

Accepted Manuscript

Title: A touch with words: Dynamic synergies between manual actions and language

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PII: S0149-7634(15)30291-8

DOI: <http://dx.doi.org/doi:10.1016/j.neubiorev.2016.04.022>

Reference: NBR 2425



To appear in:

Received date: 16-11-2015

Revised date: 14-4-2016

Accepted date: 27-4-2016

Please cite this article as: García, Adolfo M., Ibáñez, Agustín, A touch with words: Dynamic synergies between manual actions and language. *Neuroscience and Biobehavioral Reviews* <http://dx.doi.org/10.1016/j.neubiorev.2016.04.022>

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A touch with words: Dynamic synergies between manual actions and language

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Highlights

- We review 108 experiments involving manual responses to hand-related verbal units.
- Such units either facilitate or delay manual actions in different time windows.
- Effects depend on verbal and motor demands, and the time-lag between both processes.
- We model key findings using dynamic neural-network and predictive-coding tenets.
- Our model paves the way for new basic and applied research on embodied cognition.

Abstract

Manual actions are a hallmark of humanness. Their underlying neural circuitry gives rise to species-specific skills and interacts with language processes. In particular, multiple studies show that hand-related expressions –verbal units evoking manual activity– variously affect concurrent manual actions, yielding apparently controversial results (interference, facilitation, or null effects) in varied time windows. Through a systematic review of 108 experiments, we show that such effects are driven by several factors, such as the level of verbal processing, action complexity, and the time-lag between linguistic and motor processes. We reconcile key empirical patterns by introducing the Hand-Action-Network Dynamic Language Embodiment (HANDLE) model, an integrative framework based on neural coupling dynamics and predictive-coding principles. To conclude, we assess HANDLE against the backdrop of other action-cognition theories, illustrate its potential applications to understand high-level deficits in motor disorders, and discuss key challenges for further development. In sum, our work aligns with the ‘pragmatic turn’, moving away from passive and static representationalist perspectives to a more dynamic, enactive, and embodied conceptualization of cognitive processes.

Keywords: language embodiment; hand-related language; manual-action networks; predictive coding; enactive cognition.

1 Introduction

Our hands, no less than our verbal or social skills, are a hallmark of humanness. Perhaps partially due to changes in the noncoding sequence HACNS1 (Prabhakar et al., 2008), these extremities have become increasingly complex since the days of the *Homo habilis* (Almeciya et al., 2015; Marzke and Marzke, 2000; Napier, 1962). Relative to other primates, we possess shorter and more stress-resilient palms, straighter and more articulated fingers, and larger fully opposable thumbs (Young, 2003). Such adaptations support a vast species-specific skill set: they allow us to draw highly detailed landscapes, play inspiring melodies, and manipulate the most varied tools. Less obviously, manual processes also interact with our language processing mechanisms, as we argue in this paper.

Neurally speaking, hand actions are subserved by a significant proportion of the sensorimotor cortex (Martuzzi et al., 2014), Broca's area (Nishitani et al., 2005), the cerebellum (van der Zwaag et al., 2013), and other subcortical structures (Radman et al., 2013). Though highly specialized (Hashimoto et al., 2013), such broad circuits are intimately involved in multiple cognitive processes. For instance, cortical and subcortical motor-related regions are engaged by both execution and imagery of visually guided movements (Binkofski et al., 2000), including manual and mental rotation (Parsons et al., 1995). Likewise, the above areas have been implicated in verbal processing, which supports the view that language networks may have evolved from regions originally devoted to gesture (Cartmill et al., 2012; Corballis, 2003). More particularly, in

line with embodied views of language (Barsalou, 1999; Gallese and Lakoff, 2005), this functional synergy may be critical for the construal of verbal semantics (van Elk et al., 2014).

To shed light on the issue, we examined how ongoing manual actions interact with hand-related expressions (HREs) –namely, verbal units which denote or imply manual activity. Specifically, we reviewed over 100 experiments requiring overt manual responses in the context of HREs. Our general prediction was that such expressions would distinctively resonate in hand motor networks, resulting in either interference or facilitation of concurrent movements. To account for the main patterns identified, we developed a framework called Hand-Action-Network Dynamic Language Embodiment (HANDLE). This model, rather than explaining motor action or embodied semantics on their own, specifically accounts for the situated coupling of both domains by reference to activation thresholds in relevant networks. Its goal is to provide an overarching interpretation of the empirical corpus it addresses. In short, we aim to specify key functional determinants of language embodiment while examining the continuous interplay of varied neurocognitive processes.

2 Background and research aims

The most widely cited demonstrations of hand-specific language-induced motor resonance come from neuroscientific research. Crucially, as shown in Figure 1, HREs elicit somatotopic activations in motor and premotor regions (e.g., Aziz-Zadeh et al., 2006; de Vega et al., 2014; Hauk

et al., 2004; Pulvermüller, 2005; Tettamanti et al., 2005), and their processing is facilitated upon transcranial magnetic stimulation of the hand motor area (Buccino et al., 2005; Gianelli and Dalla Volta, 2014; Papeo et al., 2009).

-----Insert Figure 1 about here-----

Despite certain inconsistencies (Arevalo et al., 2012; Cardona et al., 2013; Postle et al., 2008), such evidence indicates that verbal units alluding to hands are grounded in effector-specific circuits –for a meta-analysis, see Jirak et al. (2010). However, HRE processing in these studies was not accompanied by *concurrent execution of variously complex manual actions*. This phenomenon, known as motor-language coupling (García & Ibáñez, 2014a; Ibáñez et al., 2013; Melloni et al., 2015), involves the situated *integration* of verbal processes and deliberate bodily movements, creating cross-domain effects which do not emerge in exclusively linguistic or exclusively motor tasks.

Only a few studies have assessed the brain correlates of binding HREs with congruent and incongruent *ongoing* hand movements (for informative exceptions, also included in this work, see Aravena et al., 2010; Glenberg et al., 2008b; Ibáñez et al., 2013; Melloni et al., 2015). Conversely, such effects have been more extensively assessed in behavioral studies. Through strategic manipulations of stimulus- and task-

related variables, multiple experiments have examined whether and when manual actions and HREs facilitate or interfere with each other. Though blind to neuronal correlates, this evidence may offer critical insights into language embodiment and situated cognition at large.

At first sight, individual results are so varied that the field may appear chaotic. Available studies use different tasks and stimuli, and report different effects (interference, facilitation, null results) in various time windows. However, a joint analysis of the evidence may reveal systematic temporal and functional patterns. Previous reviews have assessed broad aspects of motor-language coupling (e.g., Cardona et al., 2013; Fischer and Zwaan, 2008; García and Ibáñez, 2014a; García and Ibáñez, in press) without a specific concern for any single effector. Moreover, recent papers revising such crosstalk with a focus on ongoing hand movements discuss very few studies and fail to disentangle the role of critical variables (Borghi et al., 2010; Chersi et al., 2010). The ensuing proposals are thus empirically underdetermined to characterize fine-grained determinants of language embodiment.

To circumvent such limitations, we conducted an overarching review of reciprocal effects between HREs and manual actions. Our analysis contemplated 108 experiments reported in 51 papers, including varied linguistic units (from various classes of single words to simple and complex sentences), movement types (e.g., single-key presses, object-targeted manual actions), and theoretical contrasts (e.g., semantic vs. form-level processing, congruent vs. incongruent action-language couplings) –see Appendix. All the experiments involved comparisons between

HREs and other linguistic units, or between different types of HREs. Specifically, by analyzing the above variables, we aimed to shed light on five unresolved issues concerning the embodiment of HREs, as listed in Table 1.

By addressing these questions, we seek to establish a multi-factorial set of empirical constraints for a model of HRE embodiment –the HANDLE framework (see section 6). In doing so, we will emphasize that cognition and action are inseparable (Cartmill et al., 2012). Breaking away from isolationist approaches to each domain can bring us closer to understanding this particular form of neurocognition as an integrative phenomenon.

3 Study selection criteria and review method

The 108 experiments reviewed below were selected following two criteria. First, task performance had to require a manual response, involving finger, hand, wrist, and/or arm movements (e.g., key pressing, hand displacing, object grasping). Second, at least one experimental condition had to involve HREs, namely: verbs denoting manual actions, nouns denoting manipulable objects, adjectives implying manual affordances of objects, adverbs associated with gestures or movement direction. These units were respectively termed hand-related verbs (HRVs), nouns (HRNs), adjectives (HRAjds), and adverbs (HRAjds). Throughout the review, we targeted contrasts and subdesigns that specifically compared

congruent and incongruent action-language couplings. Importantly, while several experiments were reported as part of a single study, almost all of them were performed by different samples, which guarantees independence of the results and allows for more robust generalizations.

To maximize comprehensiveness in our literature compilation, we performed several searches in PubMed combining relevant keywords (e.g., ‘language’, ‘action language’, ‘hands’, ‘hand motor area’, ‘motor resonance’, ‘effector specificity’, ‘embodiment’, ‘affordances’). We also looked for papers citing relevant theoretical proposals, such as the Indexical Theory (Glenberg and Robertson, 2000), the Action-based Language model (Glenberg and Gallese, 2012), the Theory of Event Coding (Hommel et al., 2001), and Pulvermüller’s Hebbian model (Pulvermüller, 2005). Each hit was set aside for in-depth analysis and its references were individually scrutinized in search of further relevant studies.

All selected papers were reviewed via a systematic procedure. First, we identified the experiments and/or subdesigns which met our inclusion criteria. Second, we reviewed each experiment/subdesign summarizing the following information: (a) sample description; (b) stimuli and conditions; (c) task variables (including type of manual action, level of linguistic processing, and temporal relation between HREs and hand responses); (d) motor-language integration effects (facilitation, interference, null); and (e) timing of the results. All this information is summarized in the Appendix (sections A and B, Tables A1-A9 and B1-B8).

In the quest of interpretable patterns, we first grouped the experiments according to the linguistic unit they involved, namely: single words or sentences. This principle responds to the different processing demands required by each type of unit. Compared to words, sentences impose greater executive load, involve within-trial anticipatory processes based on cloze predictability, and their greater representational detail may prolong reverberation in relevant motor circuits and lead to more situated simulations (see Glenberg and Kaschak, 2002; Marino et al., 2012). Incidentally, relevant linguistic factors are more numerous and harder to control in sentential than in lexical stimuli.

Furthermore, we distinguished between two types of motor measures. On the one hand, global aspects of action processes can be assessed by considering reaction times (RTs). These capture the time-lapse between stimulus presentation and the completion of a manual movement, offering reliable indications of the overall impact of HREs on motor circuits. On the other hand, various details of an action's unfolding are revealed by kinematic variables. Aspects such as hand movement speed, peak velocity, or finger aperture reveal the impact of HREs on an action's ongoing deployment.

Finally, manual responses in behavioral studies may fall on varied points along a continuum of motor complexity, ranging from relatively simple (e.g., object holding, single-key pressing) to considerably complex (e.g., gesturing, object grasping). Throughout our review, we paid close attention to the experiments' distinctive manual demands. These are minimal in simple tasks; in single-key presses, for instance, an individual

finger needs to be lifted a few millimeters before landing on the same key trial after trial, while the rest of the hand and arm remain static. Instead, motor demands are greater in more complex tasks; for example, in object-grasping paradigms, participants must lift an arm, twist the wrist, estimate adequate finger aperture, and wrap their hand around a distant object. Relative to single-key presses, these actions make greater use of executive control mechanisms and involve more muscular activity. Moreover, evidence from macaques shows that whereas some neurons in the premotor cortex respond to general hand-movement categories, others are sensitive to specific object affordances (e.g., precision vs. whole-hand grasps) (Fadiga et al., 2000). Similarly, manual task demands influence the involvement of motor-semantic networks during gesture comprehension (Yang et al., 2015). Thus, a model of HRE embodiment cannot be blind to the impact of motor demands.

The structure of the review is schematized in Figure 2.

-----Insert Figure 2 about here-----

4 Single-word processing

The interplay between hand-related words and manual activity was assessed in 55 experiments. The tasks required actions of varied complexity. HREs included verbs, nouns, adjectives, and adverbs from six languages (English, Italian, Dutch, French, German, and Spanish). Additional details are offered in the Appendix (section A, Tables A1-A9).

4.1 Single-word HREs and global measures of manual action

In semantic decision tasks, HRVs delay simple actions, such as single-key presses (Sato et al., 2008, Exps. 1 and 2) and hand displacements (Spadacenta et al., 2014, Exp. 1), within the first 400 ms after or during word processing. Instead, RTs are shorter if simple responses occur in a later time window (450-750 ms post-word onset) (Dalla Volta et al., 2014; Dalla Volta et al., 2009). Beyond the one-second mark, HRVs yield null RT effects (Sato et al., 2008, Exp. 2). Thus, in basic semantic tasks, the integration of HREs and simple manual actions causes early interference, followed by short-lived facilitation which then leads to null effects.

However, interference on action planning lasts considerably longer if semantic or motor demands increase. First, when an HRV is assessed for semantic congruency with an image or another word, single-key presses show long-lasting delays (700-950 ms) for same-effector pairs (Bergen et al., 2010) –Figure 3, Panel A. Such extended interference may be greater for certain types of HRVs (e.g., for ‘cutting’ than for ‘hitting’ verbs),

especially if motor networks are affected by neurodegeneration (Kemmerer et al., 2013). Second, when semantic decision is made via whole-hand displacement, HRVs delay RTs even if presented 600 ms before the ‘go’ signal (Mirabella et al., 2012, Exps. 1 through 4) –Figure 3, Panel B. Third, using a primed-word-copying paradigm, García and Ibáñez (2016) found that planning of keyboard-typing actions was differentially delayed for HRVs when processed for over one second –Figure 3, Panel C. Interestingly, the latter two studies showed that effector-specific interference decreased through time.

-----Insert Figure 3 about here-----

Note, at this juncture, that virtually all the experiments yielding interference employed stimuli which explicitly allude to hands –crucially, HRVs. However, motor-semantic integration is radically different when words refer to the *action’s goal* rather than to the effector itself (e.g., HRAdv and HRAdj). For instance, in a task which required grasping objects on opposite sides of a table, guided by the adjectives *left* or *right*, compatible conditions led to faster RTs between 500 and 550 ms (Lindemann et al., 2006, Exp. 2). Likewise, the word *eye* eased preparation of the action of picking up a magnifying glass (Lindemann et al., 2006, Exp. 1) –Figure 4. RTs for specific grasping types were also facilitated by words implying distinctive object properties (Masson et al., 2008; Tucker and Ellis, 2004). For example, names of objects which could be grabbed with either a precision or a power grasp prompted such actions on items with compatible affordances (Tucker and Ellis, 2004).

Facilitation is also observed when HREs need to be judged for congruency with action videos showing full execution of hand movements (Kelly et al., 2010; see also Springer and Prinz, 2010). These results suggest that hand motor networks are excited rather than inhibited by indications of the movement's aim or its ongoing deployment.

-----Insert Figure 4 about here-----

Finally, manual actions seem impervious to HREs in shallower processing tasks. The early single-key pressing effects reported by Sato and colleagues during semantic decision did not emerge in lexical decision (Sato et al., 2008, Exp. 3), as also shown by Pulvermüller et al. (2001, Exp. 2). Similarly, a primed lexical decision study failed to find clearly significant effects for noun pairs sharing their manner of manipulation (Myung et al., 2006; see also Spadacenta et al., 2014, Exp. 3). Moreover, when hand displacement was guided by either letter or color identification, HRVs showed no distinct effects (Mirabella et al., 2012, Exp. 4; Spadacenta et al., 2014, Exp 2). The same is true in more complex motor tasks. HRVs failed to modulate RTs during object grasping guided by letter identification (Lindemann et al., 2006, Exp. 4) or lexical decision (Boulenger et al., 2008). The latter finding was replicated by Boulenger et al. (2006) and Nazir et al. (2008), although they collapsed HRVs with verbs alluding to other effectors. Thus, when semantic access is irrelevant for task completion, HREs do not seem to induce significant motor resonance.

In sum, single-word HREs variously affect action planning. First, in low-demand semantic tasks, HRVs yield interference in early windows (0-400 ms), facilitation at later intervals (450-750 ms), and null effects beyond those time marks. However, interference may last for 1000 ms if semantic or motor demands increase. Second, manual activity is facilitated by words alluding to the action's intended effects. Finally, response planning is indifferent to HREs when semantic processing can be bypassed.

4.2 Single-word HREs and the unfolding of manual actions

In the study by Frak et al. (2010), participants listened to words while holding an object with pressure-sensitive sensors – Figure 5. HRVs significantly affected gripping, with strength increasing at 100 ms, peaking at 380 ms, and decaying after 400 ms. Also, in semantic decision tasks, those verbs selectively reduced peak velocity of finger opening and hand lifting (Dalla Volta et al., 2009, Exps. 1 and 3).

-----Insert Figure 5 about here-----

HREs also interfered with hand kinematics in gesturing and pointing studies. Bernardis and Gentilucci (2006, Exps. 1 and 2) asked participants to view one of three words (*hello, no, stop*) and respond in different ways (e.g., executing the corresponding gesture, pronouncing the word, doing both things at once). HREs delayed the execution of compatible gestures in a window of 400-550 ms after word production. Similar results were obtained by (Barbieri et al., 2009). In three experiments, participants watched videoclips of an actress performing the tasks above and responded by producing the same word, the same gesture, or both. Congruency between words and gestures systematically led to kinematic interference, even when the former were not overtly pronounced.

In addition, whole-word typing takes longer for HRVs relative to abstract verbs –although the delay is also seen for verbs denoting other effectors (García and Ibáñez, 2016). By the same token, HRVs interfere with object grasping at roughly 250 ms after word onset (Dalla Volta et al., 2009, Exp. 2) –but see Fargier et al. (2012) and Gentilucci (2003) for opposite results when semantic processing was not required. The same is true when HRVs are presented subliminally (Boulenger et al., 2008). Importantly, when object reaching is guided by letter identification, HREs have no differential impact on kinematics (Lindemann et al., 2006, Exp. 4), confirming that the observed effects are guided by semantic processing.

Once again, note that interference emerges with stimuli featuring explicit effector-specific information (words or videoclips). However, as previously noted for motor planning, kinematic variables are facilitated by HREs specifying aspects of the *action's goal*. The mechanics of pointing towards oneself or to a remote position are assisted upon reading the deictics *here* and *there*, respectively (Chieffi et al., 2009, Exp. 1). Also, grasping kinematics are prompted by compatibility between object location and HRAdvS (e.g., *up*, *down*, *near*, *far*) (Gentilucci et al., 2000; Kritikos et al., 2012). Similarly, specific grasping variables are facilitated by HRNs implying either small or large grip apertures (Glover et al., 2004, Exp. 1), or HRAdjS indicating distinctive object affordances (e.g., *long*) (Gentilucci and Gangitano, 1998). The only exception to this robust pattern are the null kinematic effects reported by (Lindemann et al., 2006) –see section 4.3 for an insight on this point.

In brief, single-word HREs interfere with the unfolding of manual activity if they explicitly allude to hands, but induce facilitation if referred to aspects of the action's intended effects. Such a pattern closely mirrors the one observed for motor planning, suggesting a relationship between integration mechanisms across processing stages.

4.3 Single-word HREs and manual actions: Brief interim assessment

Single-word HREs systematically modulate manual actions, but only when their semantic information is engaged. In tasks with low demands, HRVs delay action execution in early windows (up to 400 ms) and facilitate it between 450 and 750 ms. If semantic or motor demands increase, interference becomes long-lived (up to 1000 ms) and consistently affects action deployment. However, when HREs convey aspects of the action's goal, manual responses are facilitated.

At first glance, this summary would seem to suggest great consistency between global and kinematic measures. Yet, most studies reporting data for both dimensions coincide in a noteworthy pattern: if HREs distinctively modulate actions at a global level, they tend to have null effects on kinematics, and vice versa (see Appendix, section A, Tables A1-A9). Thus, action-semantic integration seems to involve a tradeoff between global and action-unfolding dynamics.

Finally, all this evidence offers hints to the questions in Table 1. Such issues are treated in section 6.

5 Sentence processing

Manual actions and sentential HREs were jointly assessed in 53 experiments. These included single-key pressing tasks and variations of the action-sentence compatibility effect (ACE) paradigm. Stimuli were presented in five languages: Italian, English, Spanish, German, and French. Additional details are offered in the Appendix (section B, Tables B1-B8).

5.1 Sentential HREs and global measures of manual action

Buccino et al. (2005) assessed semantic decision to simple sentences via single-key presses. Manual RTs to stimuli with HRVs were differentially delayed within a 300-400 ms window. A replication study (Gianelli and Dalla Volta, 2014) showed a similar modulation on mean RTs, although the result did not reach significance. HRVs also inhibit motor networks if framed within complex sentences, but this result is contingent on temporal and modal semantic constraints. Late delays emerge when two hand-related clauses are linked by *while* but not by *after* (de Vega et al., 2004; Santana and de Vega, 2013). However, the effect disappears if one of the HRVs is embedded in a mental clause (de Vega et al., 2004) or preceded by a negation (Aravena et al., 2012), and it is reversed if one of the clauses denotes a different effector (de Vega et al., 2004). Thus, effector-specific delays for connected hand-related clauses occur only if these are presented as simultaneous and factual.

Yet, as previously observed with isolated words, single-key responses to manual-action sentences become faster at later time windows (500-800 ms or beyond one second), suggesting an extended resonance driven by increased semantic effort. Klatzky et al. (1989) first showed that sensibility judgments to object-action phrases are facilitated if primed by congruent hand shapes. For example, the word *palm* prompts processing of the target phrase *patting a dog*. Also through sensibility judgments, Borghi and Scorolli (2009) observed that RTs to hand-action sentences are differentially facilitated if the direct object is an HRN. Similar results were reported by Marino et al. (2012), who further noted that the effect is enhanced with HRVs which highly constrain the range of possible target objects (e.g., *to water*, *to sign*). Interestingly, these results do not obtain when responses are performed with the non-dominant hand (Borghi and Scorolli, 2009; Marino et al., 2012). Hence, this longer-lasting facilitation induced by the verbs shows effector-laterality specificity.

