequence of at least 5 increasing points on the basis of thumb-index distance velocity profile) and time-to-peak of the grip aperture.

Data Analysis

Experiment 1 and *experiment 2* were first analyzed separately, following the same procedure. TrackLab 1.0 and Smart Analyzer 1.1 (BTS Bioengineering) software were used for the reconstruction of the 3D movement profiles and the extraction of kinematic parameter values. Mean values of each raw measure were first calculated for each experimental condition (separately for *experiment 1* and *experiment 2*). Raw outlier values (±2 SD) were excluded from this calculation. The assumption of normality of data distribution was verified for each kinematic parameter, to ensure the correct application of parametric statistical tests. The normally distributed mean values of each parameter were then entered in a repeated-measures ANOVA model, reflecting either the 2 × 3 × 2 (*experiment 1*) or the 2 × 3 (*experiment 2*) factorial combination, with R 2.11.1 (**www.R-project.org**). The Greenhouse-Geisser correction was used in order to control for violations of the sphericity assumption. A significance α-level of 0.05 was declared. In cases when the ANOVA revealed any significant differences in any kinematic parameters, based on our directional hypothesis (i.e., reduced interference on congruent upper limb movements by negative vs. affirmative sentences), we computed post hoc one-tailed Student *t*-tests in order to test for the difference between negative and affirmative sentences in each level of the Concreteness factor (abstract, proximal, distal) at a true significance level, by applying a Bonferroni correction for multiple comparisons (true α-level = 0.0167).

To directly compare the results between the two experiments by specifically testing for the three-way Experiment × Polarity × Concreteness interaction, we dropped the abstract level from the Concreteness factor. We thus tested the specificity of the effect on proximal action-related sentences in *experiment 1* (load on proximal musculature) with respect to the distal action-related sentences in *experiment 2* (load on distal musculature). To do so, we calculated *z* scores for reaction times and time to peak of the grip aperture of each experiment independently and used them as dependent measures in a 2 × 2 × 2 ANOVA model, with the Experiment factor as a between-subjects factor.

RESULTS

Experiment 1: Reach-to-Grasp Movement (Load on Proximal Arm Musculature)

Reaction time. We found a significant main effect of Latency [$F(1,17) = 39.53$, $P = 8.18 \times 10^{-6}$], with slower reaction times at 0 ms latency (mean 279, SE 19) than at 500 ms latency (mean 224, SE 15), and a significant Polarity × Concreteness × Latency interaction [$F(1.53,26.04) = 4.54$, $P = 0.028$]. The other main effects and interactions were not significant (all $P >$ 0.17).

Because these results showed a significant influence of Latency, we also analyzed the two levels of the Latency factor separately, as two separate 2 × 3 (Polarity × Concreteness) ANOVAs, one for data at 0 ms and the other for data at 500 ms.

At 0 ms latency, we found a significant Polarity × Concreteness interaction [$F(1.89,32.18) = 5.85$, $P = 0.008$]. Post hoc paired comparisons between the two levels of the Polarity factor for each semantic condition showed a significant PA > PN effect [$t(17) = 3.32$, $P = 0.002$; mean PA: 290 ms (SE 23), mean PN: 264 ms (SE 22)] and no significant effects for the abstract [$t(17) = -1.38$, $P = 0.91$] and distal [$t(17) = -1.61$, $P = 0.94$] conditions (Fig. 2*A*). Thus at 0 ms latency the reaction times were significantly faster, specifically for negative versus affirmative proximal sentences.

We also tested whether, not considering the effects of negative Polarity, PA selectively interfered with the reach-to-grasp movement (see Fig. 1*A*). We found weak evidence that this was the case: PA > AA, $t(17) = 1.86$, $P = 0.039$; PA > DA, $t(17) = 1.37$, $P = 0.09$.

No significant effects were found at 500 ms latency.

