

Cross-talk between Language Processes and Overt Motor Behavior in the First 200 msec of Processing

Véronique Boulenger, Alice C. Roy, Yves Paulignan, Viviane Deprez,
Marc Jeannerod, and Tatjana A. Nazir

Abstract

■ A recently emerging view sees language understanding as closely linked to sensory and motor processes. The present study investigates this issue by examining the influence of processing action verbs and concrete nouns on the execution of a reaching movement. Fine-grained analyses of movement kinematics revealed that relative to nouns, processing action verbs significantly affects overt motor performance. Within 200 msec after onset, pro-

cessing action verbs interferes with a concurrent reaching movement. By contrast, the same words assist reaching movement when processed before movement onset. The cross-talk between language processes and overt motor behavior provides unambiguous evidence that action words and motor action share common cortical representations and could thus suggest that cortical motor regions are indeed involved in action word retrieval. ■

INTRODUCTION

An increasingly popular view implies that in addition to “classical” cortical language areas, sensory and motor regions are involved in the retrieval of word meaning. Two models have been put forward to support this proposal. The first model refers to Hebbian correlation learning (Pulvermüller, 1996, 1999, 2001) and proposes that meaning-related information about words could be laid down in temporal–visual and motor areas because some words frequently co-occur in the context of visual perception (e.g., concrete nouns), whereas others frequently co-occur in the context of action execution (e.g., action verbs). The second model, on the other hand, sees language understanding as a form of mental simulation that involves a sensory-motor matching system, the so-called mirror neuron system (Gallese & Lakoff, 2005; Tettamanti et al., 2005; Rizzolatti, Fogassi, & Gallese, 2001; Rizzolatti & Arbib, 1998; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). The mirror neuron system, initially discovered in monkeys but which also exists in humans (Mason, Banfield, & Macrae, 2004; Buccino et al., 2001, 2004; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995), consists of visuomotor neurons that fire both when a monkey executes a given action and when a monkey observes the same action being performed by others (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti et al., 1996; di Pellegrino, Fadiga, Fogassi, Gallese, &

Rizzolatti, 1992). By matching observed movement onto her/his own motor repertoire, the observer uses her/his motor knowledge to recognize the action (Rizzolatti et al., 2001). The recent discovery of acoustic mirror neurons (responding to the execution and to the noise typically evoked by an action; Kohler et al., 2002) and of orofacial communicative mirror neurons (responding to the execution of a mouth action and to the observation of oral affiliative gestures, i.e., lip smacking; Ferrari, Gallese, Rizzolatti, & Fogassi, 2003) have been taken to suggest that the human mirror neuron system may code action at an abstract level, accessible by language (Gallese & Lakoff, 2005; Tettamanti et al., 2005). Hence, the perception of an action word and not the perception of the action per se would be sufficient to trigger the mirror neuron system.

Although based on different assumptions, both models see language and motor systems as sharing overlapping neuronal representations and a range of recent data seems to support this view (Buccino et al., 2005; Pulvermüller, 2005; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005; Pulvermüller, Shtyrov, & Ilmoniemi, 2005; Oliveri et al., 2004). Neuropsychological studies, for instance, have shown selective deficits for processing action words after left premotor lesions (e.g., Bak, O’Donovan, Xuereb, Boniface, & Hodges, 2001; Damasio & Tranel, 1993). Neuroimaging studies have further revealed that motor and premotor cortices are activated during processing of action words or sentences (Pulvermüller, 2005). More importantly, words designating actions performed with different body parts

Institut des Sciences Cognitives, Bron Cedex, France

elicit somatotopically organized activation, just as movement execution does (Tettamanti et al., 2005; Hauk, Johnsrude, & Pulvermüller, 2004). Studies using transcranial magnetic stimulation (TMS) have completed this picture by revealing that processing action-related words or sentences modulates the excitability of the left but not the right motor cortex (Pulvermüller, Hauk, et al., 2005; Meister et al., 2003). Buccino et al. (2005), for instance, demonstrated that listening to hand and leg action-related sentences reduced the amplitude of motor-evoked potentials (MEPs) recorded from hand and leg muscles, respectively. Furthermore, behavioral measures in this study revealed an increase of reaction time when the motor response and the words called the same effector. Related but slightly different results were observed by Pulvermüller, Hauk, et al. (2005) and Oliveri et al. (2004), who reported higher MEPs and shorter reaction times to action words (we will discuss these seemingly divergent results later).