Another set of studies assessed the impact of HRVs on hand displacement via the ACE paradigm. In its original formulation (Glenberg and Kaschak, 2002), the task requires processing sentences which denote actions toward or away from the body (e.g., *Courtney handed you the notebook* / *You handed Courtney the notebook*) and judging their sensibility by pressing a button close to or far from the body. The critical finding is that compatible conditions yield shorter RTs, even if the sentences denote abstract transfer (*Liz told you the story* / *You told Liz the story*) (Borreggine and Kaschak, 2006; De Vega et al., 2013; Diefenbach et al., 2013; Glenberg and Kaschak, 2002; Glenberg et al., 2008b; Kaschak and Borreggine, 2008; Lugli et al., 2012). The effect is specifically driven by compatibility between the HRV and the response

direction, as it disappears when sensibility judgments to either sentence type are made with single-key presses (Glenberg and Kaschak, 2002, Exp. 2B). However, this positive ACE may dissipate and even turn into interference depending on the time allotted to response planning and execution (Borreggine and Kaschak, 2006; De Vega et al., 2013; Diefenbach et al., 2013; Kaschak and Borreggine, 2008). As proposed by Diefenbach et al. (2013) and Kaschak and Borreggine (2008), responses to compatible sentences become faster if prepared around sentence onset, but are delayed if preparation occurs towards or after the end of the sentence. However, we will add that a key determinant of these effects is the time at which the response is actually executed (see section 6.3). Interference also occurs after repeated training of congruent manual movements (Glenberg et al., 2008a). Incidentally, the effect is modulated by emotional connotations (Lugli et al., 2012) and social-context variables (Gianelli et al., 2013), and it disappears when the non-dominant hand is used (Glenberg et al., 2008a, Exp. 4).

The crosstalk between manual actions and sentences with HRVs is also sensitive to specific hand shapes. This has been shown through a variation of the ACE paradigm. In it, participants are presented with two clauses. The first one depicts a situation and the second one includes a highly expectable verb denoting an open-hand or a closed-hand action (e.g., *applauding* and *hammering*, respectively). Participants must judge their sensibility by pressing a button with either an open or a closed hand –Figure 6. When performed by healthy participants, the task consistently reveals facilitation by compatibility between sentence and action (Aravena et al., 2010; Cardona et al., 2014; Ibáñez et al., 2013; Kargieman et al., 2014; Melloni et al., 2015). The effect results from a reciprocal early modulation of motor and semantic brain regions (Ibáñez

et al., 2013, Exp. 2) –Figure 7, and is robust enough to emerge even in patients with musculoskeletal (non-neural) motor alterations (Cardona et al., 2014). However, it is abolished in patients with neurodegenerative motor disorders, such as Huntington’s disease (Kargieman et al., 2014) or Parkinson’s disease (Cardona et al., 2014; Ibáñez et al., 2013; Melloni et al., 2015) –see section 7.2. On the whole, this evidence demonstrates that HRE embodiment is fine-grained, affected by motor-network damage, and specifically dependent on neural components of the motor system.

-----Insert Figure 6 about here-----

-----Insert Figure 7 about here-----

Action-goal information also facilitates more complex manual movements. In a series of experiments (Zwaan and Taylor, 2006), participants listened to sentences denoting clockwise (e.g., *sharpen the pencil*) or counterclockwise (e.g., *remove the screw*) actions and performed sensibility judgments by turning a knob either to the right or to the left. Different versions of the task consistently revealed facilitation by compatibility in an early window (100-400 ms), suggesting that the effect is localized to the moment at which the HRV is processed. By the same token, Masson et al. (2008, Exp. 2) showed that functional and volumetric affordances of HRNs in action sentences facilitate congruent grasp types on the

corresponding objects. Notably, this was the case even if the sentence did not convey a manual interaction (e.g., *kicking a calculator*). These findings align with the view that HREs evoking teleological aspects of an ongoing action assist manual motor programming.

Taken together, the data warrant three tentative conclusions. First, single-key presses are delayed by factual sentences with HRVs, but they are assisted if aspects of the action's aim are specified. Second, when whole-hand responses are involved, compatibility between sentence meaning and manual shape or direction may yield facilitation (if actions are planned early on) or interference (if response planning and execution are delayed). Third, the integration between HREs and hand-motor networks shows lateral specificity, as these effects are absent or modified when tasks are performed with the non-dominant hand.

5.2 Sentential HREs and the unfolding of manual actions

The evidence on the crosstalk between sentential HREs and manual action unfolding is scantier. Sentences with HRVs differentially increase grip force during object holding in various windows ranging from 120 to 800 ms (Aravena et al., 2012, 2014). Such effect disappears if sentences are negative (Aravena et al., 2012), or presented in a volitional (Aravena et al., 2014, Exp. 1) or non-action (Aravena et al., 2014, Exp. 2) context. This confirms that effector-specific motor resonance is not triggered unless HREs are construed as factual events. The impact of contextual

factors is such that even the presence of another person during the task may modulate manual kinematics during HRE processing (Gianelli et al., 2013). Further research is necessary to understand how action mechanics are affected by sentential stimuli.

5.3 Sentential HREs and manual actions: Brief interim assessment

Sentence-level HREs provide further evidence about the dynamics of language embodiment. First, single-finger responses are delayed if made within the 700-ms mark, but facilitated if performed afterwards. Second, facilitation effects are more pervasive for whole-hand movements which prove compatible with fine-grained aspects of the sentence's meaning (manual shape or direction). However, delaying response planning and execution tends to interfere with motor-semantic integration. Finally, such a crosstalk is sensitive to effector-laterality and (verbal or interpersonal) contextual factors. Next, we interpret these patterns in the light of the questions presented in Table 1 and introduce the HANDLE model to account for interference, facilitation, and null effects during action-language coupling in terms of activation thresholds in relevant neural circuits.

6 The Hand-Action-Network Dynamic Language Embodiment (HANDLE) model

The research reviewed above has explored language embodiment focusing on the relationship between HREs and ongoing manual responses. *Prima facie*, the disparity of results may seem baffling. Nonetheless, an overarching analysis reveals systematic mechanisms which prove consistent with promising approaches in cognitive neuroscience. To account for the general patterns identified, we propose an integrative theoretical framework: the HANDLE model.

HANDLE aims to capture key empirical patterns in the literature within a neurocognitive framework. Its goal is to characterize the role of hand motor networks in HRE processing by answering the questions listed at the outset (Table 1). To this end, it relies on basics of neural network dynamics in combination with predictive coding and non-radical embodiment principles. The model is construed as follows. First, we outline its key theoretical assumptions, informed by neurocognitive evidence. Second, we show how those commitments support a dynamic network-based framework which captures seemingly discrepant findings in the literature; we focus first on single-word HREs and then on sentential HREs. Third, we consider how the model's main systems can be anatomically implemented and hierarchically related across gross brain regions. Finally, we discuss the model's theoretical and clinical implications, and identify critical challenges for its development.

6.1 Neurocognitive assumptions

In line with the simulation framework, we propose that HREs automatically reactivate multimodal neural networks supporting our actions and perceptual experiences (Barsalou, 1999; Gallese and Lakoff, 2005; Pulvermüller, 2005). While the semantic associations triggered by language reach beyond strictly embodied foundations (Aravena et al., 2010; De Grauwe et al., 2014; García and Ibáñez, 2016; Mikulan et al., 2014; Pulvermüller, 2005), they are largely grounded in relevant sensorimotor circuits. Thus, part of the networks engaged during comprehension of an HRV like *push* are the same involved in the action of pushing (Pulvermüller, 2005). Our model also adopts principles of the predictive coding framework, a statistical Bayesian model of neurocognitive processing in which signals flowing from hierarchically higher to lower systems (feedback connections) and in the opposite direction (feedforward connections) lead to ongoing activity adjustments depending on the mismatch between situated models of the world and incoming signals (Bastos et al., 2012; Rao and Ballard, 1999). Building on these tenets, HANDLE posits that language-induced resonance is (i) fast but potentially long-lived, (ii) associatively widespread, and (iii) denotationally gradual.

First, resonance occurs early during HRE processing, but it is also modulated by controlled top-down mechanisms. To a large extent, motor resonance depends on premotor and parietal circuits (Feldman and Narayanan, 2004; Gallese and Lakoff, 2005) and subcortical action-related mechanisms (Cardona et al., 2013). Specifically, it has been observed to emerge only 22 ms after peak activation in auditory regions (Pulvermüller, 2008), and within the 170-ms mark even if no overt concomitant manual action is required (Aravena et al., 2012; Frak et al., 2010; Papeo et al., 2009). In agreement with neurophysiological research (e.g., Sah, 1996), HANDLE proposes that sensorimotor reactivations are in

principle short-lived, but they can be extended by reverberation or top-down modulations if verbal or motor demands increase. Thus, perception of a single HRV results in early and fast-decaying resonance (Frak et al., 2010), but relevant circuits will remain highly active for long periods if taxed by ongoing verbal processes (e.g., by detecting semantic commonalities between words or by integrating an HRE to its sentential context) or motor operations (e.g., planning a complex manual movement) –for related findings, see Petit et al. (1998).

Second, resonance is associatively widespread in that a linguistic unit triggers activity not just in the sensorimotor circuits it explicitly alludes to, but also in those which have become associated with the former through real-world interactions (Glenberg and Gallese, 2012; Lindemann et al., 2006). Widespread resonance may result from synchronous repetitive firing of probabilistically associated functional networks (König and Schillen, 1991) or from binding of information coded in different components of the same functional networks, guided by frequency-specific oscillatory neural synchrony (Gray et al., 1989) or other similar coupling processes. Both mechanisms have been implicated in predictive coding during verbal processing (Lewis and Bastiaansen, 2015). This principle finds support in neuroimaging (Grabowski et al., 1998; Grafton et al., 1997) and transcranial magnetic stimulation (Cattaneo et al., 2010) research showing premotor cortex activations during processing of tool names (i.e., HREs evoking manual affordances). By the same token, the HRV *push* not only excites the networks engaged by the action of pushing, but also a host of other networks representing relevant yet non-explicit information (e.g., movable objects, possible pushing directions).

Third, resonance is denotationally gradual because it is maximal in regions coding explicitly denoted features, and less intense in networks supporting implied associations. Neuroimaging evidence shows that blood flow changes in the left premotor region are greater for HRVs than tool names, although they reach significance in both cases (Grabowski et al., 1998). Accordingly, we propose that hearing the word *push* triggers supra-threshold activity in motor networks supporting a ‘pushing’ action, and sub-threshold activity in networks supporting potentially implied associations (e.g., multimodal perceptual attributes of movable objects or directional features of pushing orientation).

In terms of HANDLE, the difference between supra- and sub-threshold levels of activation determines whether motor resonance yields interference or facilitation. Once again, note that this is a model of motor-language coupling, and not a model of isolated language processing or motor action per se. Cortical and subcortical systems are hierarchically organized, and they exchange information in various ways. From a predictive-coding perspective (Bastos et al., 2012; Rao and Ballard, 1999), feedforward connections send information (and prediction errors) from earlier to higher areas, while feedback connections convey top-down predictions and modulate activity in hierarchically lower systems. While feedforward connections typically excite higher areas (for a review, see Bastos et al., 2012), feedback connections may both promote and suppress firing in associated systems (Friston, 2008; Rao and Ballard, 1999). Suppression may also result from competition between nodes processing error units at the same hierarchical level (Friston, 2005). Such intra-level inhibitory mechanisms would be subserved by cortical lateral connections (Bastos et al., 2012) and reflected by oscillatory activity in the low and middle gamma frequency range (Lewis and

Bastiaansen, 2015). We propose that, through an interplay of these types of connections, if two concurrent processes (one verbal, one motor) largely depend on a shared neuronal population and the first one raises activity above threshold level, then the second one will not have timely access to its required resources and will be delayed. However, if the first process raises activity below threshold level, then the second one will be primed by such pre-activation, leading to faster completion. These principles can be implemented through power laws (e.g., neuronal avalanches) and other neurodynamic phenomena (Freeman, 2009; Kozma and Freeman, 2009; Milton, 2012) which allow for bistable conditions (e.g., interference or facilitation).

Finally, note that resonance becomes significant if semantic information is directly accessed, but it is typically negligible if the verbal process bypasses conceptual information. HANDLE acknowledges that word perception automatically leads to semantic activation (MacLeod, 1991), but it proposes that such propagation will be minimal unless meaning is explicitly evoked during processing.

On the basis of these principles, HANDLE aims to capture the broad patterns emerging from the review, both at the lexical and the sentential levels.

6.2 How to HANDLE the data

6.2.1 Notational devices

To visually model the patterns emerging from the review, HANDLE represents neural network hubs as collections of nodes in relevant systems.

In figures 8-11, motor-language coupling effects are modeled interns of interactions among three types of networks: (i) hand motor networks, which are engaged by both motor and embodied semantic processes, (ii) action-goal networks, which are mainly represented in the non-motor semantic system, and (iii) lexical networks, comprising its homonymous system. In this and subsequent figures, the systems are spatially separated (and represented by colored ellipses) to ease visualization; however, as shown in Figure 12, they actually overlap and exchange signals back and forth. The lexical and semantic information explicitly denoted by an HRV is critically encoded in the lexical and hand-motor networks, respectively. For instance, circuits coding ‘palm contact’ and ‘awayness’ within the hand-motor network are necessarily activated by the verb *push*, which describes an open-hand displacement towards a more distant location. Yet, spreading activation will also trigger non-motor semantic associations, some of them represented in the non-motor semantic system. The non-motor semantic system also subserves action-goal information, which is not evoked by HRVs themselves, such as directional coordinates (e.g., *right*, *left*) and target object features (e.g., *big*, *small*) –which, as we have seen, can modulate behavioral manual responses. Such information is proposed to be grounded in other (non-motor) sensory systems and maybe even in higher-level association areas (Cardona et al., 2013; Louwerse and Jeuniaux, 2008; Mirabella et al., 2012;

Pulvermüller, 2005). Among the latter, the anterior temporal lobe plays a crucial function by integrating inputs from different sensorimotor and emotional systems to support cross-modal conceptual generalizations (Patterson et al., 2007). The role of non-motor mechanisms in processing action language (including HRVs) has actually been acknowledged in neuroanatomical models of action language (Pulvermüller, 2005) and action-language coupling (Cardona et al., 2013), as well as behavioral studies on the topic (García and Ibáñez, 2016).

Each network comprises several nodes (collections of co-activated and functionally cooperative neurons), which can be in different activity levels depending on ongoing functional dynamics (Pulvermüller, 2002). HANDLE represents them as monochrome circles. Schematically, these range from resting state (excitation = 0%) to varied sub-threshold states (excitation from 1% to 99%) to supra-threshold state (excitation = 100%). The thresholds describe the nodes' readiness to trigger the processes they are associated to. In the case of hand motor network nodes, those processes can be semantic (embodied language mechanisms) or motor (movement planning and execution). Also, the higher the threshold of a node, the stronger the spread of activation it emits.

More generally, note that the thresholds are a conceptual device to account for the three possible forms motor-language coupling: interference, facilitation, and null effects. When activation is sub-threshold, the nodes are primed; thus, they require less additional activation to fire than they would if they were at rest. Instead, when activation is supra-threshold, the nodes will be fully engaged in an ongoing process and will not be

immediately available to contribute to other processes calling on them. Also, activation states proportionally determine how much activation will spread to associated neuronal pools in other systems. For example, if action-goal networks are in a supra-threshold state (100%), associated nodes in the hand motor network will be in a high sub-threshold state (say, 75%). In terms of HANDLE, then, facilitation and interference effects are the behavioral correlate of motor commands operating on sub- or supra-threshold nodes, respectively.

The model further assumes that specific manual commands will engage only a subset of hand-motor network nodes. In other words, certain features will not be typically evoked by specific HRVs. The verb *push*, for instance, does not activate nodes coding for ‘clenched fist’ or ‘power grasp’. Accordingly, only some of the nodes in the hand-motor network will be active during processing of a specific HRE. Also, note that the proposed threshold values in the upcoming figures are merely illustrative; their actual levels may be subtly adjusted by statistical predictions driven by top-down mechanisms (Bastos et al., 2012; Friston, 2008; Rao and Ballard, 1999).

Finally, the upper part of figures 8-11 shows three critical stages to model contextual motor-language integration effects: (a) preparation, namely, unconscious preparatory activity prior to motor planning –which may begin up to one second before execution (Hallett, 2007)–; (b) HRE presentation, that is, the precise moment at which the verbal stimulus is first processed; and (c) manual action command, the moment at which motor networks become engaged to execute a hand action. HANDLE proposes that the relative activation level of critical nodes in each system at

different time stages determines whether contextual binding of motor and linguistic information will delay, facilitate, or have a null impact on the ensuing manual action.

Finally, note that the figures below are not intended to illustrate specific brain areas and connections; rather, they provide abstract principled illustrations of how network interactions may emulate the behavioral phenomena captured by HANDLE. In section 6.3, we specify how these systems may be anatomically implemented and hierarchically related across brain regions.

6.2.2 HANDLE for words

HANDLE captures the principal findings concerning single-word HREs. First, consider Figures 8 and 9, which use the verb *push* to illustrate two main results observed for semantic processing of HRVs with simple motor responses: early interference and later facilitation. As proposed above, neural networks may present a range of sub-threshold activity levels (schematically, from 0% to 99%). At 100%, supra-threshold activation is reached. The preparation of an upcoming simple response (e.g., a single-key press) raises effector-specific activity to a hypothetical 25% and associated neuronal pools (e.g., in the action-goal information network) are less intensely primed (say, 10%). Indeed, mere knowledge of an upcoming action suffices to excite the motor system (Kilner et al., 2004) –those hypothetical levels, however, may be considerably raised by inter-trial predictions (Jiang et al., 2014; Ma and Jazayeri, 2014). Subsequent presentation of the HRV *push* raises activity in relevant lexical and

hand-motor network nodes to 100% while priming associated pools (other conceptual networks would also be activated, but they are not shown in the figures). In line with the reviewed results, such activity levels would remain above threshold for approximately 400 ms –note that the peak of somatotopic activations occurs roughly 200 ms after word onset (Pulvermüller et al., 2005). If a manual response occurs within that window, or overlaps with word presentation (Boulenger et al., 2006; Dalla Volta et al., 2009; Nazir et al., 2008), the motor process leading to its execution will be delayed as its putative hubs are otherwise engaged. Importantly, motor network activity for an action may begin up to one second before its execution (Hallett, 2007). Thus, competition for common resources results in a delay for effector-congruent actions (Figure 8), arguably guided by the lateral (intra-level) and top-down inhibitory connections described in section 6.1 –these are not shown in the figures to prevent cluttering. This view aligns with studies in macaques (Kraskov et al., 2009) and humans (Mukamel et al., 2010) showing that action observation suppresses activity in a specific premotor mirror regions and slow down self-movement. HANDLE assumes that verbal stimuli trigger similar mechanisms.

-----Insert Figure 8 about here-----

However, after 400 ms, the activity level induced by the HRV *push* begins to decrease. Accordingly, if a simple motor response occurs between 450 and 750 ms, sub-threshold activity (say, 50%) primes the manual motor command, which is thus completed faster than those for effector-

incongruent actions (Figure 9). In agreement with this proposal, (Papeo et al., 2009) found that motor-evoked potentials are enhanced 500 ms after HRV processing, despite earlier modulations in the direction of interference (for a discussion, see Gianelli and Dalla Volta, 2014). Beyond the one-second mark, the activity level induced by *push* has decreased to near zero, so that simple responses occurring in that window are neither delayed nor primed. These dynamic modulations are proposed to bias the outcome of relevant control mechanisms (some of which are detailed in Glenberg and Gallese, 2012), and prove consistent with those predicted by a recent computational model (Chersi et al., 2010).

-----Insert Figure 9 about here-----

As previously stated, HANDLE proposes that additional semantic or motor demands cause reverberation within relevant neuronal pools. The main consequence is that supra-threshold levels can be retained for considerably broader time spans, leading to longer-lasting resonance and, hence, extended interference or facilitation effects. In this sense, Bergen et al. (2010) found that effector compatibility yields later interference in picture-word association. The authors interpreted this result assuming that the mirror circuits encoding same-effector actions mutually inhibit each other. HANDLE offers a somewhat different explanation. When the first hand-related stimulus is presented, relevant motor networks reach supra-threshold activity. If another hand-related stimulus is processed shortly afterwards (as was the case in such a study), most of its relevant

nodes will be inaccessible. The ensuing manual response will further compete for access to those supra-threshold nodes, resulting in significant delays.

The same principles could explain why HREs evoking action-goal information mostly yield facilitation of complex movements at later time windows (Figure 10). Consider a pushing movement guided by the HRA_{Adj} *right* (Lindemann et al., 2006, Exp. 3). Its presentation raises lexical and congruent directional information (‘rightness’) above threshold, while priming motor hubs coding right-sided manual actions (e.g., right-sided pushes). Increased preparatory activity and reverberation caused by complex motor demands extend sub-threshold activity in motor circuits beyond the 400-ms mark. Thus, the pushing movements will be faster if performed on objects located in a spatially congruent location, because verbally primed motor networks will assist programming and execution of the action routine. This is consistent with the finding that RTs are shorter when stimulus and intended action effects are spatially compatible (Hommel, 1993). The same explanation accounts for facilitation effects induced by HREs with varying manual affordances (Masson et al., 2008; Tucker and Ellis, 2004).

-----Insert Figure 10 about here-----

Nevertheless, when the task does not explicitly require semantic processing (e.g., lexical decision, letter identification), HRE presentation does not significantly raise activity levels in effector-specific or action-goal-related networks. As their threshold levels are minimally raised, they typically fail to prime or interfere with motor processes (see (Sato et al., 2008). This postulation is consistent with clinical evidence showing that shallow verbal tasks can be accomplished in the absence of semantic contributions (Sasanuma et al., 1992; Teichmann et al., 2012).