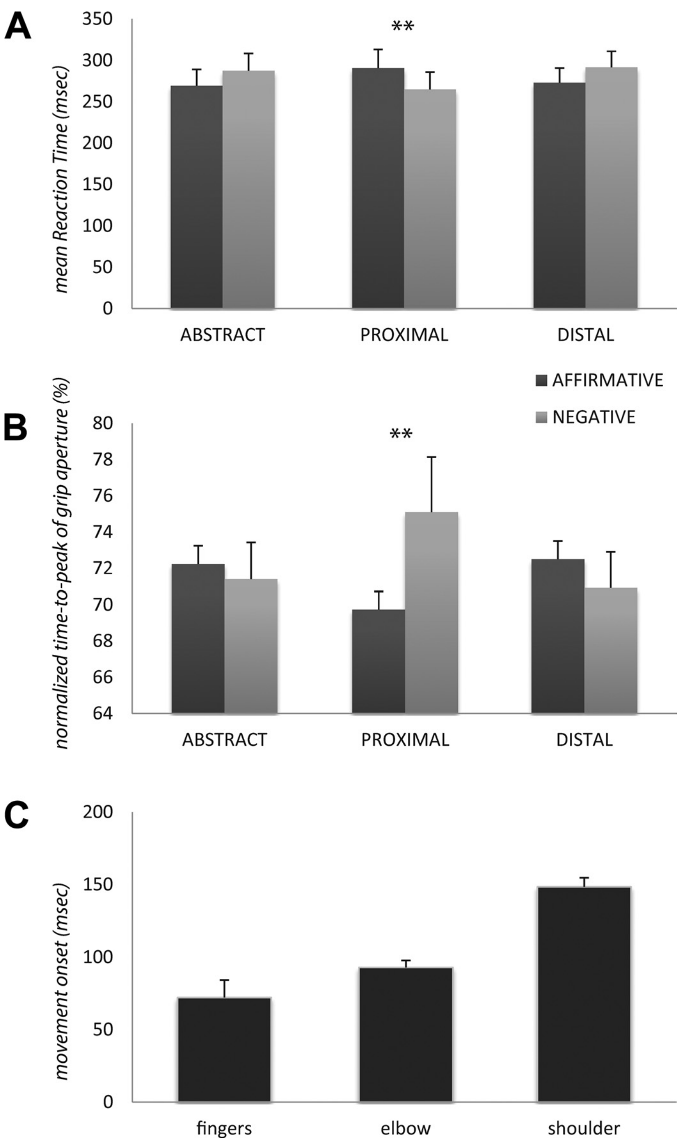

Fig. 2. Influence of sentence content on kinematic parameters of a reach-and-grasp movement (*experiment 1*: load on proximal arm musculature). Bar plots represent mean effect sizes and SE at 0 ms latency. *A*: Polarity × Concreteness interaction on reaction time. *B*: Polarity × Concreteness interaction on normalized time to peak of the grip aperture. *C*: main effect of Movement Onset: the onset of wrist movement was taken by definition as 0 ms. Significance on post hoc paired comparisons between the 2 Polarity levels (affirmative, negative) of each Concreteness condition (abstract, proximal, distal): $^{**}P < 0.01$.

Normalized time to peak of grip aperture. We found a significant Polarity × Concreteness interaction [$F(1.79,30.79) = 3.02$, $P = 0.004$]. The other main effects and interactions were not significant (all $P > 0.09$). Post hoc paired comparisons between the two levels of the Polarity factor for each semantic condition showed a significant PN > PA effect [$t(35) = -3.51$, $P = 0.0006$; mean PN: 75% (SE: 3), mean PA: 69% (SE: 3)] and no significant effects for the abstract [$t(35) = 0.66$, $P = 0.74$] and distal [$t(35) = 1.40$, $P = 0.91$] conditions (Fig. 2*B*). This indicates a delayed time to peak of the grip aperture specifically for negative versus affirmative proximal sentences.

Temporal sequence of movement onsets. For the assessment of the temporal sequence of movement onsets (wrist displacement, grip aperture, elbow flexion-extension, and shoulder flexion-extension), the basic 2 × 3 × 2 factorial combination was expanded into a 2 × 3 × 2 × 4 design by also including a Movement Onset factor (4 levels: wrist, thumb-index, elbow, shoulder). The repeated-measures ANOVA showed a main effect of Movement Onset [$F(1.82,18.16) = 68.66$, $P = 0.005$], a trend toward a significant main effect of Latency ($P = 0.08$), and no main effects of Polarity or Concreteness or interactions (all $P > 0.86$). A characteristic temporal sequence of movement onsets was found (Fig. 2*C*), with the wrist moving first (reaction time, by definition taken as 0 ms in this analysis, see MATERIALS AND METHODS), followed by the thumb-index fingers (mean 72 ms, SE 12), the elbow (mean 93 ms, SE 11), and finally the shoulder (mean 140 ms, SE 7).

Experiment 2: Grasping Movement (Load on Distal Arm Musculature)

Reaction time. We found significant main effects of Polarity [$F(1,23) = 13.78$, $P = 0.001$] and Concreteness [$F(1.50,34.50) = 5.82$, $P = 0.012$] and a significant Polarity × Concreteness interaction [$F(2,46) = 3.41$, $P = 0.041$]. Post hoc paired comparisons between the two levels of the Polarity factor for each semantic condition showed a significant DA > DN effect [$t(47) = 3.62$, $P = 0.0003$; mean DA: 222 ms (SE 15), mean DN: 185 ms (SE 16)], a significant PA > PN effect [$t(47) = 2.23$, $P = 0.015$; cf. Bonferroni-corrected α-level = 0.0167; mean PA: 214 ms (SE 16), mean PN: 195 ms (SE 16)], and no significant effect for the abstract condition [$t(47) = 0.19$, $P = 0.42$] (Fig. 3*A*). Thus in *experiment 2* the reaction times were significantly faster for negative versus affirmative distal, and to a reduced extent also proximal, sentences.

We also tested whether, not considering the effects of negative Polarity, DA selectively interfered with the grasping movement (see Fig. 1*A*). We found no significant effects: DA > AA, $t(23) = -0.27$, $P = 0.61$; DA > PA, $t(23) = 0.86$, $P = 0.19$.

Time to peak of grip aperture. We found a significant main effect of Polarity [$F(1,23) = 4.73$, $P = 0.040$] and a significant Polarity × Concreteness interaction [$F(2,46) = 4.29$, $P = 0.019$]. The other main effects and interactions were not significant (all $P > 0.21$). Post hoc paired comparisons between the two levels of the Polarity factor for each semantic condition showed a significant DN > DA effect [$t(47) = 2.82$, $P = 0.003$; mean DN: 371 ms (SE 20), mean DA: 402 ms (SE 24)], a trend toward a significant PN > PA effect [$t(47) = 1.71$, $P = 0.046$; cf. Bonferroni-corrected α-level = 0.0167], and no significant effect for the abstract condition [$t(47) =$