Despite the hitherto stimulating results, many questions remain unsolved. First, the reported results do not provide clear-cut evidence as to whether motor regions truly participate in the process of action word retrieval. In fact, as recognition of action words could prompt mental motor imagery—a phenomenon known to activate cortical motor regions (Alkhadhi et al., 2005; Jeannerod & Frak, 1999; Jeannerod, 1994)—language-related cortical motor activity could result from aftereffects of linguistic processes. The likelihood that this is the case would diminish though if cortical motor activity could be shown to arise early after word onset, that is, within the first 100–200 msec within which lexicosemantic processes are typically observed (e.g., word frequency effects or effects of word category; Sauseng, Bergmann, & Wimmer, 2004; Sereno & Rayner, 2003; Pulvermüller, 2001; Pulvermüller, Lutzenberger, & Preissl, 1999; Sereno, Rayner, & Posner, 1998; Preissl, Pulvermüller, Lutzenberger, & Birbaumer, 1995). Pulvermüller, Shtyrov, et al. (2005), who used magnetoencephalography to describe the time course of cortical activity during action word processing, provided first data in this line. Their results showed that cortical activity in the perisylvian language areas, which appeared at about 130–150 msec after action word onset, was followed by a short-lived activity in frontocentral and superior central areas at about 170–200 msec poststimulus. The present study is aimed at further substantiating this finding using behavioral measures.

Second, despite increasing evidence that action word processing engages cortical motor regions, it is unclear whether these same structures are also involved in controlling motor behavior or whether they remain “language-specific” despite their location in cortical motor regions. In other terms, would there be cross-talk between processing of actions words and overt motor behavior if the two tasks were performed concurrently?

To address these issues, we designed two experiments that allowed fine-grained analyses of the kinematics of

an arm reaching movement performed in relation to a language task. In Experiment 1, the reaching movement was performed concurrently to a visual lexical decision task with action verbs or concrete nouns and pseudowords. In Experiment 2, lexical decision was made before movement onset. As we will show, relative to concrete nouns, encoding of action verbs interferes with the concurrent execution of the reaching movement early after word/movement onset. By contrast, processing action verbs before movement onset assists subsequent motor performance.

METHODS

Participants

Nine French native volunteers (22–27 years old) participated in each of the two experiments. All were right-handed (scores between 0.58 and 0.90; Oldfield, 1971), and had normal or corrected-to-normal vision. None of the volunteers participated in both experiments.

Stimuli

Eighty-four words (42 verbs and 42 nouns) were selected from the French lexical database *Lexique* (New, Pallier, Ferrand, & Matos, 2001). Verbs, all in the infinitive form, denoted actions performed either with the hand/arm, leg, or mouth/face (e.g., paint, jump, cry). Nouns, all in singular form, referred to imageable, concrete entities that cannot be manipulated (e.g., star, cliff, meadow). Words that could be used as both nouns and verbs were excluded from the selection. Stimuli were matched for relevant lexical variables including word frequency, length in letters, number of syllables, bi- and trigram frequency, and number and cumulative frequency of orthographic neighbors (Appendix 1). Word age of acquisition was also controlled using empirical ratings performed by 20 volunteers on a seven-point scale (1 = 0–2 years; 7 = older than 13 years; Gilhooly & Logie, 1980). Word imageability was estimated following the same procedure by another 18 volunteers (0 = impossible; 6 = very easy to generate a mental image of the word). To prevent participants from focusing on word-class discrimination, they were asked to perform a lexical decision task (deciding whether a letter string is a word or not). Eighty-four pseudowords, constructed by changing one letter from real nouns or real verbs, were thus added as fillers to perform the lexical decision task. Pseudowords were either “pseudonouns” (42 items) or “pseudoverbs” (42 items) and were all pronounceable. Pseudowords were matched to words for relevant lexical variables (Appendix 1). Verbs and pseudoverbs were also carefully matched for endings, such that as many verbs as pseudoverbs (32/42) ended with “er,” which is a frequent

ending for verbs in French. All items were presented in lower case.