All the above explanations are presumed valid for responses performed with the dominant hand, as different results have been observed for non-dominant-hand actions (Marino et al., 2013). However, available evidence is not sufficient to advance any robust hypothesis on the issue. Also, the observed effects may be magnified for specific types of HREs. For example, Kemmerer et al. (2013) reported greater delays for ‘cutting’ than ‘hitting’ verbs during semantic association via single-key presses. A plausible speculation is that the networks supporting such manual action feature share more neural resources with the former than the latter verb type, resulting in greater competition for common resources and more significant delays. Further research is needed to elucidate this point.

6.2.3 HANDLE for sentences

HANDLE also offers a rationale to explain the effects of sentential HREs on manual actions. A first prediction is that effector-specific resonance extends if semantic demands increase. Thus, all effects should be longer-lasting for sentential than single-word HREs, since the former tax semantic processing to integrate features from multiple lexical units within an interpretable syntactic frame (MacDonald et al., 1994).

Confirmatory evidence comes from object-holding studies measuring grip-force variations during HRE processing. When verbal stimuli are single-word HRVs (e.g., *push*), grip force increases at 100 ms, peaks at 380 ms, and abruptly falls 400 ms after word onset (Frak et al., 2010).

However, when the same task is performed with sentences featuring such words (e.g., *he pushed the door*), grip-force modulations also occur in 320-520 and 520-800 ms windows (Aravena et al., 2012).

While the above results show extended motor resonance, the absence of overt actions does not reveal whether it manifests as interference or facilitation across time windows. Instead, studies using simple sentences show that both extended effects follow the same temporal order observed for single-word HRVs. RTs for simple manual actions are delayed if made within roughly the first 700 ms after HRV onset (Buccino et al., 2005; De Vega et al., 2013), but they are facilitated if they occur in later windows (Borghi and Scorolli, 2009; De Vega et al., 2013; Marino et al., 2012). Crucially, by requiring mid-sentence responses immediately after HRV presentation with varying stimulus-onset asynchronies, De Vega et al. (2013) showed that these effects are time-locked to the verb, as did Zwaan and Taylor (2006). Furthermore, Marino et al. (2012) demonstrated that the level of late facilitation is driven by specific semantic attributes of the HRV –it is greater for verbs which highly restrict the

range of possible objects. Thus, the same (extended) functional dynamics proposed for single-word HRVs would explain these sentence-level effects (supra-threshold resonance would yield interference, while sub-threshold resonance would favor facilitation). Importantly, extended facilitation could hardly be attributed to HRNs priming specific affordances, because these words are also present in the sentences yielding interference. Therefore, HANDLE posits that effector-specific resonance during simple-sentence processing is triggered on the fly by HRVs, and remains operative after a fully integrated simulation is achieved (for further supporting evidence, see Aravena et al., 2010; Zwaan and Taylor, 2006).

HANDLE further posits that the level of congruency between manual-action and HRV features modulates motor activity. Note that sentence-final manual responses in the above studies were arbitrarily related to the HRVs. However, as shown in ACE research, compatibility between response direction or hand shape and specific features conveyed by the HRV give rise to two distinct patterns: facilitation if the action is prepared before or shortly after sentence onset, and interference (or null effects with RTs in the direction of interference) if motor preparation occurs late during sentence processing or after its completion.

Crucially, as shown in Table B5 (Appendix), these effects occur in late time windows (700-2200 ms), within which motor network activity has decreased to sub-threshold levels. Remember that once HRV-induced reverberation begins to dwindle, motor networks enter a sub-threshold state

which assists motor commands. If specific features evoked by the HRV (e.g., ‘awayness’ in *push [the door]*) were pre-activated during motor preparation (being ready for an ‘away’ hand displacement), their sub-threshold activation will be higher than that of incongruent features (e.g., ‘towardness’). Thus, a congruent motor command (displacing the hand away from the body) will be more primed than an incongruent one (displacing the hand toward the body), resulting in facilitation by compatibility (Figure 11, Panel A). Instead, if motor preparation is withheld until near or past the end of the sentence, no such preliminary priming occurs. Moreover, the sudden decision of which action to execute causes a quick burst of activity in relevant motor networks, leading congruent HRV features (e.g., those evoked by *push [the door]*) to surpass threshold. Subsequent actions must compete for unavailable resources, thus being delayed relative to incompatible actions (Figure 11, Panel B).

-----Insert Figure 11 about here-----

Finally, note that if a directional movement (e.g., away) is repeatedly trained before the ACE task, sentences with spatially congruent HRVs (e.g., *push [the door]*) yield interference (Glenberg et al., 2008a). HANDLE offers the following explanation. Repeated activation of away movements modulates feedforward and feedback connections between language and motor systems and significantly extends motor-network reverberation, keeping it active throughout processing of an upcoming sentence. When a spatially congruent HRV (e.g., *push*) appears, nodes coding compatible directional features (‘awayness’) easily reach supra-threshold level. A congruent movement will thus be delayed following the same

principles described above. However, HANDLE also recognizes that subtle variations in threshold levels, guided by verbal and motor demands, top-down predictions, and random activity shifts, determine whether ACE modulations reach significance.

Note that these ACE results have also been explained through other rationales. These include the feature-binding account (based on the Theory of Event Coding) (Borreggine and Kaschak, 2006) and the feature-activation account (Kaschak and Borreggine, 2008), which discuss the difference between activation and integration of directional features. Such views differ from the present model in three main respects. First, while HANDLE does not deny that lexical information becomes integrated for a richer simulation after full sentence processing, it posits that effects emerging at that stage are still largely driven by HRV-induced modulations. In this sense, it aligns with neurophysiological ACE evidence that N400 modulations are time-locked to the verb's ending, and that motor-language integration occurs *during* sentence processing rather than upon sentence completion (Amoruso et al., 2013; Aravena et al., 2010; Zwaan and Taylor, 2006). Second, while those accounts focus mainly on the time allotted to response planning, HANDLE adds that a key determinant of the effects is *when the manual response actually occurs* –including concrete neurofunctional hypotheses for the observed results. Third, while those proposals are confined to ACE research, HANDLE captures various other phenomena at both word and sentence levels. In this sense, our model seems to offer a more integrative framework.

Finally, HANDLE acknowledges the effect of contextual constraints in complex sentences. Bergen et al. (2010) showed that effector compatibility between single words and pictures systematically delays manual responses. However, de Vega et al. (2004) and Santana and de Vega (2013) reported late interference and enhanced N400 modulations when two hand-related clauses are linked by *while* but not by *after*. While these results would seem to reflect the impact of a fully integrated (post-sentential) simulation, this is not necessarily the case. Instead, sentence-level processing may well rely on successive graded predictions about plausible upcoming semantic categories, as suggested by recent predictive-coding approaches to language (Hagoort, 2013; Lewis and Bastiaansen, 2015; Pickering and Garrod, 2007).

Accordingly, we propose an ongoing dynamic account of the phenomenon. Hand motor networks are excited beyond threshold by the first HRV. Then, as activity in those networks decreases below threshold, the word *while* primes nodes of all those actions that can be simultaneously performed. Since most manual actions are mutually exclusive (or at least not typically executed at the same time), other-effector features benefit more from the priming induced by *while* –probabilistically, they are more likely to occur. Hence, a second HRV will be at a disadvantage relative to, say, a leg-related verb (more of whose semantic nodes will already be in sub-threshold activity). No such difference would occur for the word *after*, which would equally prime both manual and non-manual motor networks. Thus, whereas *while* would seem to induce same-effector interference, it may actually be favoring different-effector facilitation.

Also, it was found that when two successive clauses feature different effectors, RTs are faster if they are linked by *while* as opposed to *after* (de Vega et al., 2004). This result can be explained following the same principles invoked so far. A first verb activates nodes in its corresponding effector's network. Then, the word *after* equally primes nodes for all action types, as both same- and different-effector actions can be performed in succession. Instead, the word *while* propagates most of its priming potential to different-effector networks only, as same-effector networks can less plausibly co-occur. This means that different-effector verbs will be receiving more priming from *while* than from *after*, thus reaching higher sub-threshold levels and leading to faster processing.

Note that the above effects disappear if the HRVs are preceded by expressions indicating non-factuality, such as negation adverbs (e.g., *do not paint*) (Aravena et al., 2012) and verbs implying unreality –e.g., *thought of painting* (de Vega et al., 2004) or *wants to soap his shirt* (Aravena et al., 2014). We propose that words explicitly evoking non-factuality reduce motor resonance of following HRVs to negligible levels, which thus fail to prime or interfere with upcoming manual responses. Once again, HANDLE proposes that this effect is guided by word-level information and ongoing top-down predictions rather than by integrative post-sentential simulations. Critical support for this view comes from Glenberg and Kaschak (2002), who showed that the ACE occurs in imperative sentences. As it happens, the imperative mode construes a non-factual scenario in the absence of words explicitly indicating unreality. This is consistent with the claim that effector-specific effects visible after full sentence processing are largely driven by distinctive effects of individual words.

6.3 Anatomical implementation of HANDLE's main systems

HANDLE involves multiple interacting and overlapping systems. Such systems exchange information dynamically, continuously adjusting activity levels in one another via bottom-up and top-down connections. Their overall architecture is diagrammed in Figure 12.

-----Insert Figure 12 about here-----

In addition to low-level (e.g., visual and auditory) mechanisms, which are not depicted in Figure 12, HANDLE comprises four main systems: a lexical system, a hand action system, and two semantic systems –one comprising embodied mechanisms and another one supporting non-motor conceptual information, which includes action-goal information.

The lexical system, which supports word-form processing, mainly engages temporal and temporo-occipital regions (Fiebach et al., 2002; Hickok, 2009; Pulvermüller, 1999). During word perception, it sends bottom-up signals to both semantic systems. These, in turn, convey predictions back to the lexical system, creating probabilistic expectations of which nodes would be activated next, both trial-after-trial and word-after-word in

sentence processing. This loop is crucial to implement progressive predictions, implicit inter-trial learning, and threshold adjustments proposed to operate during sentence-level HREs (see section 6.3).

Lexical input drives activity in the two semantic systems. In particular, HRE-induced resonance engages embodied motor semantics, which shares critical sensorimotor substrates with the hand action system –including M1, the primary and supplementary motor areas, Broca’s area, the basal ganglia, and parietal areas (Cardona et al., 2013; Feldman and Narayanan, 2004; Gallese and Lakoff, 2005). Effector-specific interference and facilitation largely depend on reciprocal connections between these overlapping systems. For example, consider the experiments requiring single-key pressing in response to single words. At the beginning of a trial, preparatory activity in hand motor networks conveys statistically derived predictions to associated networks in the lexical and embodied-semantics systems. When the stimulus word appears, the level of gross or effector-specific resonance it induces (or absence thereof) modulates how many prediction errors are sent back to the hand action system. Ensuing statistical computations influence the action system’s internal dynamics, yielding interference, facilitation, or null results, as explained in section 6.3.

Also, HANDLE posits that linguistic meaning is not reducible to embodied mechanisms (Mahon and Caramazza, 2008; Mikulan et al., 2014; Patterson et al., 2007). Additionally, HREs imply activity in regions supporting non-motor conceptual information, including Wernicke’s area,

the superior temporal sulcus, and, crucially, the anterior temporal lobe (Patterson et al., 2007; Visser et al., 2009). These areas are presumed to partially support action-goal-related information as well as higher-level concepts resulting from the integration of unimodal inputs from diverse brain regions. Non-motor and embodied semantics influence activity levels on each other by virtue of both bottom-up and top-down connections, mutually constraining specific patterns of motor resonance. Also, their interaction determines the construal of integrated semantic representations (e.g., upon full sentence processing) while influencing the mapping of lexico-semantic information on syntactic frames. The latter processes have been proposed to depend on regions already contemplated by the model, such as Broca's area, the inferior parietal cortex, and the basal ganglia (Hagoort, 2013, 2014; Lewis and Bastiaansen, 2015).

In sum, HANDLE is not a purely associationist model. The threshold adjustments described in sections 6.2 and 6.3 depend on bottom-up and top-down connections within and among these (and other) systems. Moreover, note that illustrative percentages ascribed to sub- and supra-threshold states are not fixed; rather, they vary dynamically relative to the systems' activation history, probabilistic learning, situated influences, and even random noise. In particular, the idea is that spreading activation and ensuing interference and facilitation effects are largely driven by experience-based probabilistic predictions (Bastos et al., 2012; Friston, 2008; Rao and Ballard, 1999), which are subtly readjusted by task-related factors, such as motor complexity, control demands, and even inter-trial statistical learning. That being said, the actual impact of each of the postulated inter-areal connections is not yet fully understood. Recent theoretical efforts (e.g., Hagoort, 2013; Lewis and Bastiaansen, 2015;

Pickering and Garrod, 2007) show that predictive coding approaches can pave the way for a dynamic conception of language processing in the brain. Not only is HANDLE compatible with these perspectives, but it also offers temporally and functionally defined hypotheses which could be explored and more directly tied to this promising framework. Below, we discuss some of the theoretical implications of the model and outline outstanding challenges for its development.

7 Assessment, implications, and challenges

7.1 Motor resonance as a synergistic and enactive phenomenon

Several cognitive models tacitly or otherwise assume that action and high-order domains are independent from each other –see Wheeler (2005). In particular, the ‘classical sandwich’ approach (Hurley, 2008) assumes a radical separation among perception, thinking, and action, each of which would rely on different representations and processes. This separatist view pervades both modular and interactionist theories of language (Pickering and Garrod, 2013).

These conceptions are deeply challenged, if not altogether falsified, by embodiment research (Barsalou, 1999; Gallese and Lakoff, 2005).

However, many embodied accounts of cognition portray sensorimotor resonance as a passive phenomenon, thus incarnating a reflexive

conception of brain function (Raichle, 2010). We will argue, instead, that brain function is proactive rather than reflexive, as it is intrinsically geared towards the active anticipation of the system's upcoming states.

We propose that the effects captured by HANDLE are not mere passive brain responses. Rather, what we are observing is the crosstalk between two overlapping strains of anticipatory activity: to deal with the demands of motor-language coupling, the brain proactively modulates its systems' states in an attempt to adapt to ongoing and upcoming demands (Raichle, 2010). For instance, motor preparation to grasp a magnifying glass activates a cognitive scheme which constrains the systems' expectations about its own future states. This manual action is probabilistically associated with relatively systematic perceptual, linguistic, and semantic experiences, which the brain actively tries to anticipate. In fact, previous motor experience induces enhanced anticipation and semantic processing of incoming stimuli (Amoruso et al., 2014). Our claim is that the brain works proactively by biasing its activation levels for possible input connections guided by the objects' round shape, refractory properties, estimated weight, and associated semantic and lexical information. In this sense, both gross and effector-specific resonance are brought about by the brain's intrinsic activity.

The proposed intertwining of action and language resembles previous theories of "action cognition" (Gentsch et al., 2015), although HANDLE partially deviates from most extant approaches. Regarding the grounding of cognition in action, our model highlights the active blending of

action and language, involving both “low” and “high” levels at motor and linguistic domains, but based on the primacy of *current* actions for bidirectional action-language effects. Thus, in agreement with common coding, HANDLE assumes an action-perception cycle centred in real actions and high-level linguistic processes. Also, our model resembles ideomotor theory (Shin et al., 2010) in proposing bidirectional automatic sensory-motor links (with relative independence of both processes), although our focus is on language and manual actions. HANDLE also aligns with the Theory of Event Coding (Hommel et al., 2001) in acknowledging the synchronization and fine-grained coupling of action-perception interactions. Note, however, that HANDLE dispels the need for a separate and specific common code, as all key effects can be explained by reference to an emergent co-activated network.

Furthermore, HANDLE agrees with internal model theories in postulating directional restrictions among bidirectional pathways. At the same time, it goes beyond forward models of motor control (Shadmehr et al., 2010) by explaining the relation between action and language, rather than that between purely motor control and learning. Moreover, as detailed above, HANDLE incorporates key predictive-coding tenets (active inference, top-down/bottom-up restrictions), although it also includes associative/Hebbian mechanisms. At the same time, our model deviates from predictive coding (Friston et al., 2011) as it does not identify perception (in this case, language perception) with prediction –which would be just one component of language comprehension. In this sense, HANDLE supposes that motor resonance is used for internal prediction but

without requiring an “emulator of the body”. While this is consistent with emulation theory (Grush, 2004), HANDLE is different in that actual movement execution is critical for the action-perception coupling effects it captures.

Resembling simulation theories, our model implies some level of isomorphism among real, observed, or linguistically inferred actions and the primary source of sensorimotor activity. Moreover, although HANDLE resembles mirror system theory in its assumption of sensorimotor resonance (Rizzolatti and Craighero, 2004), it does not propose a separate subpopulation of neurons as the single putative mechanism for action observation and execution. Finally, our model follows motor imagery theory (Vogt et al., 2013) and perceptual symbols theory (Barsalou, 2007) in framing simulation and conceptual processing as reactivations of sensorimotor states, but, once again, it does not restrict resonance to such mechanisms.

In sum, our approach is partially consistent with active cognition approaches: it assumes non-radical embodiment principles, it integrates processes and regions at low and high levels, and, more distinctively, it focuses on ongoing actions rather than on action observation/imagery. Thus, our framework stands out from previous proposals by following the “pragmatic turn” from a more passive and static representationalist perspective to a more dynamic conceptualization of cognition as enactive action (Engel et al., 2013). In other words, the key distinctive feature of HANDLE is that in its explanandum, active cognition involves current activities, highlighting the critical role of ongoing actions per se. Thus,

HANDLE provides an empirical framework to understand the links between cognition (in particular, language processes) and action as defined by enactive (Varela et al., 1992), action-oriented (Clark, 1999), and sensorimotor contingency approaches (O'Regan and Noe, 2001). In terms of HANDLE, cognition is a form of practice where language and current actions are intertwined. The model meets most prerequisites of the pragmatic turn: cognition can generate structures by action, the cognitive agent is immersed in the task domain, meaning is acquired by the role of context of action, and functional properties of cognition are framed as inseparable from embodied systems (Engel et al., 2013).

7.2 Clinical applications of hand-specific motor-language coupling research

A non-dichotomical conception of action and cognition may even have clinical implications. Since HREs partially depend on the motor system, they could give us hints on its integrity. Accordingly, studies on the crosstalk between manual action and HREs may contribute to the early detection of motor diseases, such as Parkinson's disease and Huntington's disease (García and Ibáñez, 2014a), which show specific action language impairments (Bocanegra et al., 2015). While multiple reports indicate that language and motor skills are dissociable (Arbib, 2006; Geschwind, 1965; Papagno et al., 1993), a novel approach in neurodegenerative disease research is to explore the disruption of *their natural coupling*.

We have reviewed compelling evidence that, in healthy individuals, manual responses to sentences denoting open- or closed-hand actions are faster if the hand assumes a compatible shape (section 5.1 and Table B6 in the Appendix). This natural effect (positive ACE) is altered in Parkinson's disease patients. The disturbance was first documented by Ibáñez et al. (2013), who found that early-stage patients, with non-severe motor difficulties, exhibited an abolished ACE even when tested during the 'on' phase of levodopa or a dopamine agonist. Importantly, the deficit was independent from general cognitive impairment or executive dysfunction. Such a finding was replicated by Cardona et al. (2014) and (Melloni et al. (2015)). The former report further demonstrated that this behavioral pattern was specifically triggered by frontostriatal damage. The latter showed that it was accompanied by aberrant frontotemporal connectivity and reduced cortical motor modulations, which were predicted by the level of basal-ganglia volume and atrophy.

Finally, another study reported the same pattern in Huntington's disease patients and, more crucially, in their *asymptomatic* first-degree relatives (Kargieman et al., 2014). The relatives had a mean age of 29 years, whereas the mean age of disease onset for the patients was 39. This suggests that effector-specific action-language coupling deficits may appear even 10 years before motor symptoms become manifest, which suggests a promising avenue for early detection and timely application of intervention strategies. We propose that the assessment of other fine-grained effects captured by HANDLE may further contribute to this incipient line of research, with implications for motor disorders at large. In

particular, selected paradigms informing HANDLE could be complemented with tasks tapping dissociable language domains –such as noun processing, which is mostly spared in these conditions (for a review, see García and Ibáñez, 2014a).

7.3 Looking ahead: outstanding challenges for the HANDLE model

HANDLE leads to specific hypotheses and leaves open several questions. All of these may be explored in further research, allowing for theoretical refinements. The model's key predictions are listed in Box 1.

Box 1. Key empirical predictions of the model

1. The dynamic impact of HRVs on concurrent manual actions always starts as interference and only then may pave the way for facilitation effects.
2. HREs conveying action-goal information mainly facilitate concurrent manual movements.
3. As motor or semantic demands increase, the above effects become longer-lasting.
4. The locus of motor resonance is semantic rather than lexical.
5. Motor-language coupling effects in sentence-level HREs are guided by on-the-fly predictions which are successively reconfigured following word-by-word constraints.
6. ACEs manifest as facilitation if manual responses are planned before or shortly after sentence onset, but they may turn into interference if responses are withheld until near or past the end of the sentence.

These predictions have important theoretical implications to understand the organization of verbal semantics and its relationship with embodied mechanisms. First, HANDLE proposes that the dynamic impact of HRVs on concurrent manual actions always starts as interference and only then may pave the way for facilitation effects. This could be explored with paradigms employing various SOAs and including different levels of congruency between verbal and motor processes in early windows. In addition, HANDLE posits that the functional manifestation of HRE embodiment is very sensitive to the task's motor and semantic demands. This heretofore unexplored issue could inspire novel studies leading to more context-sensitive views of action-language coupling. This aim can also be pursued through direct testing of the time windows proposed for interference, facilitation, and null effects. In this sense, behavioral manual-action data could be complemented with high-temporal-resolution neuroscientific methods, as sparsely done in previous studies (e.g., Aravena et al., 2010; Glenberg et al., 2008b; Ibáñez et al., 2013; Melloni et al., 2015).