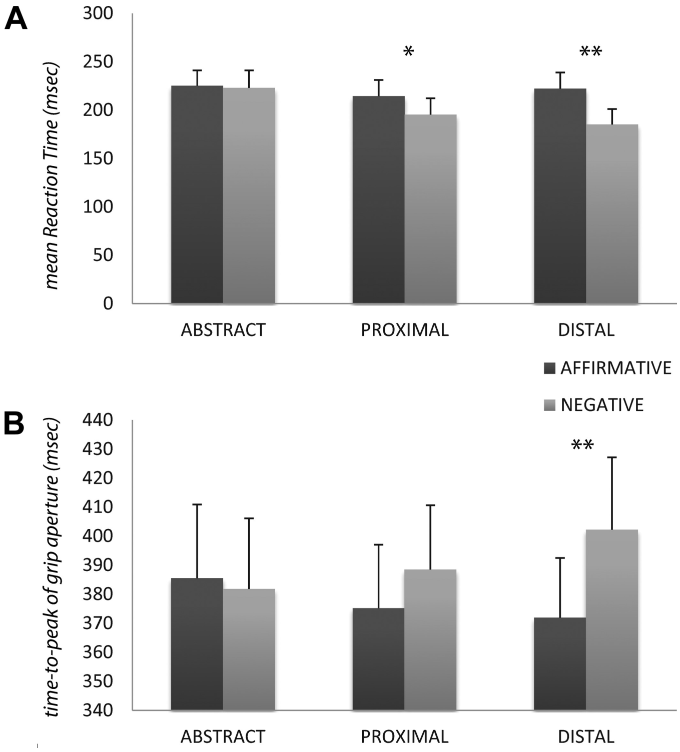

Fig. 3. Influence of sentence content on kinematic parameters of a grasp movement (*experiment 2*: load on distal arm musculature). Bar plots represent mean effect sizes and SE. *A*: Polarity × Concreteness interaction on reaction time. *B*: Polarity × Concreteness interaction on time to peak of the grip aperture. Significance on post hoc paired comparisons between the 2 Polarity levels (affirmative, negative) of each Concreteness condition (abstract, proximal, distal): $^*P < 0.05$, $^{**}P < 0.01$.

−9.43, $P = 0.66$] (Fig. 3*B*). This indicates a delayed time to peak of the grip aperture for negative versus affirmative distal sentences.

Experiment × Polarity × Concreteness Interactions

Reaction time. We found a significant Experiment × Polarity × Concreteness interaction [$F(1,40) = 11.50$, $P = 0.001$], clearly confirming the dissociation with faster reaction times specifically for PN in *experiment 1* and specifically for DN in *experiment 2* (Fig. 4*A*).

Time to peak of grip aperture. We found a significant Experiment × Polarity × Concreteness interaction [$F(1,40) = 7.41$, $P = 0.009$], clearly confirming the dissociation with delayed time to peak of the grip aperture specifically for PN in *experiment 1* and specifically for DN in *experiment 2* (Fig. 4*B*).

Analysis of Subjective Verb Frequency Ratings

Experiment 1. The subjective estimates of verb frequency, which were temporally completely detached within each trial from the measured kinematics, were required to ensure that the participants maintained their attention focused on the auditory linguistic stimuli. We found a trend toward a significant main effect of Polarity [$F(1,17) = 4.43$, $P = 0.051$] and no significant main effects of Concreteness or Latency or significant two- or three-way interactions between the three factors (all $P > 0.28$). This indicates that the subjects may have been moderately sensitive to the Polarity manipulation, even though they were not informed of the presence of Polarity and Concreteness factors in the presented stimuli. Importantly, the subjective verb frequency ratings significantly correlated with the verb frequency ratings taken from the Italian Corpus of Lexical Frequency, both when considering affirmative (Spearman's S = 16,639, $P = 9.4 \times 10^{-6}$, $\rho = 0.54$) and negative (Spearman's S = 16,577, $P = 8.2 \times 10^{-6}$, $\rho = 0.54$) sentences. Thus the balancing of lexical verb frequency across experimental conditions with the Italian Corpus of Lexical Frequency was not significantly altered from the subjective perspective of the participants during lexical-semantic decoding of the stimuli.

Experiment 2. We found neither significant main effects of Polarity or Concreteness nor a significant interaction between the two factors (all $P > 0.10$). As for *experiment 1*, in *experiment 2* the subjective verb frequency ratings also significantly correlated with the verb frequency ratings taken from the Italian Corpus of Lexical Frequency for both affirmative (Spearman's S = 15,790, $P = 3.1 \times 10^{-6}$, $\rho = 0.56$) and negative (Spearman's S = 18,884, $P = 1.2 \times 10^{-4}$, $\rho = 0.47$) sentences.

Experiment 1 vs. experiment 2. When comparing the subjective frequency ratings expressed by the participants in *experiment 1* with those expressed by the participants in *experiment 2*, as a measure of stimulus processing consistency, we found a significant correlation for both affirmative (Spearman's S = 8,141, $P = 4.2 \times 10^{-13}$, $\rho = 0.77$) and negative (Spearman's S = 12,546, $P = 1.7 \times 10^{-8}$, $\rho = 0.65$) sentences. This indicates that the subjective frequency ratings assigned to each verb of the experimental set were highly consistent across the two participant groups.