Also, HANDLE implies that the mental lexicon is mainly structured following semantic rather than form-level constraints. Thus, the model opposes views of lexical organization based on grammatical class distinctions (Laiacina and Caramazza, 2004; Shapiro and Caramazza, 2003), and aligns with emergentist approaches acknowledging semantic/pragmatic and distributional features as key constraints for the structure of lexical systems (Vigliocco et al., 2011). Finally, HANDLE establishes that, with sentential stimuli, motor-language integration is guided by on-the-fly word-by-word predictions rather than upon full sentence processing (Amoruso et al., 2013; Aravena et al., 2010; Zwaan and Taylor,

2006). This claim could lead to valuable contributions to the field, as it highlights the dynamic nature of embodiment, proves amenable to predictive-coding principles, and may thus favor the integration of motor-language coupling research with more general, cutting-edge perspectives on neurocognition.

In addition, HANDLE gives rise to several questions for further research. Three of them concern microanatomic brain dynamics: what are the putative excitatory and inhibitory neuronal mechanisms assumed by the model?; what is the relative weight of bidirectional connections among the model's systems?; how do top-down predictions and bottom-up errors modulate threshold levels on a more specific neurophysiological level? These questions could be addressed through a combination of anatomical/functional connectivity approaches (via DTI and fMRI), electromagnetic measures of rapid coupling-decoupling and synergic brain dynamics, and direct intracranial recordings offering enhanced spatiotemporal precision in simultaneous measurements of motor and language areas. Unlike the latter technique, which allows for ecological studies of motor-language integration, the first two do not currently allow for complex movements. However, incipient methodological breakthroughs are likely to overcome this caveat. In particular, recent developments for the analysis of PET (Brown et al., 2006) and EEG (Ojeda et al., 2014) data allow to measure brain activity during complex movements. Moreover, the combination of task-evoked neural responses and resting network analysis can provide a robust approach to test the predictions of HANDLE. While the former method allows assessing the relative segregation and integration of information across brain regions during a task (Friston, 2011), the latter can show whether neuronal

populations within a given region are differentially sensitive to a feature of interest (Grill-Spector and Malach, 2001). These issues could also be examined through computational modeling, as illustrated by Chersi et al. (2010).

Additional questions concern the impact of contextual variables on the observed effects. HANDLE stems from studies requiring manual responses during HRE processing. Comparing behavioral and neurocognitive patterns between such tasks and others requiring no overt action (e.g., action observation, passive language comprehension) could reveal the specific impact of *ongoing* activities on language-induced motor resonance. Further insights into the situatedness of language embodiment can be gained by manipulating verbal or interpersonal affective factors during action-language coupling tasks (see Gianelli et al., 2013; Lugli et al., 2012; Spadacenta et al., 2014). It would also be important to increase ecological validity through designs involving naturalistic dialogue in interactive settings (García and Ibáñez, 2014b), including action-rich scenarios such as sport arenas, dance floors, or playgrounds.

Moreover, the model triggers questions regarding the plasticity of hand-specific action-language coupling. It would be interesting to assess how and when the observed effects become established during ontogenesis, especially since gesturing abilities in children predict language development (Rowe and Goldin-Meadow, 2009a, b). Also, building upon findings by Glenberg et al. (2008a), future research could assess whether sustained training in either manual actions or HRE processing affects performance in the other domain. This line of research could have

important implications for both language learning and motor rehabilitation. Yet, the most captivating translational question surrounding HANDLE is this one: can the predictions of HANDLE be used to detect early signs of incident or future motor disorders? The results surveyed in section 7.2 suggest that action-language tasks may tap the integrity of the motor system (see also Bocanegra et al., 2015; García and Ibáñez, 2014a). Breakthroughs in this direction could afford clinical practitioners with an efficient, low-cost tool to foster pre-symptomatic detection of neural atrophy and thus favor timely intervention.

Finally, new questions emerge regarding verbal expressions alluding to non-manual phenomena. For example, do similar effects occur for motor-language coupling involving other effectors (e.g., foot responses to foot-related expressions)? Would such integration dynamics behave in the same way as those captured by HANDLE? And do such functional and temporal patterns of embodiment manifest with other word types –e.g., abstract words in relation to emotional systems (see Naccache et al., 2005)? Answers to these queries could dramatically increase our understanding of how language processes are rooted in non-language-specific neurocognitive mechanisms.

8 Conclusion

It seems that our brains develop a *sensus communis* by integrating and co-construing ongoing actions and action semiotics. Accordingly, action deployment cannot be reduced merely to motor proficiency (Ni Choisdealbha and Reid, 2014). Implicitly or explicitly, action involves meaning

and intention. Very early on, philosophical phenomenology captured one side of this dimension, claiming that material things depend on the bodily configuration of the experiencing subject (Husserl, 1952). Yet, at the same time, bodily actions are shaped by the situated linguistic background. In this review, we have shown that action involves an implicit and complex blending with verbal semantics. Different meaningful processes are temporally intermingled by a specific combination of internal bodily actions and external linguistic stimuli.

Action-language coupling, in terms of HANDLE, involves the automatic and simultaneous contextual binding of actions and verbal information. HANDLE seeks to account for fine-grained contextual integration effects between action and language through neural coupling dynamics and predictive-coding principles. This basic and minimalistic contextual modulation can be extended to other processes. In fact, HANDLE is consistent with models of contextual perception (Bar, 2004) and contextual social cognition (Baez et al., in press; Ibáñez and Manes, 2012). Frameworks such as these contribute to forging a situated outlook on embodied cognition.

Focusing on manual actions and HREs, HANDLE captures dynamic aspects of this functional crosstalk while providing a unifying framework for multiple and disparate findings in the literature. Our model shows that action and semantics do not blend in a straightforward, unidirectional fashion. Rather, their combination gives rise to a complex, fine-grained synthesis yielding interference or facilitation at different time-scales, guided by verbal, motor, and task-related factors. On these premises, HANDLE motivates new hypotheses and questions to be addressed in the

near future. Available and future methodological developments will allow for more precise testing of the model's predictions through a combination of behavioral, electrophysiological, and neuroanatomical techniques. Exploring these possibilities may generate groundbreaking research into motor-language coupling, language embodiment, and situated cognition at large.

Acknowledgments

This work was partially supported by grants from CONICET, CONICYT/FONDECYT Regular (1130920), FONCyT-PICT 2012-0412, FONCyT-PICT 2012-1309, and the INECO Foundation.

Conflict of interest

None to declare.

Appendix

Section A: Summary of experiments involving single-word HREs

Experiments are organized in terms of increasing motor demands (as detailed in Table 1 in the main manuscript). Within each paradigm, experiments are further subclassified according to the required processing level (semantic, lexical, perceptual).

Table A1. Object-holding experiments.

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
Frak <i>et al.</i> (2010)	<i>N</i> = 6 Lang: Fr Hand: R Age: 15-52*	35 HRVs 35 non-manipulable concrete nouns	Counting occurrences of a word in a word list while holding cylinder with index and thumb	Change of grip force by HRVs but not nouns	Increase at 100 ms, peak at 380 ms, and abrupt fall 400 ms after word onset

NOTES: Fr: French; R: right-handed; HRVs: hand-related verbs; *: range.

Table A2. Finger-opening experiments.

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand action	Effect timing
Dalla Volta <i>et al.</i> (2009), Exp. 1	<i>N</i> = 16 Lang: It Hand: R Age: 20-27*	10 HRVs 10 foot verbs 10 abstract verbs	Go/no-go finger opening guided by pre-execution semantic decision (does the verb involve action?)	Null effect on RT Interference (reduced peak velocity)	~80 ms after word onset

NOTES: It: Italian; R: right-handed; HRVs: hand-related verbs; *: range; RT: reaction time.

Table A3. Single-key pressing experiments (guided by semantic-level processing).

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand action	Effect timing
Sato <i>et al.</i> (2008), Exp. 1	<i>N</i> = 24 Lang: It Hand: R Age: 24**	10 HRVs 10 foot verbs 10 abstract verbs	Go/no-go button pressing guided by pre-execution semantic decision (does the verb involve action?) Go signal within a 150 ms window	Interference	Delay of 35 ms starting at 315 ms after word onset

Sato <i>et al.</i> (2008), Exp. 2	<i>N</i> = 24 Lang: It Hand: R Age: 23**	10 HRVs 10 foot verbs 10 abstract verbs	Same as above Go signal at 150 or 1150 ms after word presentation	Interference only in the early delivery condition (150 ms after word onset)	Delay of 15 ms starting at 272 ms after word onset
Dalla Volta <i>et al.</i> (2014)	<i>N</i> = 26 Lang: It Hand: R Age: 27.5**	25 HRVs 25 foot verbs 25 mouth verbs 25 abstract verbs	Semantic decision (does the verb involve action?), with index and middle fingers	Facilitation (shorter RTs) (also for foot verbs)	~720 ms after word onset
Dalla Volta <i>et al.</i> (2009), Exp. 3	<i>N</i> = 15 Lang: It Hand: R Age: 22-28*	10 HRVs 10 foot verbs	Semantic decision Compatible condition: respond to hand and foot verbs by lifting hand or foot finger, respectively Incompatible condition: vice versa	Facilitation by compatibility on RT Interference by compatibility on kinematics (peak velocity and maximal height)	~450 ms after word onset Timing of interference effect not reported
Bergen <i>et al.</i> (2010), Exp. 1	<i>N</i> = 39 Lang: Eng Hand: n/a Age: n/a	16 hand/arm action pictures 16 mouth/face action pictures 16 foot/leg action pictures	Picture-word agreement decision by key pressing Each picture followed by a verb, denoting either (i) the action shown, (ii) a same-effector action, (iii) a different-effector action	Interference for same-effector relative to different-effector verbs	Delays of ~50 ms starting at 750 ms after word onset
Bergen <i>et al.</i> (2010), Exp. 2	<i>N</i> = 21 Lang: Eng <i>N</i> = 27 Lang: Can Hand: n/a Age: n/a	12 HRVs 12 mouth verbs 12 foot/leg verbs (all verbs in the participants' L1)	Word-picture agreement decision by button pressing Each picture followed by a verb, denoting either (i) the action shown, (ii) a same-effector action, (iii) a different-effector action	Interference for same-effector relative to different-effector verbs	Delays of ~50 ms starting at 730 ms after word onset
Bergen <i>et al.</i> (2010), Exp. 3	<i>N</i> = 56 Lang: Eng Hand: n/a Age: n/a	14 HRVs 14 mouth verbs 14 foot/leg verbs	Semantic decision by key pressing (does the second verb mean roughly the same as the first one?) Each verb followed by another one denoting either (i) a synonym,	Interference for same-effector relative to different-effector verbs	Delays of ~100 ms starting at 930 ms after word onset

			(ii) a same-effector action, (iii) a different-effector action		
Bergen <i>et al.</i> (2010), Exp. 4	<i>N</i> = 40 L2 Eng users Lang: Eng Hand: R Age: n/a	16 hand/arm action pictures 16 mouth/face action pictures 16 foot/leg action pictures	Picture-word agreement decision by key pressing Each picture followed by a verb denoting either (i) the action shown, (ii) a same-effector action, (iii) a different-effector action	Interference for same-effector relative to different-effector verbs	Delays of ~115 ms starting at 930 ms after word onset
Kemmerer <i>et al.</i> (2013)	PD <i>N</i> = 10 Age: 75.5** conts <i>N</i> = 10 Age: 71.5** Lang: Eng Hand: R	24 'hitting' HRVs 24 'cutting' HRVs 24 leg verbs 24 mouth verbs 24 state verbs 24 mental verbs	Semantic similarity judgment task, with key presses by right or left index fingers to choose the verb on the right or left, respectively.	PD and conts: interference on 'cutting' relative to 'hitting' and mouth verbs	PD: delay of 100-400 ms after 2400 ms conts: delay of 100-200 ms after 2100 ms
Kelly <i>et al.</i> (2009), Exp. 1	<i>N</i> = 29 Lang: Eng Hand: R Age: n/a	16 action videos as primes Filler videos 5 types of target videos: 1. speech and gest comp with video 2. comp speech, weakly incomp gest 3. comp speech, strongly incomp gest 4. comp gest, weakly incomp speech 5. comp gest, strongly incomp speech	Semantic relatedness judgment (is any part of the target, speech or gesture, related to the prime?) guided by video watching	Facilitation: faster RTs by dual compatibility No RT effect among incomp conditions More errors to strongly than weakly incomp items	comp 740 ms, incomp 790-850 ms
Kelly <i>et al.</i> (2009), Exp. 2	<i>N</i> = 41 Lang: Eng Hand: R Age: n/a	Same as in Exp. 1	Semantic relatedness judgment (is speech in target related to prime?) guided by video watching	Null RT effect	----

NOTES: PD: Parkinson's disease patients; conts: healthy controls; It: Italian; Eng: English; Can: Cantonese; R: right-handed; n/a: not available; HRVs: hand-related verbs; *: range; **: mean; RT: reaction time; gest: gesture; comp: compatible; incomp: incompatible; non-significant results are reported if crucial to the study's overall results.

Table A4. Single-key pressing experiments (guided by lexical-level processing).

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand action	Effect timing
Sato <i>et al.</i> (2008), Exp. 3	<i>N</i> = 12 Lang: It Hand: R Age: 22**	10 HRVs 10 foot verbs 20 non-words	Go/no-go button pressing guided by pre-execution lexical decision Go signal 150 ms after word onset	Null effect	-----
Pulvermüller <i>et al.</i> (2001)	Exp. 1 <i>N</i> = 20 Lang: Ger Hand: R Age: 23.3** Exp. 2 <i>N</i> = 17 Lang: Ger Hand: R Age: 23.2**	32 HRVs 32 face verbs 32 leg verbs	Lexical decision by key pressing	Exp. 1: HRVs faster than leg but slower than face verbs Exp 2: No differences between HRVs and leg or face verbs	RTs are misreported. In text, face verbs faster than HRVs; but bar charts show the contrary. Also, HRV results not discussed
Myung <i>et al.</i> (2006), Exp. 1	<i>N</i> = 34 Lang: Eng Hand: n/a Age: n/a	28 word pairs with HRNs sharing manner of manipulation 28 pairs with nouns lacking semantic or visual features 28 pairs with non-word targets	Primed lexical decision by key pressing	Null effect (reported as marginally significant facilitation, with $p = .08$)	Related pairs: 1175 ms Unrelated pairs: 1201 ms

NOTES: It: Italian; Ger: German; Eng: English; R: right-handed; **: mean; n/a: not available; HRVs: hand-related verbs; HRNs: hand-related nouns; RT: reaction time; non-significant results are reported if crucial to the study's overall results.

Table A5. Hand-displacement experiments.

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
Mirabella <i>et al.</i> (2012), Exp. 1	<i>N</i> = 18 Lang: It Hand: R Age: 26**	10 HRVs 10 foot verbs 10 abstract verbs	Go/no-go hand displacement guided by pre-execution semantic decision (does the verb involve action?) Go signal 53.2 or 332.5 ms after word onset (verb visible until end)	Interference on RT Null effect on kinematics	lasted until ~335 ms after signal onset

			of trial)		
Mirabella <i>et al.</i> (2012), Exp. 2	<i>N</i> = 13 Lang: It Hand: R Age: 24**	10 HRVs 10 foot verbs 10 abstract verbs	Same as above Go signal 53.2 or 332.5 ms after word onset (verb visible for same duration as the go signal)	Interference on RT Kinematic data not reported	lasted until ~360 ms after signal onset
Mirabella <i>et al.</i> (2012), Exp. 3 ^a	<i>N</i> = 12 Lang: It Hand: R Age: 23**	10 HRVs 10 foot verbs 10 abstract verbs	Same as above Go signal presented within a 400 ms window	Interference on RT Kinematic data not reported RTs faster as SOA increased (interference decreased through time)	lasted until ~450 ms after signal onset
Mirabella <i>et al.</i> (2012), Exp. 3b	<i>N</i> = 13 Lang: It Hand: R Age: 22**	10 HRVs 10 foot verbs 10 abstract verbs	Same as above Go signal presented within a 1000 ms window	Interference on RT Kinematic data not reported RTs faster as SOA increased (interference decreased through time)	lasted until ~600 ms after signal onset
Spadacenta <i>et al.</i> (2014), Exp. 1	<i>N</i> = 30 Lang: It Hand: R Age: 25.2**	6 HRVs, negative connotation 6 HRVs, neutral connotation 6 leg verbs 6 abstract verbs	Go/no-go hand displacement guided by pre-execution semantic decision (does the verb involve action?) Go signal 53.2 or 332.5 ms after word onset (verb visible until end of trial)	Interference of HRVs Facilitation of negative HRVs relative to neutral HRVs	With 53.2 ms SOA, delay of 10-20 ms starting 420 ms after word onset With 332.5 ms SOA, delay of 10-20 ms starting 240 ms after word onset
Spadacenta <i>et al.</i> (2014), Exp. 3	<i>N</i> = 30 Lang: It Hand: R Age: 25.2**	8 HRVs with negative connotation 6 HRVs with neutral connotation 8 leg verbs 24 pseudowords	Go/no-go hand displacement guided by pre-execution lexical decision Go signal 53.2 or 332.5 ms after word onset (verb visible until end of trial)	Facilitation of HRVs over leg verbs Interference of negative HRVs relative to neutral HRVs	With 53.2 ms SOA, delay of 10-30 ms starting at 485 ms after word onset With 332.5 ms SOA, delay of 5-20 ms starting 285 ms after word onset

NOTES: It: Italian; R: right-handed; **: mean; HRVs: hand-related verbs; RT: reaction time; SOA: stimulus-onset asynchrony; non-significant results are reported if crucial to the study's overall results.

Table A6. Pointing/gesturing experiments.

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
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Bernardis <i>et al.</i> (2006), Exps. 1 and 2	<i>N</i> = 28 Lang: It Hand: R Age: 21-24*	Three visually presented words (<i>hello</i> , <i>no</i> , <i>stop</i>) and a pseudoword	Respond in one of four ways: 1. do indicated gesture 2. utter letter string 3. gesture while saying letter string 4. utter words while doing meaningless arm action	Interference on kinematics by compatibility	Gesture execution delayed 170 ms starting at 375 ms after word production
Barbieri <i>et al.</i> (2009), Exp. 1	<i>N</i> = 8 Lang: It Hand: R Age: 23-28*	Clips with actress (i) uttering <i>hello</i> or <i>no</i> , (ii) doing gesture for 'hello' or 'no', (iii) uttering <i>hello</i> or <i>no</i> with congruent gesture	Respond to the video by producing the same communication signals emitted by the actress	Interference on kinematics by simultaneous gesture and word uttering	180-210 ms after completion of actress' gesture/word
Barbieri <i>et al.</i> (2009), Exp. 2	<i>N</i> = 16 Lang: It Hand: R Age: 23-26*	Clips with actress doing gesture for either 'hello' or 'no', while uttering words <i>hello</i> , <i>no</i> or <i>grasp</i>	Respond to the video by either producing the same word and gesture, or just the gesture	Interference on kinematics for congruent trials, both uttering or silently repeating the word	180-210 ms after completion of actress' gesture/word
Barbieri <i>et al.</i> (2009), Exp. 3	<i>N</i> = 10 Lang: It Hand: R Age: 25-37*	Clips with actress doing gesture for either 'hello' or 'no', while uttering words <i>hello</i> , <i>no</i> or <i>yellow</i>	Respond to the video by simultaneously producing the same word and gesture	Interference on kinematics for congruent trials	190-215 ms after completion of actress' gesture/word
Chieffi <i>et al.</i> (2009), Exp. 1	<i>N</i> = 12 Lang: Eng Hand: R Age: 19-32*	Tokens showing the words <i>here</i> or <i>there</i> or X-string of letters, placed close to or far from the subject	Word reading while pointing towards oneself or to a remote position	Facilitation of kinematics (index peak velocity) by compatibility	-----

NOTES: It: Italian; Eng: English; R: right-handed; *: range.

Table A7. Object-grasping experiments.