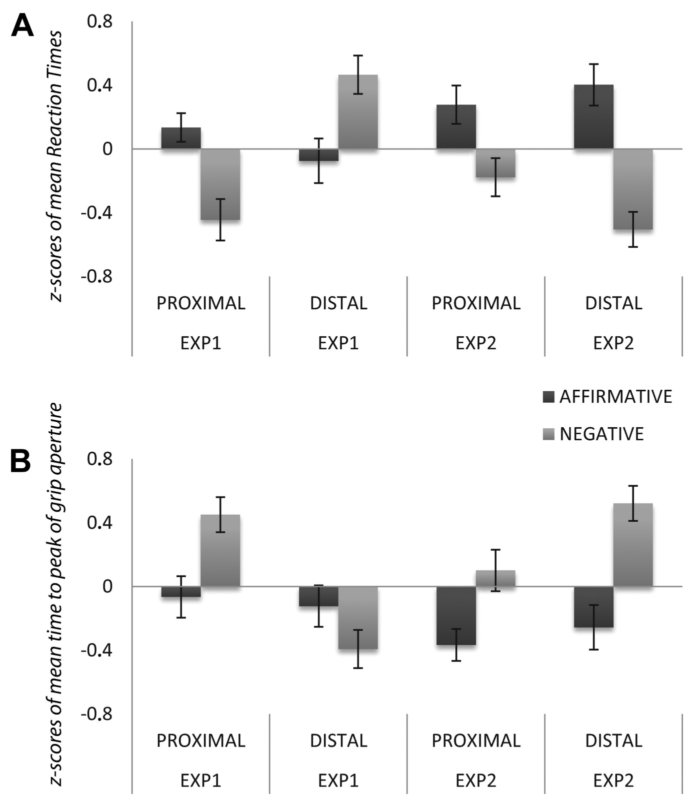

Fig. 4. Experiment × Polarity × Concreteness interactions (*experiment 1* vs. *experiment 2*). Bar plots represent *z* scores and SE. *A*: Experiment × Polarity × Concreteness interaction on reaction time. *B*: Experiment × Polarity × Concreteness interaction on time to peak of the grip aperture.

DISCUSSION

We hypothesized a disembodiment effect of sentential negation, consisting of a computational load reduction in concept-specific embodied neural systems that thus become more free to support concurrent tasks (Fig. 1*A*). Accordingly, we found that sentences describing actions involving arm musculature interfered less with kinematic parameters of congruent upper limb movements when presented in negative compared to affirmative form. In *experiment 1*, requiring a reach-to-grasp movement (Fig. 1*B*), we found faster reaction times and delayed time to peak of the grip aperture, selectively for negative versus affirmative proximal sentences, with no significant effects for either abstract or distal sentences. In *experiment 2*, requiring grasping without reaching (Fig. 1*C*), we found faster reaction times and delayed time to peak of grip aperture for negative versus affirmative distal sentences, a comparable, though reduced in size, reaction time effect for proximal sentences, and no effects for abstract sentences.

We interpret this dissociation across the two experiments, which was confirmed by the Experiment × Polarity × Concreteness interactions, as due to the factorial combination of a higher load on proximal versus a higher load on distal arm musculature for movement and sentences. Distal sentences did not contain descriptions of actions heavily involving the proximal arm musculature, but almost exclusively the distal musculature. Therefore, distal sentences did not interfere significantly with the kinematic parameters of the reach-to-grasp movement of *experiment 1*, which was characterized by a heavier load on proximal musculature, but only interfered with the grasp without reaching movement of *experiment 2*, which was characterized by a heavier load on distal musculature. Proximal sentences, in turn, contained descriptions of actions predominantly involving the proximal arm musculature but to some extent also involving the distal musculature (due to the hand interactions with target objects inherent to the employed transitive verbs). This may explain why proximal sentences clearly interfered with the kinematic parameters of *experiment 1* but to a more limited extent also with the movement onset measured by reaction times in *experiment 2*. Moreover, another possible source of difference between the two types of action-related sentences is due to the greater effort implied by action verbs referred to proximal arm musculature, given that the degree of effort associated with movements has been shown to modulate premotor region responses (Moody and Gennari 2010). Such a difference could particularly explain the partial effects for proximal sentences found in *experiment 2*.

Our interpretation of the results of *experiments 1* and *2* rests on the notion advanced by embodied and grounded theories of cognition (Barsalou 1999, 2008; Gallese and Lakoff 2005; Glenberg and Kaschak 2002) that concepts involve an automatic simulation of the corresponding primary neural processes. Thus accessing the conceptual content of words relies on the same somatic, sensory, or motor primary neural processes that are engaged by their semantic referents (Ghio and Tettamanti 2010; Pulvermüller 2005; Pulvermüller and Fadiga 2010; Tettamanti and Moro 2012; Willems and Hagoort 2007). Under circumstances in which both the linguistic access to conceptual knowledge and the primary processes (e.g., hand action-related language and hand movements) simultaneously compete for the utilization of the same neural resources, mutual interference effects can be observed (Boulenger et al. 2006; Buccino et al. 2005; but see Papeo et al. 2009 showing interference effects only at the postconceptual level). The notion of embodied conceptual systems was assumed here at a fine-grained level of lexical-semantic specificity, as reflected, on the one hand, by the distinction between sentences related to upper limb actions, showing Polarity effects, and abstract sentences, not showing any Polarity effects, and, on the other hand, between proximal and distal sentences, showing a dissociation pattern in *experiments 1* and *2*. Thus the observed dissociation points back to the separability of the neural systems controlling for movements involving either proximal or distal arm musculature.