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
Boulenger <i>et al.</i> (2008)	<i>N</i> = 25 Lang: Fr Hand: R Age: 27.5**	70 HRVs 70 non-manipulable nouns 140 consonant strings	Object grasping with pre-execution subliminal word presentation	Null RT effect Interference on kinematics (reduced wrist acceleration amplitude); same effect for consonant strings	0-350 ms after word onset
Boulenger <i>et al.</i> (2006), Exp. 1	<i>N</i> = 9 Lang: Fr Hand: R Age: 22-27*	42 action verbs (hand/arm, leg/foot, mouth/face) 42 non-manipulable nouns 42 pseudoverbs 42 pseudonouns	Go/no-go object grasping guided by mid-execution lexical decision	Null RT effect Interference on kinematics (reduced wrist acceleration peak and amplitude)	160-180 ms after word onset

				Effect not exclusive HRVs	
Boulenger <i>et al.</i> (2006), Exp. 2	<i>N</i> = 9 Lang: Fr Hand: R Age: 22-27*	Same as Exp. 1	Go/no-go object grasping guided by pre-execution lexical decision	Null RT effect Facilitation of kinematics (increased wrist acceleration peak) Effect not exclusive HRVs	550-580 ms after word onset
Nazir <i>et al.</i> (2008)	<i>N</i> = 9 Lang: Fr Hand: R Age: n/a	Same as Boulenger <i>et al.</i> (2006)	Go/no-go object grasping guided by mid-execution lexical decision	Null RT effect Interference on kinematics (reduced amplitude of wrist deceleration peak) Effect not exclusive to HRVs	observed when words appeared 50 and 200 ms post action onset
Lindemann <i>et al.</i> (2006), Exp. 1	<i>N</i> = 24 Lang: Dut Hand: R Age: n/a	Words <i>mouth</i> and <i>eye</i> , indicating the goal locations of the actions 2 unrelated words 5 pseudowords	Go/no-go object (cup or magnifying glass) grasping or finger lifting guided by lexical decision	Grasping: initiation facilitated by compatibility between object and goal- location word Finger lifting: no effect No facilitation of kinematic variables	comp 521 ms, incomp 538 ms
Lindemann <i>et al.</i> (2006), Exp. 2	<i>N</i> = 24 Lang: Dut Hand: R Age: n/a	Words <i>left</i> and <i>right</i> , indicating the locations of objects on table 2 unrelated words 5 pseudowords	Go/no-go object (cup or magnifying glass) grasping or finger lifting guided by lexical decision	Finger lifting: initiation facilitated by compatibility Grasping: no effect No facilitation of kinematic variables	comp 504 ms, incomp 524 ms
Lindemann <i>et al.</i> (2006), Exp. 3	<i>N</i> = 15 Lang: Dut Hand: R Age: n/a	Words <i>mouth</i> and <i>eye</i> , indicating the goal locations of the actions 4 unrelated human-body-part words 6 animal names	Go/no-go object (cup or magnifying glass) grasping guided by semantic decision (does the word denote a human body part?)	Grasping: initiation facilitated by compatibility with action-consistent words No facilitation of kinematic variables	comp 474, incomp 490 ms
Kritikos <i>et al.</i> (2012), Exp. 1	<i>N</i> = 19 Lang: Eng Hand: R Age: 22.4**	9 <i>up</i> synonyms 9 <i>down</i> synonyms 10 non-words	Upon seeing a word, utter it while reaching for and grasping an object with thumb and index by its upper or lower end according to where in the screen the word appeared	Facilitation of movement initiation by compatibility of word and location	~950 ms
Kritikos <i>et al.</i> (2012), Exp. 2	<i>N</i> = 11 Lang: Eng Hand: R	9 <i>up</i> synonyms 9 <i>down</i> synonyms 10 non-words	Upon seeing a word, utter it while reaching for and grasping an object with thumb and index by its upper	Facilitation of movement initiation and maximum hand height by compatibility of word and location, with object	~940 ms

	Age: 22.4**		or lower end according to where in the screen the word appeared In a second run, do the same without a physical object (imagine where the object would have been)	present and absent	
Gentilucci & Gangitano (1998)	<i>N</i> = 6 Lang: It Hand: R Age: 20-29*	Large and small objects showing a printed adjective (<i>long</i> or <i>short</i>)	Object grasping with index and thumb	Facilitation of reaching kinematics increased for word <i>long</i> (peak acceleration, velocity, deceleration)	-----
Tucker & Ellis (2004)	<i>N</i> = 73 Lang: Eng Hand: n/a Age: n/a	16 pictures of natural objects 16 pictures of man-made objects 16 HRNs (natural objects) 16 HRNs (man-made objects) Half in each set required precision grasps (small objects), half required power grasps (large objects)	Semantic decision (natural or man-made) by grasping an object with either a precision or a power grasp	Facilitation of RTs by compatibility of affordance, for both images and words	Words: comp 595 ms, incomp 620 ms
Masson <i>et al.</i> (2008), Exp. 1	<i>N</i> = 20 Lang: Eng Hand: n/a Age: n/a	6 HRNs evoking functional actions 6 HRNs evoking volumetric actions 6 HRNs evoking a functional and a volumetric action	Object grasping via a functional (aerosol, palm, poke, trigger) or a volumetric (horizontal grasp, horizontal pinch, vertical grasp, vertical pinch) hand action, primed by an HRN	Facilitation of RTs by compatibility, only for functional actions Facilitation when cue appeared after full word (not on mid-word appearance), for functional actions, and when cue was related to prime	29 ms shorter for comp, in 1120-1150 ms window
Lindemann <i>et al.</i> (2006), Exp. 4	<i>N</i> = 20 Lang: Dut Hand: R Age: n/a	Words <i>mouth</i> and <i>eye</i> , indicating the goal locations of the actions 4 unrelated action words ending with D or G 6 unrelated words ending with other letters	Go/no-go object (cup or magnifying glass) grasping guided by letter identification (does the word end with D or G?)	Null effect	-----
Mirabella <i>et al.</i> (2012), Exp. 4	<i>N</i> = 12 Lang: It Hand: R Age: 24**	5 HRVs 5 foot verbs 5 abstract verbs	Go/no-go hand displacement guided by color identification (is the verb printed in green?)	Null verb type effect	-----
Spadacenta <i>et al.</i> (2014),	<i>N</i> = 30 Lang: It	3 HRVs, negative connotation 3 HRVs, neutral connotation	Go/no-go hand displacement guided by color identification (is the verb	Null effect	-----

Exp. 2	Hand: R Age: 25.2**	3 leg verbs 3 abstract verbs	printed in green?) Go signal 53.2 or 332.5 ms after word onset (verb visible until end of trial)		
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NOTES: Fr: French; Dut: Dutch; Eng: English; It: Italian; R: right-handed; **: mean; *: range; n/a: not available; HRVs: hand-related verbs; RT: reaction time; comp: compatible; incomp: incompatible; non-significant results are reported if crucial to the study's overall results.

Table A8. Object-reaching-and-displacement experiments.

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
Dalla Volta <i>et al.</i> (2009), Exp. 2	<i>N</i> = 15 Lang: It Hand: R Age: 20-25*	10 HRVs 10 foot verbs 10 abstract verbs	Go/no-go object grasping and displacement guided by pre-execution semantic decision (does the verb involve action?)	Null effect on RT (reach and grasp) Interference (less reach peak velocity)	~250 ms after word onset
Gentilucci (2003)	<i>N</i> = 16 Lang: Eng Hand: R Age: 21-25*	Object showing a printed verb (<i>place</i> or <i>lift</i>), or an adjective (<i>lateral</i> or <i>high</i>) or a consonant string	Object grasping and displacement	Facilitation of reaching kinematics by verb <i>place</i> and of placing kinematics by verb <i>lift</i> (peak velocity) No effect caused by adjectives	-----
Fargier <i>et al.</i> (2012), Exp. 1	<i>N</i> = 21 Lang: Fr Hand: R Age: 28.3**	Manual-verb pair: <i>grasp-put down</i> Non-verb pairs	Object grasping and displacement while uttering a word-pair (one word per movement) Also, non-verbalization condition	Facilitation of grasping movement (higher amplitude of wrist speed and acceleration peaks, with overall faster movement) Facilitation of displacement (higher wrist velocity amplitude and deceleration peaks)	Effect on grasping speed, 875 ms after movement onset
Fargier <i>et al.</i> (2012), Exp. 2	<i>N</i> = 16 Lang: Fr Hand: R Age: 21.4**	Manual-verb pair: <i>grasp, put down</i> Non-manual verb pair: <i>squat, run</i> Non-motor-verb pair: <i>food, pepper</i>	Object grasping and displacement while uttering a word-pair (one word per movement) Also, non-verbalization condition	No effect on word production onset Facilitation of grasping (higher wrist speed amplitude and deceleration peaks) Facilitation of displacement (higher wrist velocity peak amplitude)	-----
Gentilucci <i>et al.</i> (2000),	<i>N</i> = 6 Lang: It	Large and small objects showing a printed adverb (<i>near</i> or <i>far</i>),	Object grasping and lifting with index and thumb	Facilitation of reaching kinematics increased for the word <i>far</i> (peak	-----

Exp. 1	Hand: R Age: 22.8**	placed close to or far from subject		acceleration and speed) Facilitation of peak speed and finger aperture by compatibility	
Gentilucci <i>et al.</i> (2000), Exp. 2	<i>N</i> = 6 Lang: It Hand: R Age: 20.8**	Large and small objects showing a printed adverb (<i>near</i> or <i>far</i>) or no word at all, placed at a congruent distance relative to subject	Object grasping and lifting with index and thumb	Increase of finger aperture velocity and maximal finger aperture by word <i>far</i> relative to <i>near</i>	-----
Gentilucci <i>et al.</i> (2000), Exp. 4	<i>N</i> = 10 Lang: It Hand: R Age: 22.6**	Same as above, with words <i>large</i> and <i>small</i>	Object grasping and lifting with index and thumb	Increase of finger aperture velocity and maximal finger aperture by word <i>large</i> relative to <i>small</i>	-----
Gentilucci <i>et al.</i> (2000), Exp. 5	<i>N</i> = 6 Lang: It Hand: R Age: 20.1**	Large and small objects showing a printed adverb (<i>high</i> or <i>low</i>), placed high or low relative to subject	Object grasping and lifting with index and thumb	Facilitation (increased arm peak velocity) for the word <i>high</i>	-----
Gentilucci <i>et al.</i> (2000), Exp. 6	<i>N</i> = 6 Lang: It Hand: R Age: 20.7**	Same as above, with words <i>up</i> and <i>down</i>	Object grasping, lifting, and placing downwards with index and thumb	Facilitation (increased arm peak acceleration) for the word <i>up</i>	-----
Gentilucci <i>et al.</i> (2000), Exp. 7	<i>N</i> = 6 Lang: It Hand: R Age: 20.7**	Same as above	Object grasping, lifting, and placing upwards with index and thumb	Facilitation (increased arm peak acceleration) for the word <i>down</i>	-----
Glover <i>et al.</i> (2004), Exp. 1	<i>N</i> = 12 Lang: It Hand: R Age: n/a	5 HRNs denoting objects which can be gripped with small apertures 5 HRNs denoting objects which can be picked with large apertures	Reading a word and then reaching for, grasping, and lifting an object	Increased grip aperture early when reaching large-object words, which progressively decayed as motion progressed	-----

NOTES: It: Italian; Eng: English; Fr: French; R: right-handed; *: range; **: mean; HRVs: hand-related verbs; HRNs: hand-related nouns; RT: reaction time; non-significant results are reported if crucial to the study's overall results.

Table A9. Keyboard-typing experiments.

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
García & Ibáñez	<i>N</i> = 33 Lang: Sp	10 HRVs 10 other-effector verbs	Keyboard-based primed-verb copying	Interference of motor primes and targets on typing onset (higher for	Typing onset 850-880 ms after verb onset

(2016)	Hand: R Age: 25.4**	10 abstract verbs (90 trials, 9 prime-target conditions)		HRV than other-effector primes) Interference of motor primes on full-verb typing Facilitation of full-verb typing by prime-target semantic congruency	Full-verb typing 1630-1650 ms after word onset
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NOTES: Sp: Spanish; *: range; HRVs: hand-related verbs.

Section B: Summary of experiments involving sentential HREs

Experiments are organized in terms of increasing motor demands (as detailed in Table 1 in the main manuscript). Where appropriate, experiments are further subclassified according to sentence complexity.

Table B1. Object-holding experiments.

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
Aravena <i>et al.</i> (2012)	<i>N</i> = 24 Lang: Fr Hand: R Age: 22.9**	35 affirmative Ss with HRVs 35 negative Ss with HRVs 35 Ss with nouns lacking motor associations	Counting Ss including country names (to ensure attention) while gripping a force sensor	Increased grip force for affirmative HRV Ss No modulation for negative HRV Ss	320-520 ms and 520-800 ms after word onset
Aravena <i>et al.</i> (2014), Exp. 1	<i>N</i> = 25 Lang: Fr Hand: R Age: 21.7**	35 Ss with HRVs, focus on action 35 Ss with HRVs, focus on volition 35 Ss with nouns lacking motor associations	Listening to Ss while holding a grip-force sensor	Increase in grip force only for Ss focused on action	In three time windows: 120-320, 320-520, and 520-800 ms
Aravena <i>et al.</i> (2014), Exp. 2	<i>N</i> = 19 Lang: Fr Hand: R Age: 21.7**	37 Ss with HRVs, action context 37 Ss, pseudoverbs, action context 37 Ss, non-act verbs, action context	Listening to Ss, while holding a grip-force sensor	Increase in grip force for action-action and action-pseudoverb Ss	In three time windows: 120-320, 320-520, and 520-800 ms

		37 Ss, non-act verbs, non-act context			
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NOTES: Fr: French; R: right-handed; **: mean; HRVs: hand-related verbs; non-act: non-action.

Table B2. Single-key pressing experiments (with simple sentences).

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
Buccino <i>et al.</i> (2005), Exp. 2	<i>N</i> = 20 Lang: It Hand: R Age: 19-28*	20 HRV Ss 20 foot-verb Ss 20 abstract-verb Ss 30 “catch” Ss	Semantic judgment (does the sentence involve action?) by pressing a switch with the hand or the foot	Interference by effector compatibility	HRV Ss: comp 320 ms, incomp 302 ms Foot-verb Ss: comp 392 ms, incomp 376 ms
Gianelli & Dalla Volta (2014), Exp. 2	<i>N</i> = 44 Lang: It Hand: R Age: n/a	20 HRV Ss 20 foot-verb Ss 20 abstract-verb Ss 30 “catch” Ss	Semantic judgment (does the sentence involve action?) by pressing a switch with hand or foot	Null effect, with mean RTs showed that hand responses to HRV Ss were slower than to foot-verb Ss	388 vs. 372ms

NOTES: It: Italian; *: range; n/a: not available; S: sentence; HRVs: hand-related verbs; RT: reaction time; comp: compatible; incomp: incompatible; non-significant results are reported if crucial to the study's overall results.

Table B3. Single-key pressing experiments (with complex sentences).

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
De Vega <i>et al.</i> (2004), Exp. 1	Exp. 1A <i>N</i> = 44 Lang: Sp Hand: R Age: n/a Exp. 1B <i>N</i> = 23 Lang: Eng Hand: R Age: n/a	40 stories; key Ss: simultaneous actions (<i>while</i>) with same eff (hand) 40 stories; key Ss: successive actions (<i>after</i>) with same eff (hand) 40 stories; key Ss: simultaneous actions (<i>while</i>) with different effs 40 stories; key Ss: successive actions (<i>after</i>) with different effs 20 control stories,	Sensibility judgment by key pressing (right after key sentence)	Both experiments: Interference on same-effector Ss and facilitation of different-effector Ss if the adverb was <i>while</i> as opposed to <i>after</i>	Exp. 1A Same effector: <i>while</i> 2445 ms, <i>after</i> 2157 ms Different effector: <i>while</i> 2241 ms, <i>after</i> 2336 ms Exp. 1B Same effector:

		half simultaneous, half successive Half the key Ss in each condition were sensible, half nonsensical 60 filler stories			<i>while</i> 1880 ms, <i>after</i> 1797 ms Different effector: <i>while</i> 1768 ms, <i>after</i> 1843 ms
De Vega <i>et al.</i> (2004), Exp. 2	<i>N</i> = 60 Lang: Ger Hand: R Age: n/a	Same-effector stories in Exp. 1. Half key clauses headed by <i>thought of</i> (unreality), and half headed by <i>begin to</i> (reality)	Sensibility judgment by key pressing (right after key sentence)	Interference on <i>begin to</i> Ss and facilitation if the adverb was <i>while</i> as opposed to <i>after</i> No such difference for <i>thought of</i> Ss	<i>begin to</i> Ss: <i>while</i> 2360 ms, <i>after</i> 2297 ms <i>thought of</i> Ss: <i>while</i> 2543 ms, <i>after</i> 2308 ms
Santana & de Vega (2013), Exp. 1	<i>N</i> = 25 Lang: Sp Hand: R Age: 20.4**	40 nonsensical Ss: simultaneous actions (<i>while</i>) with same eff (hand) 40 sensible Ss: successive actions (<i>after</i>) with same eff (hand) 30 filler sensible Ss: simultaneous actions (<i>while</i>) with same eff (hand) 30 nonsensical filler Ss: successive actions (<i>after</i>) with same eff (hand) 40 fillers	Sensibility judgment by key pressing	Interference on <i>while</i> Ss relative to <i>after</i> Ss	<i>while</i> Ss: 1160 ms <i>after</i> Ss: 1011 ms
Santana & de Vega (2013), Exp. 2	<i>N</i> = 25 Lang: Sp Hand: R Age: 21.9**	35 incongruent S: simultaneous actions with same eff (hand) 35 congruent sensible Ss: simultaneous actions (one perceptual, one manual) 35 congruent filler Ss: simultaneous actions (one motor, one perceptual) 35 incongruent anomalous fillers	Sensibility judgment by key pressing	Interference on motor-motor Ss relative to perceptual-motor and anomalous Ss	Motor-motor: 1328 ms Percept-motor: 1191 ms

NOTES: Sp: Spanish; Eng: English; Ger: German; *: range; **: mean; n/a: not available; S: sentence; eff: effector; non-significant results are reported if crucial to the study's overall results.

Table B4. Single-key pressing experiments (with verb-noun pairs).

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
Klatzky <i>et al.</i> (1989), Exp. 1	<i>N</i> = 16 Lang: Eng Hand: n/a Age: n/a	4 words involving key hand shapes 20 sensible object-action phrases 10 nonsensical object-action phrases	Sensibility judgment of a target phrase primed by hand-shape or neutral words, by key-pressing	Facilitation by all hand-shape words relative to neutral words	Within 1000 and 1100 ms
Klatzky <i>et al.</i> (1989), Exp. 2	<i>N</i> = 13 Lang: Eng Hand: n/a Age: n/a	4 words involving key hand shapes 20 sensible object-action phrases 10 nonsensical object-action phrases	Sensibility judgment of a target phrase primed by hand-shape or neutral words, by key-pressing	Facilitation by all hand-shape words relative to neutral words	Within 1000 and 1100 ms
Klatzky <i>et al.</i> (1989), Exp. 3	<i>N</i> = 13 Lang: Eng Hand: n/a Age: n/a	4 words involving key hand shapes 20 sensible object-action phrases 10 nonsensical object-action phrases	Sensibility judgment of a target phrase primed by hand-shape or neutral words, by key-pressing (without explicit request of attention to prime)	Facilitation by full hand-shape primes relative to neutral words	Within 1050 and 1150 ms
Borghi & Scorolli (2009), Exp. 1	<i>N</i> = 13 Lang: It Hand: R Age: n/a	Verb-noun pairs 12 dominant-hand verbs with noun manipulated by dominant hand 12 dominant-hand verbs with noun bimanually manipulated 12 either-hand verbs with noun manipulated by dominant hand 12 either-hand verbs with noun bimanually manipulated 48 nonsensical filler pairs	Sensibility judgment by key pressing with either the right of the left finger	Facilitation of right-hand and left-hand responses to sensible and nonsensical Ss, respectively Facilitation of dominant-hand-verb pairs	right 572 ms, left 711 ms 78 ms faster
Borghi & Scorolli (2009), Exp. 2	<i>N</i> = 22 Lang: It Hand: R Age: n/a	Verb-noun pairs: 12 HRVs with object nouns	Sensibility judgment by key pressing with either the right of the left finger	Interference of right-hand and left-hand responses to sensible and nonsensical Ss, respectively	right 863 ms, left 701 ms

		12 foot verbs with object nouns 48 nonsensical filler pairs			
Borghi & Scorolli (2009), Exp. 3	<i>N</i> = 38 Lang: It Hand: R Age: n/a	Verb-noun pairs: 28 HRVs with object nouns 28 mouth verbs with object nouns 56 nonsensical filler pairs	Sensibility judgment by key pressing with either the right of the left finger	Facilitation of right-hand responses to sensible Ss	-----
Borghi & Scorolli (2009), Exp. 4	<i>N</i> = 8 Lang: It Hand: R Age: n/a	Verb-noun pairs: Combination of hand, foot, and mouth verbs in Exps. 2 and 3	Sensibility judgment by key pressing with either the right of the left finger	Facilitation of right-hand responses to sensible hand vs. foot Ss Facilitation of mouth over hand Ss	136 ms faster 70 ms faster
Marino <i>et al.</i> (2012)	<i>N</i> = 22 Lang: It Hand: R Age: 21.5**	Verb-noun pairs: 12 low-freedom verbs with HRN 12 low-freedom verbs with non-graspable noun 12 high-freedom verbs with HRNs 12 high-freedom verbs with non-graspable noun 48 nonsensical filler pairs	Sensibility judgment by key pressing with either the right of the left finger	Sensible pairs: Facilitation of low-freedom verbs Facilitation of high-freedom verbs followed by non-graspable nouns Non-sensible pairs: Facilitation of low-freedom verbs Facilitation of right-hand responses for pairs with HRNs Left-hand disadvantage, mainly in Ss with HRNs	46 ms faster 34 ms faster 16 ms faster 28 ms faster All within 1130-1190 ms

NOTES: Eng: English; It: Italian; *: range; n/a: not available; R: right-handed; HRV: hand-related verb; HRN: hand-related noun.

Table B5. Hand-displacement ACE experiments.