Studies in humans, using TMS to elicit motor evoked potentials, evidenced how maps for proximal and distal upper limb muscles in the primary motor cortex are somatotopically arranged (Teitti et al. 2008), though largely overlapping (Devanne et al. 2006). The high degree of overlap probably facilitates complex muscle orchestration for programming and executing movements that involve both proximal and distal muscles, such as reach-to-grasp (Devanne et al. 2006; Melgari et al. 2008). In the macaque monkey, cortical stimulation studies found clearly separable premotor cortex representations for proximal forelimb movements involving reaching for grasping and for distal forelimb movements involving grasping without reaching (Gentilucci et al. 1988, 1989). In humans, however, proximal and distal maps in the premotor and supplementary motor cortices were not clearly separable with TMS (Teitti et al. 2008). As an explanation for such disparate findings, it has been proposed that both the primary motor cortex and the premotor cortex of monkeys and humans may not be primarily organized according to somatotopy but rather display a discontinuous somatic topography with multiple overlapping maps (Graziano 2006). These overlapping maps may differentiate different types of actions involving the upper limbs based on, in particular, the goal or meaning of the actions (possibly involving several upper limb parts in orchestration), the position of the hand, and the position of the target in the peripersonal space (Fernandino and Iacoboni 2010). The combination of these organization factors leads to a motor repertoire for specific upper limb actions, such as reaching or grasping, thus pointing to separable neural systems controlling for proximal reaching versus distal grasping movements.

These factors characterizing the organization of the primary motor and premotor cortices must be closely considered for the interpretation of the kind of kinematic parameters modulated by proximal and distal sentences in *experiments 1* and *2*. In *experiment 1* both an "early" kinematic parameter (reaction times) and a "late" kinematic parameter (grip aperture) were concerned. Similarly, in *experiment 2* the modulations concerned both early (reaction times) and late (grip aperture) kinematic parameters. This apparent overlap may be taken to speak against a concept-specific disembodiment effect of negation for sentences describing actions involving proximal versus distal arm musculature. In particular, if we were to attribute a strictly somatotopic organization to the motor cortex, we should have expected that grip aperture, which results from the action of distal arm muscles controlling for the extension of the thumb and index finger, should be modulated by distal sentences, irrespective of *experiments 1* and *2*. However, as noted above, the motor cortex organization primarily reflects factors other than somatotopy, such as the action type and the positions of both the hand and the target in the peripersonal space. It is therefore essential to consider that the same kinematic parameters were measured differently across *experiments 1* and *2*, and thus represent different kinematic phenomena in the two experiments. In *experiment 1*, requiring a reach-to-grasp movement, the reaction times reflected the activity of proximal musculature initiating the reaching movement (see also the discussion below), whereas the time to peak of the grip aperture was measured at an intermediate location between the hand start position and the location of the target object, namely, at a time point at which there is an ongoing orchestrated activity between proximal arm muscles controlling for the reaching kinematics and distal arm muscles controlling for the thumb-index aperture. This complex orchestrated muscular activity, as we have seen, is coded in specific motor cortical maps coding for reaching of the hand for an object at specific peripersonal space coordinates. It is therefore not surprising that such a relatively higher load on proximal reaching components in *experiment 1* resulted in significant reaction times and grip aperture effects for proximal but not for distal sentences. In *experiment 2*, in turn, the required kinematics was a grasping movement close to the position of the target object, with virtually no reaching movement required: reaction times were measured from the thumb-index distance velocity profile (rather than from the wrist velocity profile as in *experiment 1*), and thus this "early" effect was initiated by the activity of distal muscles, just like the "late" grip aperture effect. The distal grasping action required in *experiment 2* is most likely coded in specific motor cortical maps, distinct from those targeted by the reach-to-grasp movement required in *experiment 1*. It is therefore again not surprising that such a relatively higher load on distal grasping components in *experiment 2* resulted in significant reaction times and grip aperture effects for distal sentences. In addition, as already noted, the actions described by proximal verbs also marginally involved the distal arm musculature, and thus possibly also some distal kinematic action components (see Table 1), thus providing a plausible rationale for the more limited significant effects for proximal sentences in *experiment 2*.

A caveat to the interpretation of the present results in terms of interference reduction by negative action-related sentences on congruent movements is that our results only present weak evidence for an implied premise, namely, that in the affirmative polarity case action-related language and movement interfere on kinematic parameters, as shown by a previous study (Boulenger et al. 2006). Only in *experiment 1* did we find an effect of increased interference by affirmative proximal sentences with respect to affirmative abstract sentences. No comparable effects were found in *experiment 2*. There are some experimental differences that may explain such discrepancy between our study and that of Boulenger et al. (2006). First, while the latter authors used nonmanipulable object nouns as a control condition, we used abstract sentences. Abstract concepts are generally associated with increased processing difficulty with respect to concrete object-related concepts, because of the well-known concreteness effect (Schwanenflugel et al. 1988). The increased processing difficulty may have partially compensated for the relative advantage resulting from the lack of interference between abstract conceptual-semantic processing and upper limb movements, thus weakening the observable kinematic effects. Second, Boulenger et al. (2006) only employed a reach-to-grasp movement comparable to the movement required in our *experiment 1*. No distal grasp-only movements as required in our *experiment 2* were previously investigated in combined language-movement kinematic studies. Reference indicating the effect size of interference for affirmative language under the distal movement conditions of *experiment 2* is therefore lacking. In sum, the present study may have not provided the optimal conditions to replicate the interference effect of affirmative action-related language, and altogether this is a limitation of the present study. Perhaps using a different effector (e.g., foot action-related sentences) might have provided a more effective control condition than either abstract or distal versus proximal sentences. However, what matters here, in our view, is that we were able to demonstrate a clear kinematic effect for negative versus affirmative sentences, and that this effect, which we confidently interpret as an interference reduction (see also below), was specific for congruent action-related meanings compared with incongruent action-related and control abstract meanings.

Several aspects of our pattern of results deserve detailed consideration. First, our interpretations are based on the assumption that the participants in our study actually accessed the conceptual semantic content of the auditory experimental sentences. While there is little doubt that lexical-semantic access upon auditory word processing is a fast and automatic process (Friederici 2012), it could in principle well be that our participants did not listen attentively to the auditorily presented sentences, thus compromising the processing of auditory word forms and associated lexical-semantics altogether. That this was not the case is demonstrated by the highly significant correlations between the subjective verb frequency ratings collected in both experiments and the verb frequency ratings taken from the Corpus of Lexical Frequency of Written Italian (Laudanna et al. 1995). Not only were the subjective verb frequency ratings consistent with the linguistic corpus for both affirmative and negative sentences, but they were also highly consistent across the two groups participating in *experiments 1* and *2*, which consisted of entirely different subjects. Clearly, such a close correspondence would not have been observed if even a small subset of participants had not properly encoded the verb stimuli. As a consequence, we can be confident that conceptual semantic processing of the experimental sentences actually occurred.

Second, a significant Polarity $\times$ Concreteness $\times$ Latency interaction in the reaction times measured in *experiment 1*, as well as the subsequent post hoc tests, indicated that a significant modulation by negative proximal sentences was present when the reach-to-grasp movement was prompted at 0 ms but not when it was prompted at 500 ms after sentence presentation. As explained in the introduction, the Latency factor was introduced in *experiment 1* in order to account for the two-step simulation hypothesis of negation processing (Kaup et al. 2007). According to this hypothesis, the mental simulation of the factual state of affairs implied by sentential negation only occurs after the simulation of the counterfactual negated state of affairs, with a time delay of several hundred milliseconds (Anderson et al. 2010; Kaup et al. 2006; Lüdtke et al. 2008). Our results are not consistent with the two-step simulation hypothesis and with our related initial hypothesis, since they indicate that the effect of sentential negation on reaction times that can be measured at 0 ms movement latency has already disappeared after 500 ms. This suggests that the processing of negation occurs very early when listening to simple and short declarative sentences such as those used in the present experiment. The sentence presentation modality used in the present study markedly differs from the complex sentence-picture verification paradigm that has typically been used in studies leading to the two-step simulation hypothesis, in which there was a strong emphasis on inferring the correct truth value conveyed by sentential negation (Kaup et al. 2007). In fact, in circumstances under which the factual and counterfactual truth values must be put in direct opposition to choose the correct sentence-to-picture match from alternative choices, it may be necessary to engage in the explicit mental simulation of the affirmative sentence meaning first, followed by the negative meaning, in serial order, leading to two temporally disjoint mental representations. By contrast, under more passive sentence listening conditions that do not require a truth value verification, negation processing may occur earlier, following a principle of reduced accessibility of the negated information (Kaup 2001; Kaup and Zwaan 2003; MacDonald and Just 1989). This explanation would also be consistent with the lack of evidence in favor of the two-step simulation hypothesis in our previous fMRI study (Tettamanti et al. 2008), in which we also used a passive sentence listening task, even though such negative result must be considered with caution because of the limited temporal resolution of fMRI.

Third, we showed in *experiment 1* that the reach-to-grasp movement was characterized by a consistent temporal sequence of movement onsets, with the wrist moving first, followed by thumb-index finger, elbow, and shoulder. Thus the reaching movement was initiated by muscular activity that caused the wrist to move first. A wrist movement in the sagittal plane can be best explained by either a forearm pronosupination or a shoulder rotation. Other explanations, such rotations of elbow or shoulders, could not be evaluated by our model based on projections on the sagittal plane alone. However, all the viable explanations lead to the conclusion that, whatever the starter of the reaching movement, it involved proximal musculature. This explains why in *experiment 1* a significant effect of negation on reaction times was produced by proximal but not by distal sentences.

Fourth, negative versus affirmative sentences with semantic content congruent to the requested movement were associated with faster reaction times but with delayed time to peak of grip aperture. While the finding of faster reaction times can be rather intuitively understood under the disembodiment effect hypothesis as the consequence of a reduced interference compared with affirmative sentences (Buccino et al. 2005), the delay in time to peak requires further consideration. That the latter findings might also reflect a disembodiment effect clearly follows—as concisely anticipated in formulating our experimental hypotheses—from knowledge of kinematic variations in the reach-to-grasp movement that arise as a consequence of adverse movement conditions (Castiello 2005). In healthy subjects, for instance, grasping slippery objects leads to a larger grip aperture earlier during the reaching trajectory compared with grasping rough-surfaced objects (Smeets and Brenner 1999). Patients with optic ataxia, who present abnormalities in grasping kinematics (Jeannerod 1986), have been shown to adopt an exaggerated anticipatory grip aperture that correlates poorly with object size (Jeannerod et al. 1994). Furthermore, movements thoroughly planned in advance and guided by a feedforward strategy, as opposed to poorly planned movements adjusted online by a feedback strategy, are typically associated not only with faster reaction times but also with delayed times to peak of wrist acceleration and grip aperture, indicating a more precise performance (Gage et al. 2007; Lin et al. 2007). We therefore interpret our grip aperture findings as evidence of an interference of affirmative action-related sentences on congruent movements, which is reversed by the disembodiment effect of negation, leading to delayed times to peak for negative sentences.