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
Glenberg & Kaschak (2002)	Exp. 1 <i>N</i> = 44 Lang: Eng	40 sensible toward S pairs, imperative 20 sensible toward S, indicative (concrete	Sensibility judgment by moving hand to a button close to or far away from the body	Facilitation by compatibility (positive ACE)	Reduction of 50-100 ms starting at 1250 or 1650 ms

	Hand: R Age: n/a Exp. 2A N = 70 Lang: Eng Hand: R Age: n/a	transfer) 20 sensible toward S pairs, indicative (abstract transfer) 40 sensible away S pairs, imperative 20 sensible away S pairs, indicative (concrete transfer) 20 sensible away S pairs, indicative (abstract transfer) 80 nonsense Ss			
Glenberg & Kaschak (2002), Exp 2B	N = 72 Lang: Eng Hand: R Age: n/a	Same as above	Sensibility judgment by pushing a button with either the index finger	Null effect	-----
Borreggine & Kaschak (2006)	N = 48 (per exp.) Lang: Eng Hand: R Age: n/a	20 sensible toward Ss (concrete transfer) 20 sensible away Ss (concrete transfer) 20 sensible toward Ss (abstract transfer) 20 sensible away Ss (abstract transfer) 40 nonsense Ss	Go/no-go sensibility judgment by pressing a button located close to or away from the body Guided by trial-per-trial instructions on whether YES was the close of the far button	Exp. 1 (inst at S onset): facilitation by compatibility (positive ACE) Exp. 2 (inst 50 ms post S): null effect Exp. 3 (inst 500 ms post S): null effect, mean RTs towards negative ACE Exp. 4 (inst 1000 ms post S): null effect, mean RTs towards negative ACE	Exp. 1: comp 700 ms, incomp 1000 ms
Kaschak & Borreggine (2008)	N = 48 (per exp.) Lang: Eng Hand: R Age: n/a	Same as Borreggine & Kaschak (2006)	Sentence memorization with trial-by-trial instructions to press a button located either close to or away from the body (instruction always presented <i>during</i> sentence processing, as each sentence lasted roughly 2300 ms)	Exp. 1 (inst 500 ms post S onset): facilitation by compatibility (positive ACE) Exp. 2 (inst 1500 ms post S onset): null effect Exp. 3 (inst 2000 ms post S	Exp. 1: comp 1475 ms, incomp 1575 ms (only for 'towards' Ss)

				onset): null effect, mean RTs towards negative ACE	
Glenberg <i>et al.</i> (2008a), Exp. 1	<i>N</i> = 20 Lang: It Hand: R Age: n/a	20 sensible toward Ss (concrete transfer) 20 sensible toward Ss (abstract transfer) 20 sensible away Ss (concrete transfer) 20 sensible away Ss (abstract transfer) 40 sensible no-transfer Ss 120 nonsensical Ss (half concrete, half abstract)	Sensibility judgment by moving hand to a button close to or far away from the body	Facilitation by compatibility (positive ACE) for both concrete transfer and abstract transfer Ss	concrete Ss: 31 ms faster abstract Ss: 48 ms faster
Lugli <i>et al.</i> (2012), Exp. 1	<i>N</i> = 24 Lang: It Hand: R Age: n/a	8 sensible Ss, toward movement of “positive” object (target: <i>oneself</i>) 8 sensible Ss, toward movement of “negative” object (target: <i>oneself</i>) 8 sensible Ss, away movement of “positive” object (target: <i>another person</i>) 8 sensible Ss, away movement of “negative” object (target: <i>another person</i>) 32 nonsensical Ss	Sensibility judgment by pulling the mouse toward the body or by pushing it away	Facilitation by compatibility (positive ACE) only for <i>oneself</i> Ss with toward movements Facilitation of positive objects with <i>oneself</i> Ss Interference of negative objects with away movements	1497 ms 1480 ms 1647 ms
Lugli <i>et al.</i> (2012), Exp. 2	<i>N</i> = 22 Lang: It Hand: R Age: n/a	Same as in Exp. 1, but targets were specific positive (e.g., <i>friend</i>), or specific negative (e.g., <i>enemy</i>), or generic (e.g., <i>another person</i>)	Sensibility judgment by pulling the mouse toward the body or by pushing it away	Facilitation by compatibility (only for <i>oneself</i> Ss with toward movements) Facilitation of away movements by generic specific positive targets Facilitation of <i>oneself</i> Ss by	1296 ms 1405 and 1415 ms 1266 ms

				positive objects Facilitation of specific positive targets Ss by positive objects	1429 ms
Diefenbach <i>et al.</i> (2013), Exp. 1	N = 16 Lang: Ger Hand: R Age: 24.8**	40 Ss describing transfer of objects towards body 40 Ss describing transfer of objects away from body 40 Ss describing transfer of info 40 Ss describing reception of info 80 neutral, no-transfer Ss Half the Ss in each condition were sensible, half nonsensical	Go/no-go sensibility judgment by pushing a button (distant from or close to the body, depending on the condition), with cue signal appearing simultaneously with sentence	Interference by compatibility (negative ACE)	2000-2050 ms
Diefenbach <i>et al.</i> (2013), Exp. 2	N = 40 Lang: Ger Hand: R Age: 24.4**	40 Ss: object transfer toward body 40 Ss: object transfer away from body 40 Ss: transfer of info 40 Ss: reception of info 80 neutral, non-transfer Ss Half the Ss in each condition were sensible, half nonsensical	Go/no-go sensibility judgment by pushing a button (distant from or close to the body, depending on the condition), with cue signaling the direction of the yes response visible only for 500 ms, and appearing at variable SOAs before and after sentence onset	Facilitation by compatibility (positive ACE) with cue at S onset Interference by compatibility (negative ACE) with cue 500 ms after S onset	Facilitation at ~2100 ms Interference at ~2150 ms
De Vega <i>et al.</i> (2013), Exp. 1	N = 105 Lang: Sp Hand: R Age: n/a	24 Ss: transfer away from body 24 Ss: transfer towards body 48 filler Ss: non-transfer verbs (mostly cognition)	Responding to the action verb (when it “jumped” forwards or backwards on the screen) by pressing either a “toward” or an “away” key	350 ms SOA: facilitation by compatibility (positive ACE) 100 and 200 ms SOA: interference by compatibility (negative ACE) Greater interference when response occurred 350 ms after word onset (compared to 100 and	350 ms SOA: 901 ms 100 ms SOA: 783 ms 200 ms SOA: 762 ms Difference of ~15 ms between comp and incomp

				200 ms)	
De Vega <i>et al.</i> (2013), Exp. 2	<i>N</i> = 49 Lang: Sp Hand: R Age: n/a	Same as Exp. 1	Responding to the action verb (when it changed colors) by pressing either a “toward” or an “away” key	Interference by compatibility (negative ACE)	Difference of roughly 26 ms between comp and incomp
Glenberg <i>et al.</i> (2008b) Exp 1	<i>N</i> = 37 Lang: Eng Hand: R Age: n/a	10 sensible toward Ss, concrete objects 10 sensible away Ss, concrete objects 10 sensible no-transfer Ss, concrete objects 10 sensible toward Ss, abstract objects 10 sensible away Ss, abstract objects 10 sensible no-transfer Ss, abstract objects 60 nonsense Ss	Sensibility judgment pressing a button with a single right-hand finger after being trained in displacing beans away from or towards the body	Interference by compatibility (negative ACE)	-----
Glenberg <i>et al.</i> (2008b) Exp 2	<i>N</i> = 42 Lang: Eng Hand: R Age: n/a	Same as Exp. 1	Lexical decision pressing a button with a single right-hand finger after being trained in displacing beans away from or towards the body	Null effect	-----
Glenberg <i>et al.</i> (2008b) Exp 3	<i>N</i> = 76 Lang: Eng Hand: R Age: n/a	The Ss described no movement, but events near or far from grammatical subject (third vs. second person singular)	Same as Exp. 1	Null effect	-----
Glenberg <i>et al.</i> (2008b) Exp 4	<i>N</i> = 148 Lang: Eng Hand: R Age: n/a	Same as Exp. 1	Sensibility judgment pressing a button with a single right-hand or left-hand finger after being trained in displacing beans away from or towards the body	Interference by compatibility (negative ACE), only when using right hand	----
Gianelli <i>et al.</i> (2013)	<i>N</i> = 24 Lang: It Hand: R Age: n/a	16 sensible Ss: toward movement of “positive” object (target: <i>oneself</i>) 16 sensible Ss: toward movement of “negative” object (target: <i>oneself</i>) 16 sensible Ss: away movement of “positive” object (target: <i>another person</i>)	Sensibility judgment by pulling the mouse toward the body or by pushing it away Condition 1: participant alone Condition 2: examiner present	Null ACE on RT and kinematics in the individual condition Facilitation of nouns with grasp- related properties when related to the <i>another person</i> target, only in the social condition	-----

		16 sensible Ss: away movement of “negative” object (target: <i>another person</i>) 32 nonsensical Ss		Also, RTs and kinematics modulated by presence or absence of another person in the room	
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NOTES: Eng: English; It: Italian; Sp: Spanish; **: mean; n/a: not available; S: sentence; inst: instruction; ACE: action-sentence compatibility effect; comp: compatible; incomp: incompatible; non-significant results are reported if crucial to the study's overall results.

Table B6. Hand-shape ACE experiments.

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
Aravena <i>et al.</i> (2010)	<i>N</i> = 26 Lang: Sp Hand: R Age: 22.4**	52 Ss with open-hand HRVs 52 Ss with closed-hand HRVs 52 Ss: non-manual/non-motor verbs All in third person	Sensibility judgment by pressing button with open or closed hand-shape	Facilitation by compatibility (positive ACE), for open and closed hand trials Faster RTs to neutral than comp and incomp trials (position-free effector specificity)	comp 679 ms, incomp 1034 ms
Ibáñez <i>et al.</i> (2013), Exp. 1	<i>N</i> = 17 PD, 15 conts Lang: Sp Hand: R Age**: PD: 62.7; conts: 61.3	Same as Aravena <i>et al.</i> (2010)	Sensibility judgment by pressing button with open or closed hand-shape	Facilitation by compatibility (positive ACE) in conts Null ACE in PD Faster RTs to neutral than comp and incomp trials (position-free effector specificity)	comp 980 ms, incomp 1210 ms comp and incomp 1180 ms
Ibáñez <i>et al.</i> (2013), Exp. 2	<i>N</i> = 2 epileptic patients Lang: Sp Hand: R Age: 24, 31	Same as Aravena <i>et al.</i> (2010)	Sensibility judgment by pressing button with open or closed hand-shape	Insufficient <i>N</i> for statistical analysis	-----
Cardona <i>et al.</i> (2014), Exp. 1	<i>N</i> = 10 MO, 10 conts Lang: Sp Hand: R Age**: MO: 40.6;	Same as Aravena <i>et al.</i> (2010)	Sensibility judgment by pressing button with open or closed hand-shape	Facilitation by compatibility (positive ACE) for MO and conts Faster RTs to neutral than comp and incomp trials (position-free effector specificity)	MO: comp 900 ms, incomp 950 ms conts: comp 830 ms, incomp 940 ms

	conts: 40.7				
Cardona <i>et al.</i> (2014), Exp. 2	<i>N</i> = 10 TM, 10 conts Lang: Sp Hand: R Age**: TM: 44.6; conts: 44.8	Same as Aravena <i>et al.</i> (2010)	Sensibility judgment by pressing button with open or closed hand-shape	Facilitation by compatibility (positive ACE) for TM and conts Faster RTs to neutral than comp and incomp trials (position-free effector specificity)	TM: comp 890 ms, incomp 1000 ms conts: comp 890 ms, incomp 1000 ms
Cardona <i>et al.</i> (2014), Exp. 3	<i>N</i> = 15 PD, 15 conts Lang: Sp Hand: R Age**: PD: 62.3; conts: 61.3	Same as Aravena <i>et al.</i> (2010)	Sensibility judgment by pressing button with open or closed hand-shape	Null ACE for PD Facilitation by compatibility (positive ACE) for conts Faster RTs to neutral than comp and incomp trials (position-free effector specificity)	PD: comp 1160 ms, incomp 1160 ms conts: comp 900 ms, incomp 1210 ms
Kargieman <i>et al.</i> (2014)	<i>N</i> = 18 HD, 18 conts; 19 HD rels, 19 conts. Lang: Sp Hand: R Age**: HD: 43; conts: 43.2; HD rels: 29; conts: 29.5	Same as Aravena <i>et al.</i> (2010)	Sensibility judgment by pressing button with open or closed hand-shape	Null ACE for HD and HD rels Facilitation by compatibility (positive ACE) for conts Faster RTs to neutral than comp and incomp trials (position-free effector specificity)	HD: comp 1236 ms, incomp 1217 ms HD rels: comp 995 ms, incomp 1003 ms HD conts: comp 920 ms, incomp 1000 ms HD rels conts: comp 950 ms, incomp 1027 ms
Melloni <i>et al.</i> (2015)	<i>N</i> = 14 PD, 13 conts Lang: Sp Hand: R Age**: PD: 56; conts: 54.7	Same as Aravena <i>et al.</i> (2010)	Sensibility judgment by pressing button with open or closed hand-shape	Null ACE for PD Facilitation by compatibility (positive ACE) for conts	PD: comp 1522 ms, incomp 1495 ms conts: comp 805 ms, incomp 1013 ms

NOTES: Sp: Spanish; **: mean; PD: Parkinson's disease patients; conts: healthy controls; MO: melitis optica patients; TM: traverse myelitis patients; HD: Huntington's disease patients; rels: relatives; S: sentence; ACE: action-sentence compatibility effect; comp: compatible; incomp: incompatible; non-significant results are reported if crucial to the study's overall results.

Table B7. Knob-turning ACE experiments.

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
Zwaan & Taylor (2006), Exp. 2	<i>N</i> = 58 Lang: Eng Hand: R Age: 18.3**	9 sensible Ss (clockwise actions) 9 sensible Ss (c-clockwise actions) 54 fillers (18 sensible, 36 not)	Sensibility judgment by turning a knob either to the right of to the left	Facilitation by compatibility (positive ACE)	comp 237 ms, incomp 275 ms
Zwaan & Taylor (2006), Exp. 3	<i>N</i> = 39 Lang: Eng Hand: R Age: 19**	8 sensible Ss (clockwise actions) 8 sensible Ss (c-clockwise actions) 54 fillers (18 sensible, 36 not)	Sensibility judgment while monitoring a rotating cross by pressing a button either to the right of to the left	Facilitation by compatibility (positive ACE) when action direction and cross direction matched. So, comprehension was easier when concurrent visual stimulus moved in the same direction	comp 124 ms, incomp 177 ms
Zwaan & Taylor (2006), Exp. 4	<i>N</i> = 60 Lang: Eng Hand: R Age: 19.3**	Same as Exp. 3	Self-paced reading with chunk processing indicated by turning a knob either to the right of to the left (followed by comprehension question)	Facilitation by compatibility (positive ACE) in the verb region, but not afterwards	comp 358 ms, incomp 380 ms
Zwaan & Taylor (2006), Exp. 5	<i>N</i> = 42 Lang: Eng Hand: R Age: 18.8**	8 sensible Ss (clockwise actions) 8 sensible Ss (c-clockwise actions) 32 fillers	Self-paced reading with chunk processing indicated by pressing the spacebar (with concurrent visual stimulus implying rotation either to the right or to the left)	Facilitation by compatibility (positive ACE) in the verb region, but not afterwards (comprehension was easier when the concurrent visual stimulus moved in the same direction)	Between 380 and 400 ms

NOTES: Eng: English; **: mean; S: sentence; c-clockwise: counterclockwise; ACE: action-sentence compatibility effect; comp: compatible; incomp: incompatible.

Table B8. Object-grasping experiments.

Experiment	Participants	Stimuli	Task	Interaction between HREs and hand actions	Effect timing
Masson <i>et al.</i> (2008), Exp. 2	<i>N</i> = 84 Lang: Eng Hand: n/a Age: n/a	288 Ss including combinations of: 6 HRNs evoking functional actions 6 HRNs evoking volumetric actions 6 HRNs evoking a functional and a volumetric action	Object grasping via a functional (aerosol, palm, poke, trigger) or a volumetric (horizontal grasp, horizontal pinch, vertical grasp, vertical pinch) hand action, primed by either a verb or a noun in a sentence	Facilitation of functional actions by attention verbs Facilitation of volumetric and functional actions by non-manual action verbs	comp: 15 ms faster, between 1100-1200 ms

		4 attention verbs evoking no action			
		4 non-manual action verbs			

NOTES: Eng: English; n/a: not available; S: sentence; HRNs: hand-related nouns; comp: compatible; incomp: incompatible.

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Figure captionS

Figure 1. Schematic illustration of the cortical systems for language and action. (A) Somatotopy of the motor and premotor cortex. The approximate location of the face/articulators, arm/hand and foot/leg representations. **(B) Connections between the language and action systems.** Inferences about corticocortical links in humans are based on neuroanatomical studies in monkeys. The arrows indicate longdistance cortico-cortical links. **(C) Semantic somatotopy model of action word processing.** Distributed neuronal assemblies bind information about word forms and the actions to which they are semantically linked. Because action words can relate to different body parts (for example, ‘lick’, ‘pick’ or ‘kick’), the cortical distributions of their neurocognitive networks differ. A1, core region of the primary auditory cortex; BPO, Broca’s area, pars opercularis; BPT, Broca’s area, pars triangularis; M1, primary motor cortex; PFC, prefrontal cortex, posterior part adjacent to motor system; PMC, premotor cortex; WB, auditory belt region in Wernicke’s area; WPB, auditory parabelt region in Wernicke’s area. Reprinted by permission from Macmillan Publishers Ltd: NATURE REVIEWS NEUROSCIENCE. Pulvermuller, F., *Brain mechanisms linking language and action*. Nat.Rev.Neurosci., 2005. 6(7): p. 576-582, copyright (2005).

Figure 2. Structure of the review. Studies on the crosstalk between HREs and manual actions involve two main types of verbal stimuli: single words or sentences. Each of those stimulus types has been employed in paradigms requiring varied concomitant manual actions, ranging from simple (e.g., object holding, single-key pressing) to complex (e.g., object grasping). The studies have considered two broad measure types: global

action measures (RTs) and kinematic measures. See Appendix (Tables A1-A9 and B1-B8) for a description of the manual tasks used with each type of verbal stimulus.

Figure 3. Extended interference by increased semantic or motor demands. (A) Paradigm and results from Bergen *et al.* (2010). Verbs in three conditions for the images *run* and *scratch*. Participants viewed action images followed by a congruent or incongruent verb and decided whether both stimuli matched by pressing a button. Results in different versions of the experiment show long-lasting interference for same-effector pairs. **(B) Paradigm and results from Mirabella *et al.* (2012).** Each trial started with the presentation of a central red circle that subjects had to touch and hold for a variable period. Then, a verb was shown above the central stimulus. After a variable delay (stimulus onset asynchrony, SOA) a peripheral target appeared. Participants were asked either to touch it, if the meaning of the verb referred to a concrete action (go-trials), or to refrain from moving if it had an abstract content (no go trials). The panel shows results from Experiment 1: RTs were significantly slower when participants responded to hand-related verbs (mean \pm SEM: 336.465.86 ms) than to foot-related verbs (322.765.67 ms). Furthermore, RTs were significantly slower when the go-signal was presented after an SOA of 53.2 ms than after a SOA of 332.5 ms (412.765.77 ms vs. 246.366.7 ms). **(C) Paradigm and results from García and Ibáñez (2016).** Participants were asked to look at two successively presented verbs and type the second one as fast and accurately and possible. FLL: first-letter lag (lapse from target onset to first key press). WWL: whole-word lag (lapse from first to last key press). FLL results show that both primes and targets denoting motor actions

interfered with the initiation of typing. Interference was greater when primes denoted manual actions. Panel A: Reproduced with kind permission from Springer Science+Business Media: *Memory and Cognition*, *Body part representations in verbal semantics*, 38(7), 971-972, Benjamin Bergen, Ting-Ting-Chan Lau, Shweta Narayan, Diana Stojanovic & Kathryn Wheeler, Figure 1 and Table 1. Panel B: Reproduced with permission from Mirabella *et al.* (2012). Panel C. Reprinted from *Cognition*, 149, Adolfo M. García & Agustín Ibáñez, Hands typing hands: Action-semantic integration dynamics throughout written verb production, Pages 56-66, Copyright (2016), with permission from Elsevier

Figure 4. Paradigm and results from Lindemann *et al.* (2012). Illustration of the experimental setup. A cup (Object 1), a magnifying glass (Object 2), and a computer display were placed on the table. Participants placed their right hand on the starting position. In the object-grasping condition, participants were instructed to prepare actions associated with these objects. For example, if a cup was shown, the required action was to grasp the cup and to bring it to the mouth. The motor response associated with the magnifying glass was to grasp the object and move it to the right eye. By contrast, in the finger-lifting condition, the participants prepared a lifting of either the index or middle finger of the right hand depending on which side the depicted object was situated on the table. Importantly, the action in association with the object had to be delayed until the presentation of a word on the screen. Results on the right side show mean response latencies in the go/no-go lexical-decision task of Experiment 1 (goal locations) and 2 (spatial descriptions) as a function of the factors Action Condition and Word Consistency. Error bars represent the 95% within-subject confidence intervals. Reproduced with permission from Lindemann *et al.* (2012).

Figure 5. Paradigm and results from Frak *et al.* (2010). Functioning of the instrumented cylinder. A. The apparatus is designed to measure the orientation (h) and vertical location (x) of the applied force (P) by either the index or thumb while exerting a grip force. These parameters are computed from outputs of a F/T sensor (with axes X, Y and Z) embedded in the two half-cylinders using two T-adaptors. B. The participants were asked to lift the cylinder with the thumb and index fingers of the right hand and hold it at about 5 cm above the table. Results on the right side show normalized grip force amplitude. Grand average of normalized grip force amplitude of verbs and nouns –when they are targets– between the onset of a stimulus word until the end of the longest word duration. Compared to the nouns, the presence of verbs induced an early change in the signal following word onset. The shaded portion of the graph, starting at 260 ms and ending at 430 ms, shows the area where the two curves are significantly different ($p < .05$). Reproduced with permission from Frak *et al.* (2010).

Figure 6. Paradigm and results from Aravena *et al.* (2010). (A) open-hand (OH) motor response during sentence comprehension task. (B) closed-hand (CH) motor response during sentence comprehension task. (C) Custom-made response button. A commonly available USB joystick with analogue sticks was adapted to detect when a participant initiated a response. (D) RTs of ACE for CH group and OH group. In the former, the compatible sequence trials comprised CH sentences and the incompatible comprised OH sentences. In the latter, the compatible and incompatible effects were opposite. Vertical bars denote 0.95 confidence intervals. (E and F) N400-like effect for OH group and CH group. The channel locations of selected electrodes are shown in the grey circle. Note that the incompatible stimuli which elicits N400 amplitude enhancement are OH sentences in CH group (Panel E) and CH sentences in the OH group (Panel F). (G) ERPs from motor responses.

Compatibility effects and difference waveforms for MP and RAP. Channel locations are shown in the grey circle inside the figure. Reproduced with permission from Aravena *et al.* (2010).

Figure 7. ECoG of ACE. (A) Motor and language areas producing an ACE. Normalized position of the electrodes showing a significant ACE (compatibility effect) superimposed in a render 3D map of the canonical CH2bet from MRICron software. The figure depicts the position of electrodes evincing an ACE from both patients' grids in a common space showing the activation of IFG, STG and MTG (language-related areas) and the MFG, PM and M1 (motor-related areas). Electrode colour is indicative of iERP modulation: MP (Blue); M-N400 (Red); L-N400 (Green).

(B) Pictures of subdural grids and electrode arrays. Codes (number) of electrodes in left picture are not the same as the grid codes (D1) since it includes the electrode for triggers (number 5 in the picture). In the three schematic grids, numbers in red are indicative of significant compatibility effects observed at those sites for MP, M-N400 and L-N400 (from left to right).

(C) Time-probability charts showing the significant effects at MP in premotor/motor (M1, ventral and dorsal PM) areas and N400 windows (M-N400 localized in premotor/motor areas including M1 and ventral-dorsal PM area; and a L-N400 localized in STG, MTG and IFG).