In sum, our findings provide conclusive evidence in favor of a disembodiment effect of sentential negation. Compared with corresponding affirmative sentences, the comprehension of negative sentences is characterized by a computational load reduction in embodied conceptual representations, leaving a greater amount of neural resources available that can be exploited by competing primary processes. We also propose that the disembodiment effect of sentential negation is concept specific and follows a principle of lexical parsimony, requiring that only the affirmative form of a concept is stored in semantic memory while its negative counterpart is associated with—or possibly produced by—a transient reduction of the access to such stored semantic information. Altogether, we have demonstrated this neural specificity for closely related concepts such as proximal and distal upper limb movements (present study), as well as for more distant concepts in the abstract domain (Tettamanti et al. 2008). If sentential negation indeed blocks concept-specific semantic representations, it seems implausible that the syntactic generator of this blocking procedure itself be reduplicated in each and every concept-specific neural representation, as instead argued by Liuzza et al. (2011), stating that embodied action-related simulations in the motor system may also code for the syntactic features of negation. Indeed, the greatest challenge for future research in this field will be to elucidate how in the brain the semantic disembodiment effect of sentential negation is orchestrated at the syntactic level to promote sentence interpretation.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: E.B., A.T., P.F., and A.C. performed experiments; E.B., A.T., and M.T. analyzed data; E.B. and M.T. prepared figures; E.B., A.M., R.G., D.P., and M.T. drafted, edited and revised manuscript; E.B., A.T., P.F., A.C., A.M., R.G., D.P., and M.T. approved final version of manuscript; R.G., D.P., and M.T. conception and design of research.

REFERENCES

Anderson SE, Huette S, Matlock T, Spivey MJ. On the temporal dynamics of negated perceptual simulations. In: *Meaning, Form, and Body*, edited by Parrill F, Turner M, Tobin V. Stanford, CA: CSLI, 2010, p. 1–20.

Aziz-Zadeh L, Wilson SM, Rizzolatti G, Iacoboni M. Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Curr Biol* 16: 1818–1823, 2006.

Barsalou LW. Perceptual symbol systems. *Behav Brain Sci* 22: 577–609, 1999.

Barsalou LW. Grounded cognition. *Annu Rev Psychol* 59: 617–645, 2008.

Binder JR, Desai RH. The neurobiology of semantic memory. *Trends Cogn Sci* 15: 527–536, 2011.

Boulenger V, Roy AC, Paulignan Y, Deprez V, Jeannerod M, Nazir TA. Cross-talk between language processes and overt motor behavior in the first 200 msec of processing. *J Cogn Neurosci* 18: 1607–1615, 2006.

Buccino G, Riggio L, Melli G, Binkofski F, Gallese V, Rizzolatti G. Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. *Brain Res Cogn Brain Res* 24: 355–363, 2005.

Carpenter PA, Just MA. Sentence comprehension: a psycholinguistic processing model of verification. *Psychol Rev* 82: 45–73, 1975.

Castiello U. The neuroscience of grasping. *Nat Rev Neurosci* 6: 726–736, 2005.

Dale R, Duran ND. The cognitive dynamics of negated sentence verification. *Cogn Sci* 35: 983–996, 2011.

Devanne H, Cassim F, Ethier C, Brizzi L, Thevenon A, Capaday C. The comparable size and overlapping nature of upper limb distal and proximal muscle representations in the human motor cortex. *Eur J Neurosci* 23: 2467–2476, 2006.

Fernandino L, Iacoboni M. Are cortical motor maps based on body parts or coordinated actions? Implications for embodied semantics. *Brain Lang* 112: 44–53, 2010.

Friederici AD. The cortical language circuit: from auditory perception to sentence comprehension. *Trends Cogn Sci* 16: 262–268, 2012.

Gage WH, Zabjek KF, Hill SW, McIlroy WE. Parallels in control of voluntary and perturbation-evoked reach-to-grasp movements: EMG and kinematics. *Exp Brain Res* 181: 627–637, 2007.

Gallese V, Lakoff G. The brain's concepts: the role of the Sensory-motor system in conceptual knowledge. *Cogn Neuropsychol* 22: 455–479, 2005.

Gentilucci M, Fogassi L, Luppino G, Matelli M, Camarda R, Rizzolatti G. Functional organization of inferior area 6 in the macaque monkey. *Exp Brain Res* 71: 475–490, 1988.

Gentilucci M, Fogassi L, Luppino G, Matelli M, Camarda R, Rizzolatti G. Somatotopic representation in inferior area 6 of the macaque monkey. *Brain Behav Evol* 33: 118–121, 1989.

Ghio M, Tettamanti M. Semantic domain-specific functional integration for action-related vs. abstract concepts. *Brain Lang* 112: 223–232, 2010.

Glenberg AM, Kaschak MP. Grounding language in action. *Psychon Bull Rev* 9: 558–565, 2002.

Glenberg AM, Robertson DA, Jansen JL, Johnson-Glenberg MC. Not propositions. *J Cogn Sys Res* 1: 19–33, 1999.

Graziano M. The organization of behavioral repertoire in motor cortex. *Annu Rev Neurosci* 29: 105–134, 2006.

Hauk O, Johnsrude I, Pulvermuller F. Somatotopic representation of action words in human motor and premotor cortex. *Neuron* 41: 301–307, 2004.

Horn LR. *A Natural History of Negation*. Chicago, IL: Univ. of Chicago Press, 1989.

Jeannerod M. Mechanisms of visuomotor coordination: a study in normal and brain-damaged subjects. *Neuropsychologia* 24: 41–78, 1986.

Jeannerod M, Decety J, Michel F. Impairment of grasping movements following a bilateral posterior parietal lesion. *Neuropsychologia* 32: 369–380, 1994.

Kaup B. Negation and its impact on the accessibility of text information. *Mem Cognit* 29: 960–967, 2001.

Kaup B, Lüdtke J, Zwaan RA. Processing negated sentences with contradictory predicates: is a door that is not open mentally closed? *J Pragmat* 38: 1033–1050, 2006.

Kaup B, Zwaan RA. Effects of negation and situational presence on the accessibility of text information. *J Exp Psychol Learn Mem Cogn* 29: 439–446, 2003.

Kaup B, Zwaan RA, Lüdtke J. The experiential view of language comprehension: how is negation represented? In: *Higher Level Language Processes in the Brain: Inference and Comprehension Processes*, edited by Schmalhofer FA, Perfetti CA. Mahwah, NJ: Erlbaum, 2007, p. 255–288.

Kiefer M, Pulvermüller F. Conceptual representations in mind and brain: theoretical developments, current evidence and future directions. *Cortex* 48: 805–825, 2012.

Laudanna A, Thornton AM, Brown G, Burani C, Marconi L. Un corpus dell'italiano scritto contemporaneo dalla parte del ricevente. In: *III Giornate internazionali di Analisi Statistica dei Dati Testuali*, edited by Bolasco S, Lebart L, Salem A. Rome: Cisu, 1995, p. 103–109.

Lin K, Wu C, Wei T, Lee C, Liu J. Effects of modified constraint-induced movement therapy on reach-to-grasp movements and functional performance after chronic stroke: a randomized controlled study. *Clin Rehabil* 21: 1075–1086, 2007.

Liuzza MT, Candidi M, Aglioti SM. Do not resonate with actions: sentence polarity modulates cortico-spinal excitability during action-related sentence reading. *PLoS One* 6: e16855, 2011.

Lüdtke J, Friedrich CK, De Filippis M, Kaup B. Event-related potential correlates of negation in a sentence-picture verification paradigm. *J Cogn Neurosci* 20: 1355–1370, 2008.

MacDonald MC, Just MA. Changes in activation levels with negation. *J Exp Psychol Learn Mem Cogn* 15: 633–642, 1989.

Melgari JM, Pasqualetti P, Pauri F, Rossini PM. Muscles in "concert": study of primary motor cortex upper limb functional topography. *PLoS One* 3: e3069, 2008.

Meteyard L, Cuadrado SR, Bahrami B, Vigliocco G. Coming of age: a review of embodiment and the neuroscience of semantics. *Cortex* 48: 788–804, 2012.

Moody CL, Gennari SP. Effects of implied physical effort in sensory-motor and pre-frontal cortex during language comprehension. *Neuroimage* 49: 782–793, 2010.

Moro A. *The Boundaries of Babel*. Cambridge, MA: MIT Press, 2008.

Nieuwland MS, Kuperberg GR. When the truth is not too hard to handle: an event-related potential study on the pragmatics of negation. *Psychol Sci* 19: 1213–1218, 2008.

Oldfield RC. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9: 97–113, 1971.

Papeo L, Vallesi A, Isaja A, Rumiati RI. Effects of TMS on different stages of motor and non-motor verb processing in the primary motor cortex. *PLoS One* 4: e4508, 2009.

Pulvermüller F. Brain mechanisms linking language and action. *Nat Rev Neurosci* 6: 576–582, 2005.

Pulvermüller F, Fadiga L. Active perception: sensorimotor circuits as a cortical basis for language. *Nat Rev Neurosci* 11: 351–360, 2010.

Schwanenflugel PJ, Harnishfeger KK, Stowe RW. Context availability and lexical decisions for abstract and concrete words. *J Mem Lang* 27: 499–520, 1988.

Smeets JB, Brenner E. A new view on grasping. *Motor Control* 3: 237–271, 1999.

Teitti S, Määttä S, Säisänen L, Könönen M, Vanninen R, Hannula H, Mervaala E, Karhu J. Non-primary motor areas in the human frontal lobe are connected directly to hand muscles. *Neuroimage* 40: 1243–1250, 2008.

Tettamanti M, Buccino G, Saccuman MC, Gallese V, Danna M, Scifo P, Fazio F, Rizzolatti G, Cappa SF, Perani D. Listening to action-related sentences activates fronto-parietal motor circuits. *J Cogn Neurosci* 17: 273–281, 2005.

Tettamanti M, Manenti R, Della Rosa PA, Falini A, Perani D, Cappa SF, Moro A. Negation in the brain: modulating action representations. *Neuroimage* 43: 358–367, 2008.

Tettamanti M, Moro A. Can syntax appear in a mirror (system)? *Cortex* 48: 923–935, 2012.

Tomasino B, Weiss PH, Fink GR. To move or not to move: imperatives modulate action-related verb processing in the motor system. *Neuroscience* 169: 246–258, 2010.

Trabasso T, Rollins H, Shaughnessy E. Storage and verification stages in processing concepts. *Cogn Psychol* 2: 239–289, 1971.

Willems RM, Hagoort P. Neural evidence for the interplay between language, gesture, and action: a review. *Brain Lang* 101: 278–289, 2007.

Zanuttini R. *Negation and Clausal Structure: A Comparative Study of Romance Languages*. Oxford, UK: Oxford Univ. Press, 1997.