(D) Point-by-point p -value waveform of the compatibility effect for MP, M-N400, and L-N400. The blue lines highlight the $p < .01$ threshold. Note that in panels **C** and **D**, a value of zero on the abscissa indicates the time of the response for MP, whereas a value of zero indicates the time at which the verb was presented for M-N400 and L-N400. Note that motor areas (first and second columns) correspond to Patient 2; and language areas (third column) are from the electrodes on Patient 1. Reprinted from *Cortex*, 49(4), Agustín Ibáñez, Juan F. Cardona, Yamil Vidal Dos Santos, Alejandro Blenkmann, Pía Aravena,

María Roca, Esteban Hurtado, Mirna Nerguizian, Lucía Amoruso, Gonzalo Gómez-Arévalo, Anabel Chade, Alberto Dubrovsky, Oscar Gershanik, Silvia Kochen, Arthur Glenberg, Facundo Manes & Tristán Bekinschtein, Motor-language coupling: direct evidence from early Parkinson's disease and intracranial cortical recordings, 968-84, 2013, with permission from Elsevier.

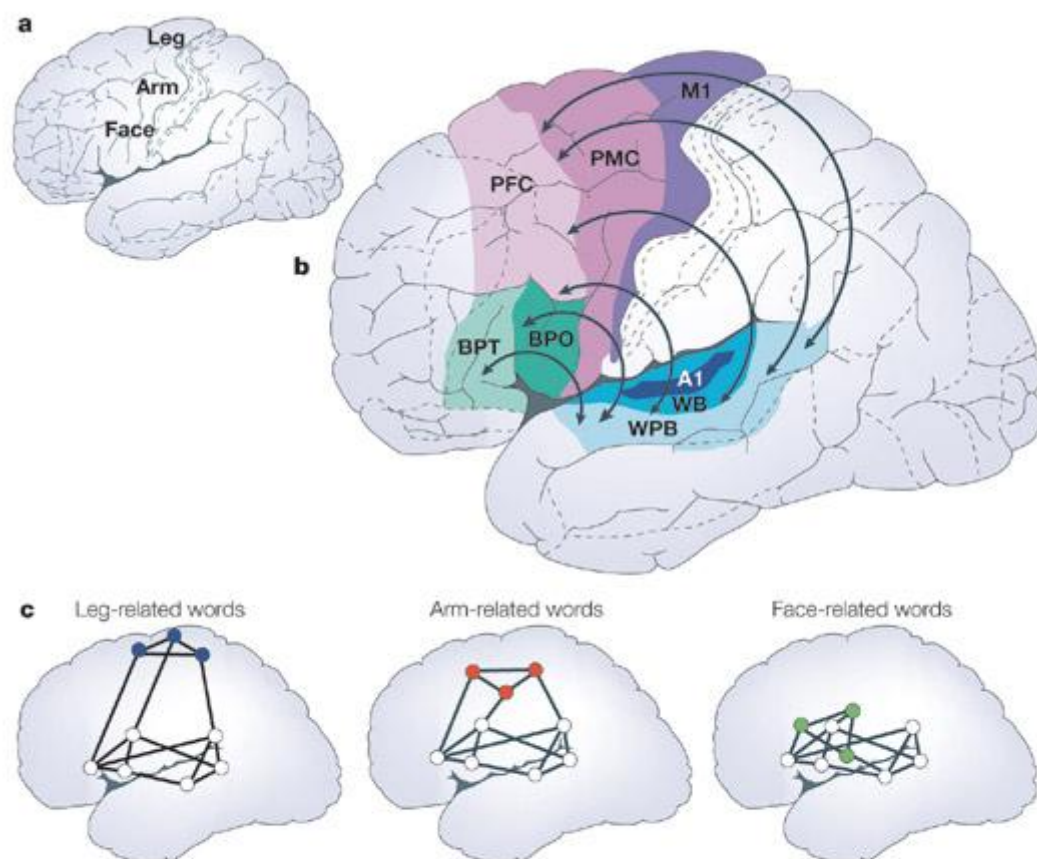
Figure 8. Semantic processing of the HRV *push* followed by a simple manual response within a 0-400 ms window. During response preparation, effector-specific motor networks are primed by anticipatory action programming. Presentation of the HRV *push* causes supra-threshold activation in lexical and relevant motor nodes engaged by semantic processing, and sub-threshold activation in associated circuits supporting goal-related information. Within 400 ms, these activity levels are maintained; thus, the incoming manual motor command fails to access (a substantial part of) its neural resources and is delayed. **Notes:** Th = threshold; grayscale in nodes indicates activity level (white = minimal; black = maximal). Vertical lines indicate bidirectional connections among the systems.

Figure 9. Semantic processing of the HRV *push* followed by a simple manual response within a 450-750 ms window. During response preparation, effector-specific motor networks are primed by anticipatory action programming. Presentation of the HRV *push* causes supra-threshold activation in lexical and relevant motor nodes engaged by semantic processing, and sub-threshold activation in associated circuits supporting goal-related information. Within 450 and 750 ms after word onset, activity levels decrease; thus, an incoming manual motor command finds (a substantial part of) its neural resources pre-activated and is facilitated. **Notes:** Th = threshold; grayscale in nodes indicates activity level (white = minimal; black = maximal). Vertical lines indicate bidirectional connections among the systems.

Figure 10. Semantic processing of the HRAdj *right* followed by a complex manual response within a 450-900 ms window. During response preparation, effector-specific motor networks are primed by anticipatory action programming. Presentation of the HRAdj *right* causes supra-threshold activation in lexical and relevant conceptual node, and sub-threshold activation in associated motor circuits (e.g., those supporting right-sided actions). High motor demands during preparation maintain activity levels well beyond the 400-ms mark; thus, an incoming manual motor command finds (a substantial part of) its neural resources pre-activated and is facilitated. **Notes:** Th = threshold; grayscale in nodes indicates activity level (white = minimal; black = maximal). Vertical lines indicate bidirectional connections among the systems.

Figure 11. HANDLE account of the ACE modulation. (A) Positive ACE (facilitation). Preparation of an ‘away’ movement raises the threshold of all relevant nodes. Presentation of a congruent HRV (e.g., *push [the door]*) causes supra-threshold activation in lexical and relevant conceptual nodes. Activation eventually begins to dwindle, but the sub-threshold level of the ‘away’ nodes still remains higher than others in the pool because they are primed by the previously prepared motion. Subsequent execution of an action involving such nodes will benefit from more priming than actions which do not access ‘away’ nodes. **(B) Negative ACE (interference).** Presentation of an ‘away’ HRV (e.g., *push [the door]*) causes supra-threshold activation in lexical and relevant conceptual nodes. Activation begins to dwindle, but sudden preparation of an ‘away’ movement raises activation of the ‘away’ nodes above threshold. Subsequent execution of an action involving such nodes will not have timely access to them, thus being delayed relative to actions which do not require them. **Notes:** Th = threshold; grayscale in nodes indicates activity level (white = minimal; black = maximal).

Figure 12. Overall architecture of the HANDLE model. HANDLE comprises four main systems: the lexical system, which supports form-level processing, mainly relies on temporal and temporo-occipital regions. The hand action system and the embodied-semantics systems, whose interaction gives rise to gross and effector-specific motor resonance, largely depend on shared regions, including M1, the primary and supplementary motor areas, Broca's area, the basal ganglia, and parietal areas. Additional conceptual information (including action-goal information) is subserved by non-motor semantic networks, crucially involving Wernicke's area, the superior temporal sulcus, and the anterior temporal lobe. All these systems profusely interact via top-down connections (which convey dynamically updated predictions) and bottom-up signals (which send driving signals and prediction errors back to higher levels). Other relevant systems (responsible for visual, auditory, and unification mechanisms) are not shown in the figure.



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Fig. 1

Fig. 2

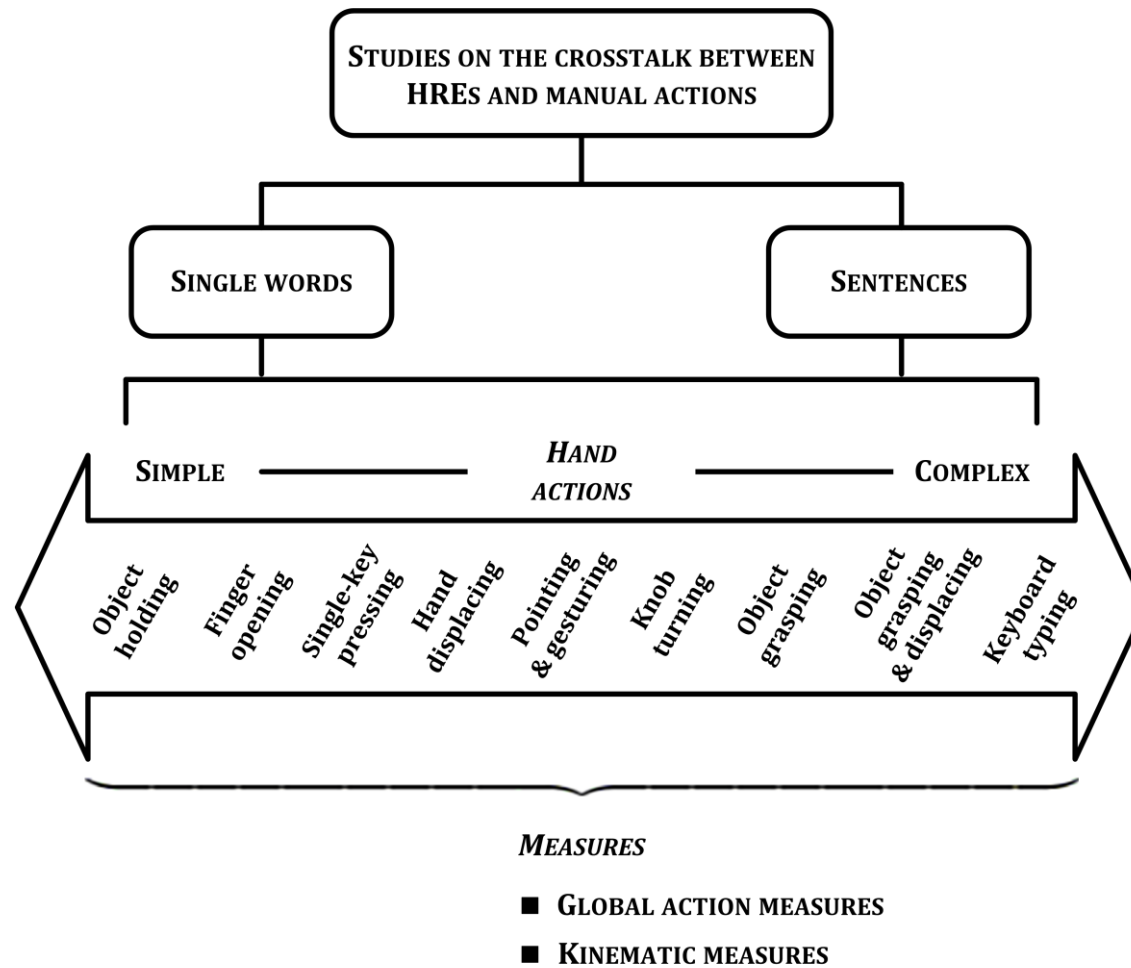
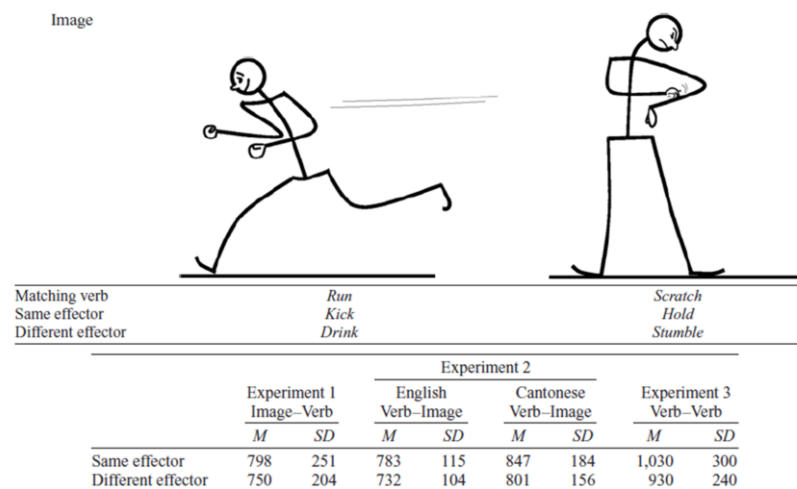
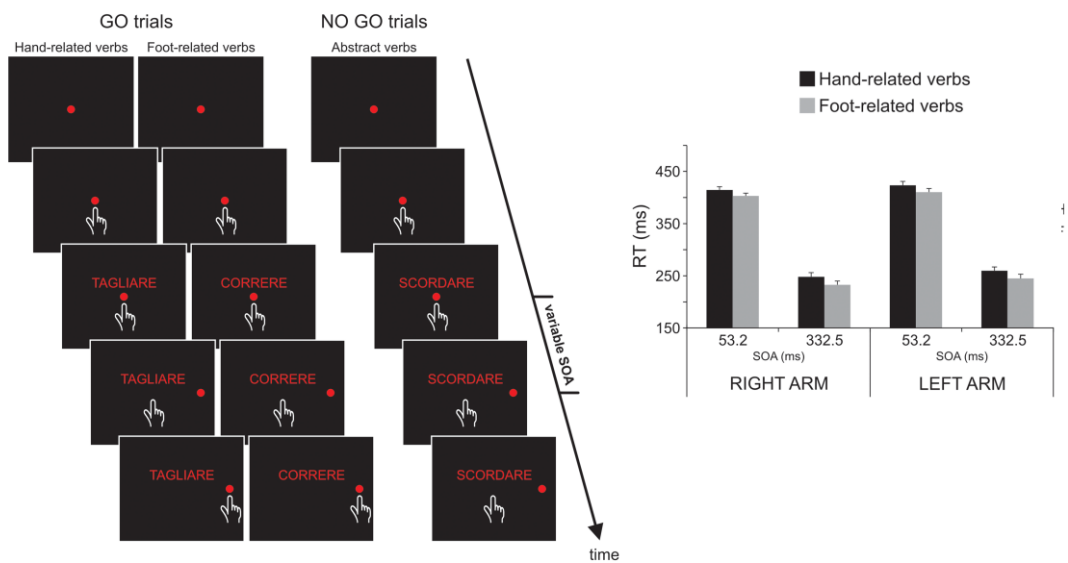


Fig. 3

(A)



(B)



(C)

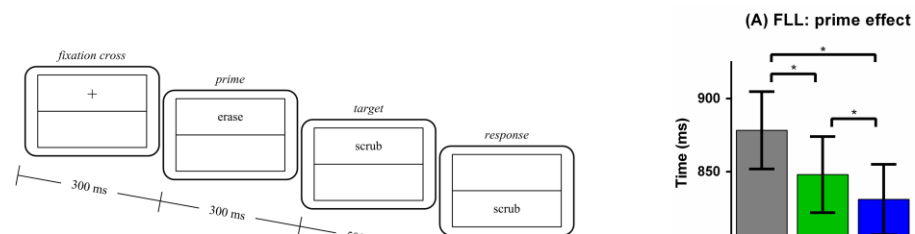


Fig. 4

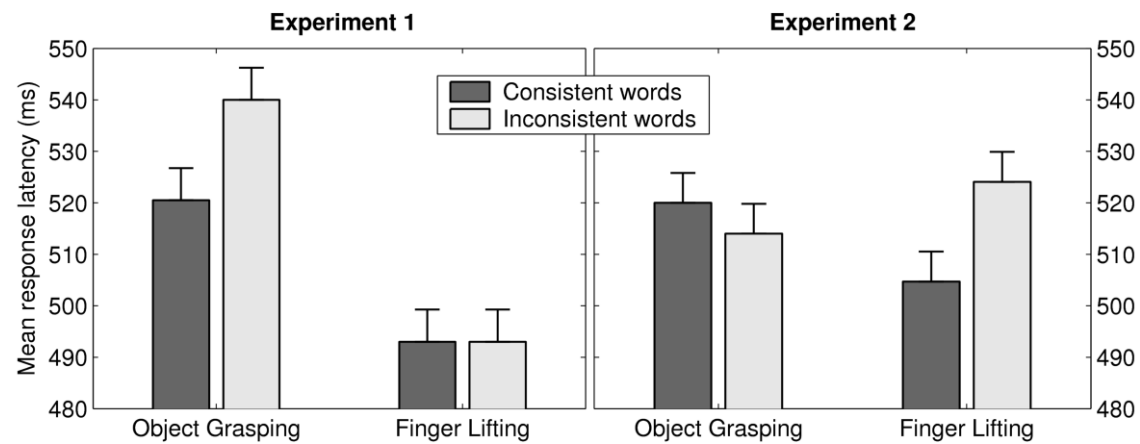
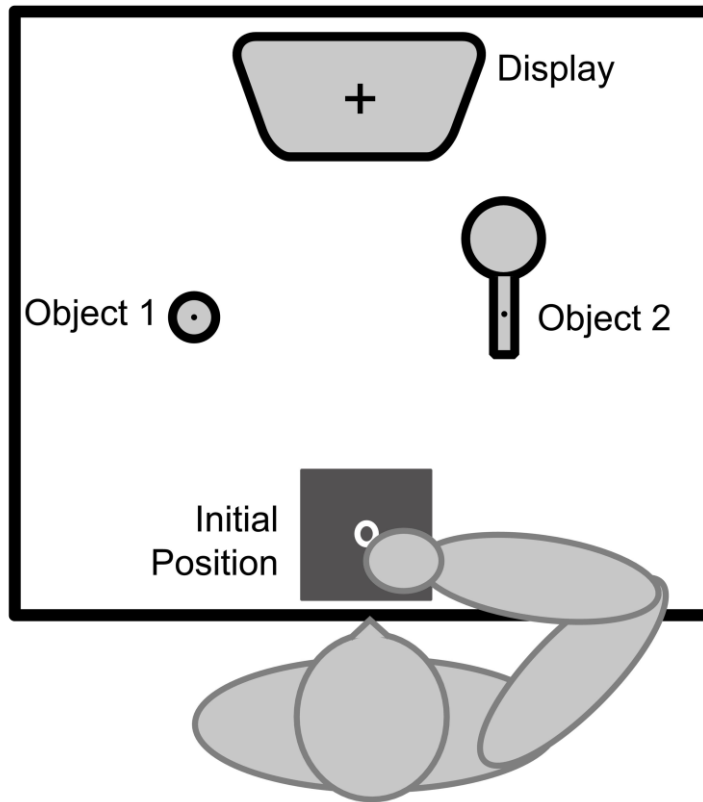


Fig. 5

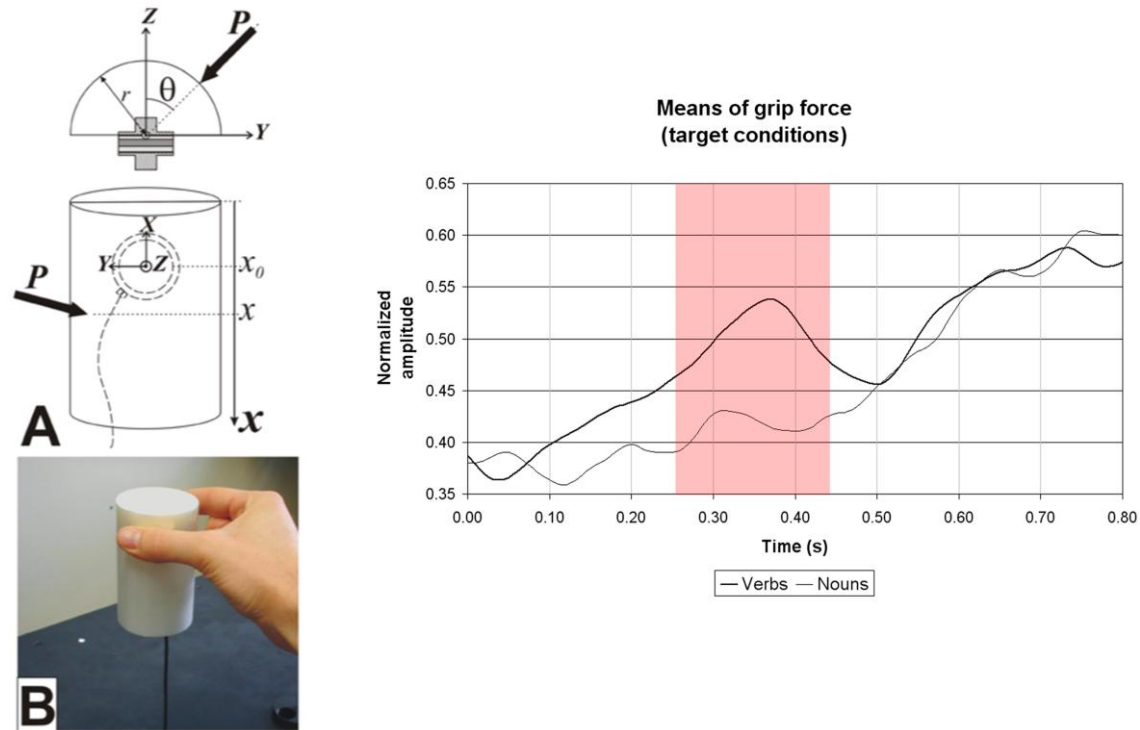


Fig. 6

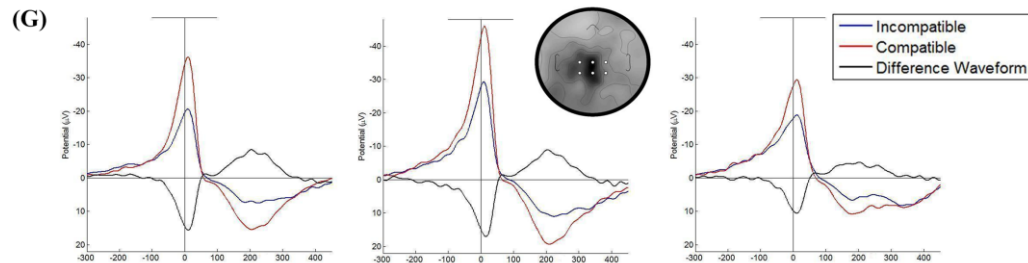
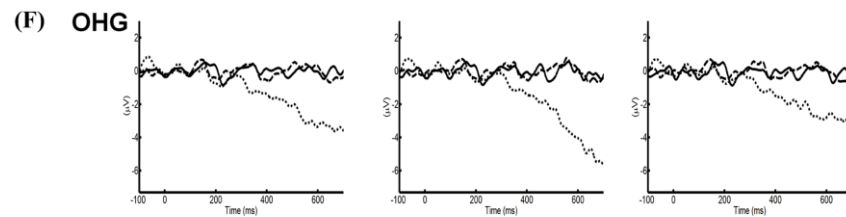
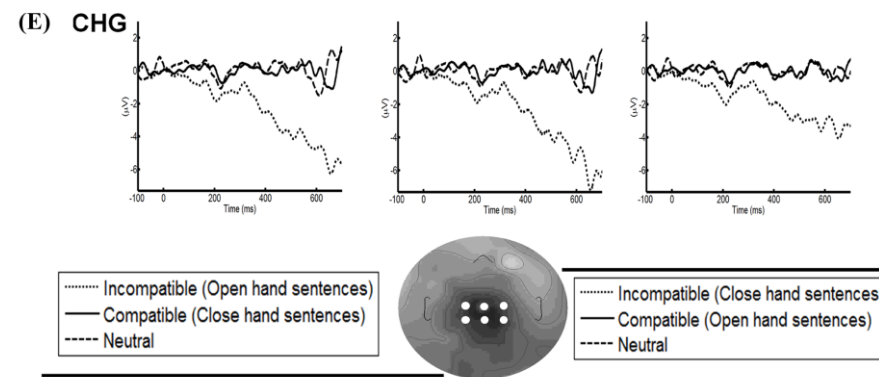
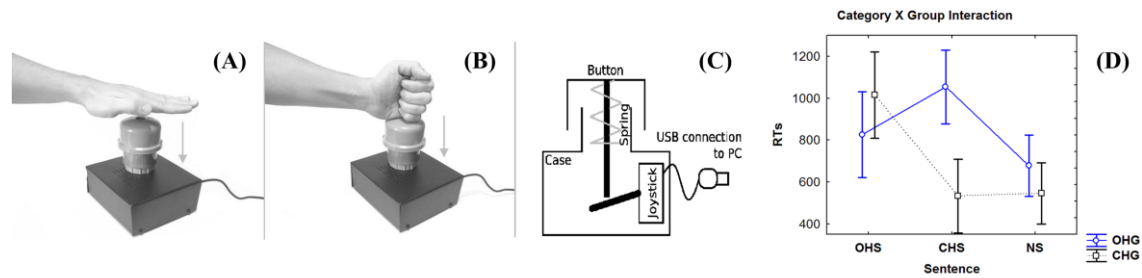


Fig. 7

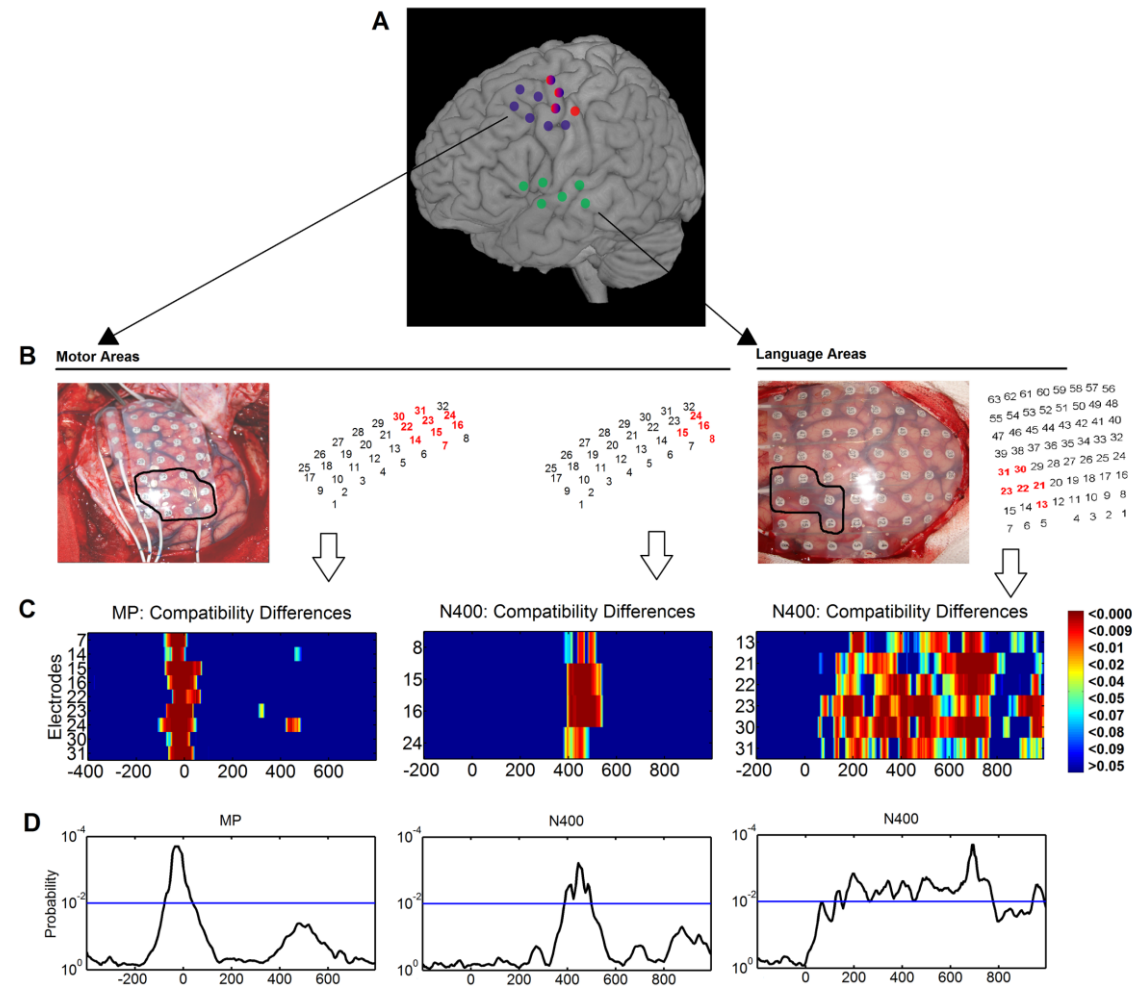


Fig. 8

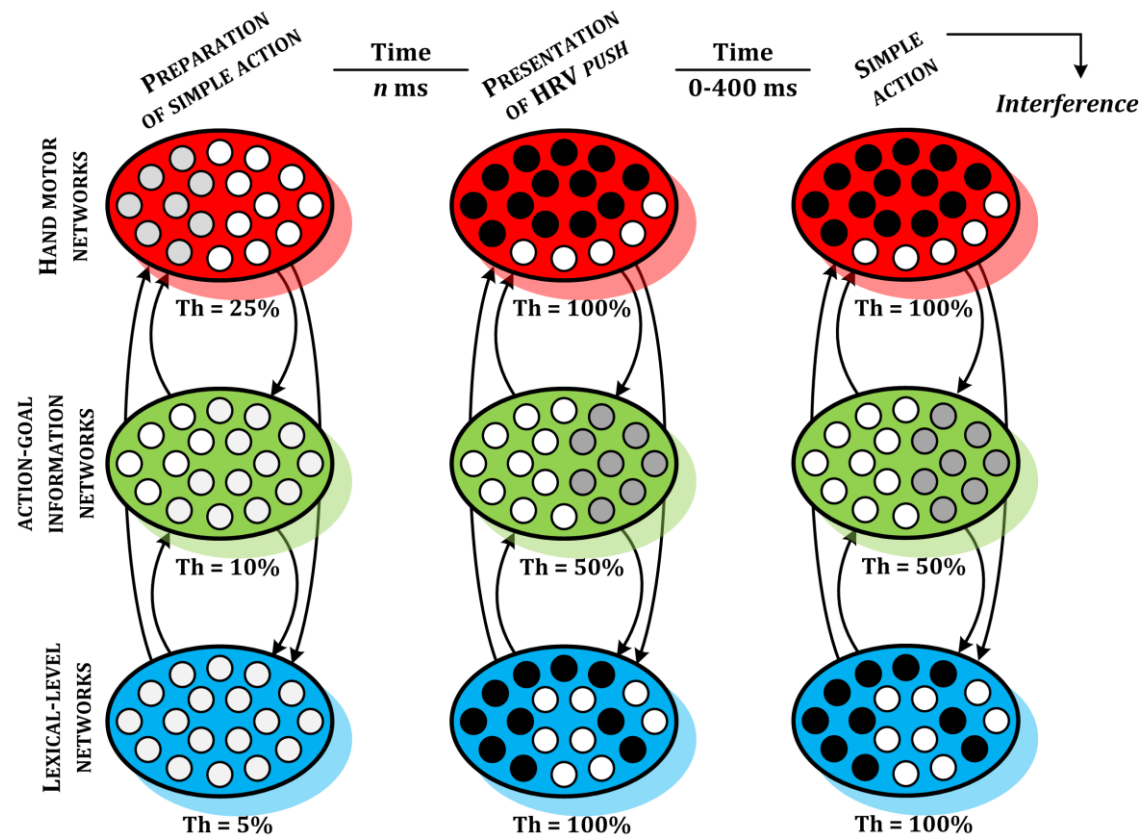


Fig. 9

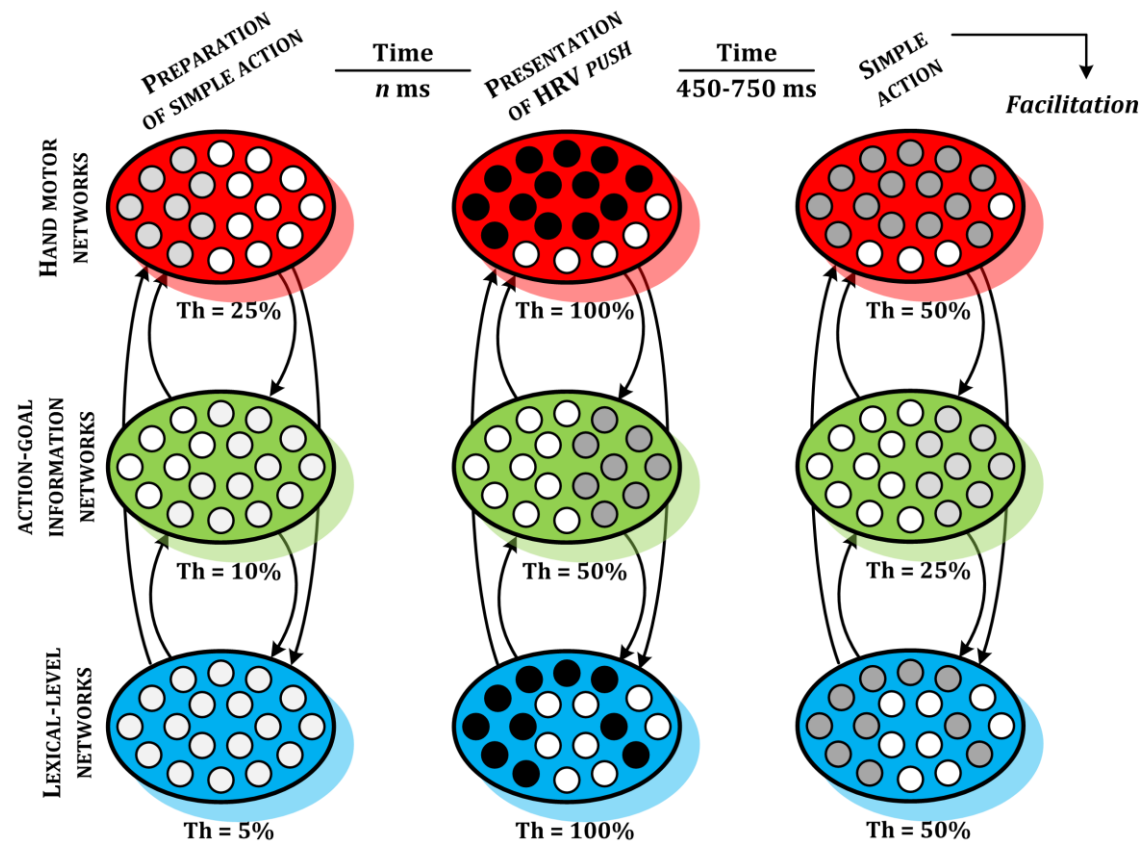


Fig. 10

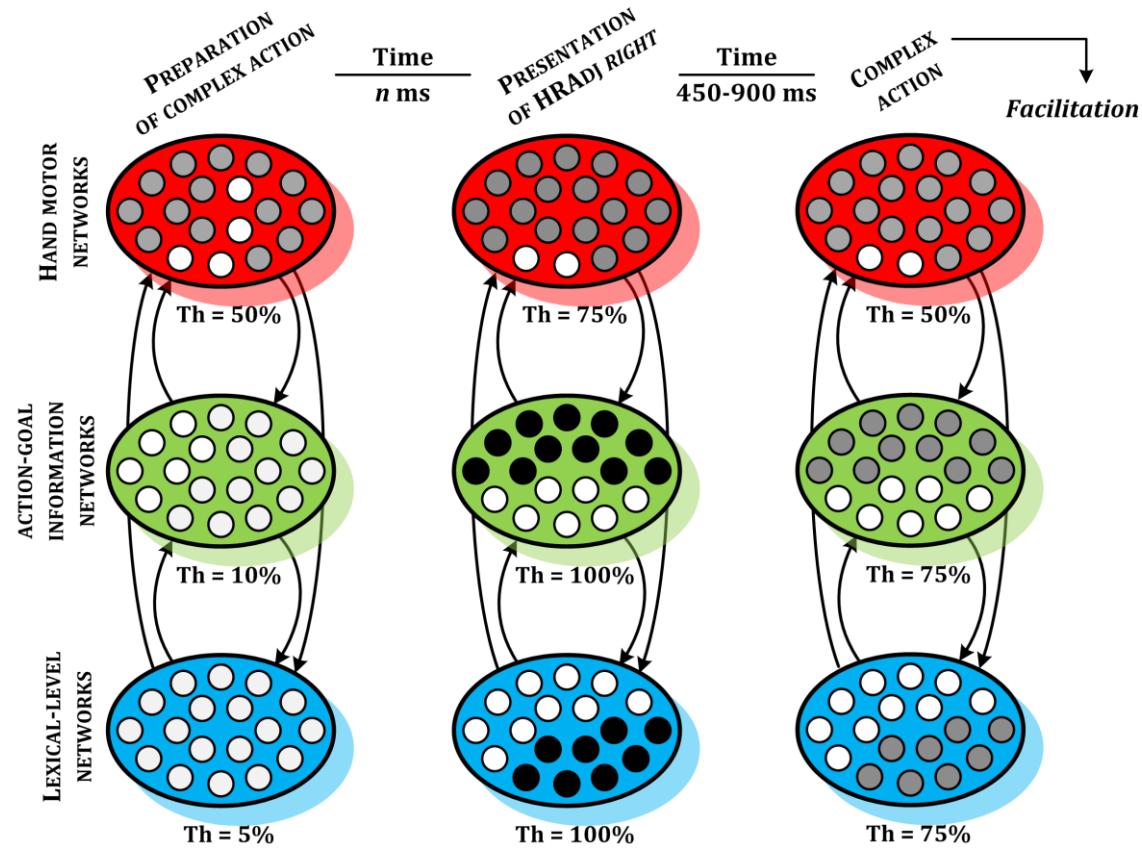


Fig. 11

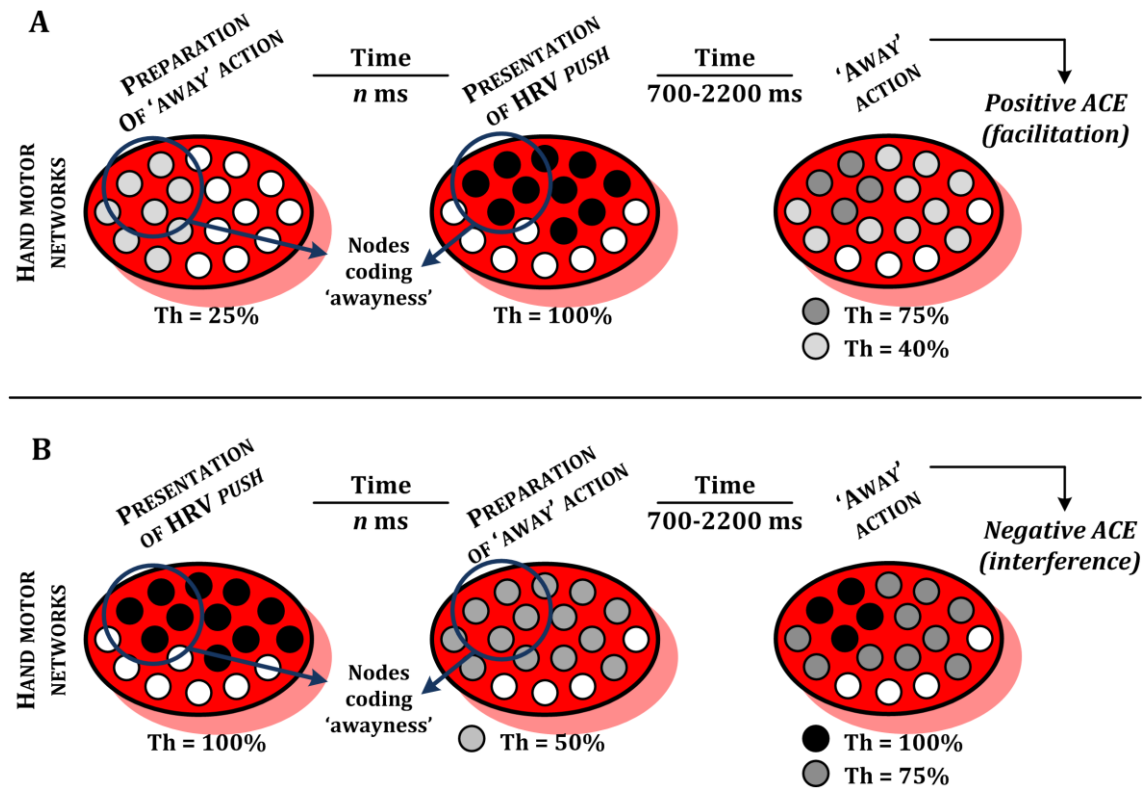
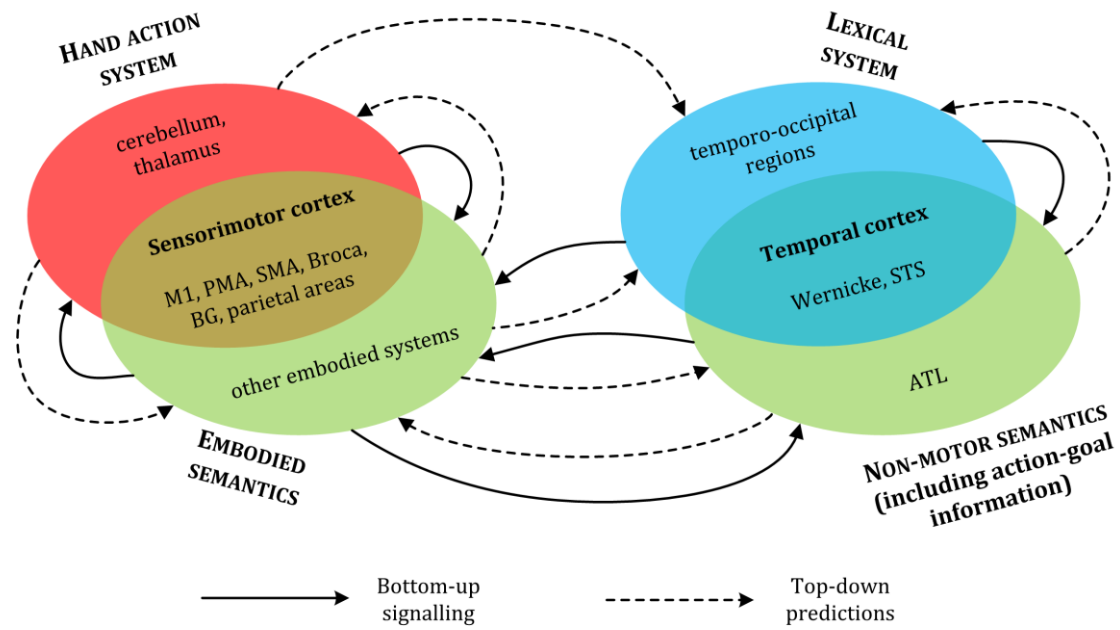


Fig. 12



Tables

Table 1. Five key issues in HRE embodiment research and their potential implications for cognitive science.

Aspects	Questions regarding the embodiment of HREs	Potential implications for neurocognitive research at large
Effect Directionality	Does the integration of HREs and manual activity yield facilitation, interference, or null effects?	Static or monotonic accounts of functional coupling may prove overly simplistic and misleading. Adopting a multimodal and dynamic approach can shed light on more intricate and ecological conceptions of healthy and pathological cognition.
Temporal Dynamicity	How does such integration unfold in the progression from planning to movement onset to its development?	
Modulation by verbal variables	Does such dynamic integration vary as a function of the linguistic unit (words vs. sentences) or the level of verbal processing (lexical vs. semantic)?	Concomitant strains of neural activity may be wrongly characterized by reference to broad theoretical domains (e.g., language and motor processing conceived as two homogeneous wholes). Moreover, considering the mutual effects of variously complex verbal and manual processes on each other may better explain inter-domain couplings in everyday cognition.
Sensitivity to motor complexity	Does such dynamic integration vary depending on how complex the motor routine is?	
Granularity	Is the embodiment of HREs sensitive enough to discriminate between varied hand shapes, positions, and gestures?	Action and high-order cognition may converge in fine-grained functional integrations and entrench bidirectional action-language processes.