Procedure

Experiment 1

Participants were asked to touch a home-pad (10 cm from their chest) with their right thumb and index finger held in a pinch-grip position while fixating a monitor (95 cm from their chest). On appearance of a white cross at the center of the monitor for 500 msec (go-signal), they had to leave the home-pad to reach and grasp a cylindrical object (height: 30 mm, diameter: 15 mm) placed in front of them (40 cm from the home-pad). The onset of the movement (i.e., leaving the home-pad) triggered the presentation of a letter string on the monitor. If the string was a word, the movement has to be carried on; if it was a pseudoword, the movement has to be interrupted to move back to the home-pad. Stimulus remained on the screen until participants grasped the object (in the word condition) or turned back to the home-pad (in the pseudoword condition). The next trial was triggered by the experimenter once participants were in the starting position. Video recording assured that participants maintained their gaze on the cylindrical object during final movement execution (word condition only). Each stimulus was proposed once, and presentation was randomized. Twenty training trials familiarized participants with the task.

Experiment 2

Material was identical to Experiment 1. Procedure differed in that the go signal was no longer a fixation cross but the letter string. As in Experiment 1, if the stimulus was a word, participants had to reach and grasp the cylindrical object. If it was a pseudoword, they had only to lift their hand from the home-pad.

Movement Recordings

An Optotrak 3020 (Northern Digital) was used to record the spatial positions of four markers (infrared light-emitting diodes), at a frequency of 200 Hz and with a spatial resolution of 0.1 mm. One marker was taped on the wrist. The three remaining markers were fixed on the experimental setup to define a space in which all recorded movements were systematically placed from participant to participant.

Data Analysis

A second-order Butterworth dual-pass filter (cutoff frequency = 10 Hz) was used for raw data processing. Movements were then visualized and analyzed using

Optodisp software (INSERM-CNRS-UCBL; Thevenet, Paulignan, & Prablanc, 2001). Kinematic parameters for the word condition were assessed for each individual movement. We analyzed movement time (i.e., time elapsed between the onset of the movement and the grasping of the target object) and latency and amplitude of wrist acceleration/deceleration peaks. Movement onset was determined as the first value of a sequence of at least 11 increasing points on the basis of wrist velocity profile. End of movements was determined similarly, starting from the end and going backward. Peak latencies were defined as the time elapsed between movement onset and peak. In Experiment 2, we additionally measure reaction time defined as the time elapsed between word onset and movement onset. All kinematic parameters were determined for each individual trial and were averaged for each participant as a function of word category. Trials in which participants made errors or anticipated movement execution were excluded from the analysis.

RESULTS

Experiment 1

A total of 11.64% of trials were excluded from the analysis (5.56% for nouns vs. 6.08% for verbs). Analyses of movement parameters revealed that individual wrist acceleration peaks appeared later and were smaller during displays of action verbs than during displays of concrete nouns in 8 out of 9 participants (Table 1a). An analysis of variance (ANOVA) with repeated measures confirmed that word group had a significant influence on these two variables [peak latency: 160 msec for nouns vs. 177 msec for verbs, $F(1,8) = 6.12$, $p = .0380$; for peak amplitude: 3994 mm/sec² for nouns vs. 3871 mm/sec² for verbs, $F(1,8) = 8.77$, $p = .0180$]. None of the other movement parameters showed significant differences between the two word categories. As wrist acceleration peak is indicative of initial muscular contractions, longer latency and smaller amplitude suggest that perceiving action verbs interferes with the execution of the movement.

For better illustration of the phenomenon, in Figure 1A, we plot wrist acceleration profiles, normalized between 0% and 100% of time, averaged over items and participants. Note that by averaging entire movement profiles, slightly different values for latencies and amplitudes of wrist acceleration/deceleration peaks are obtained when compared with the values presented in Table 1 (see Appendix 2 for details about differences between the two analyses).

Experiment 2

A total of 7.93% of trials were excluded from the analysis (4.76% for nouns vs. 3.17% for verbs). Reaction time

Table 1. Mean Latency and Amplitude for the Wrist Acceleration and Deceleration Peaks, and Total Movement Time for Each Participant While Processing Nouns and Verbs for (a) Experiment 1 and (b) Experiment 2

Participants	Wrist Acceleration Peak								Wrist Deceleration Peak				Total Movement time (msec)	
	Latency (msec)				Amplitude (mm/sec ²)				Latency (msec)		Amplitude (mm/sec ²)		Nouns	Verbs
	Nouns		Verbs		Nouns		Verbs		Nouns	Verbs	Nouns	Verbs	Nouns	Verbs
	Total	Total	Arm	Others	Total	Total	Arm	Others	Total	Total	Total	Total	Total	Total
<i>a) Experiment 1</i>														
P1	128	126	124	128	5341	5027	5125	4938	522	523	-4231	-4004	852	842
P2	155	158	159	156	6251	6240	5740	6672	457	455	-4512	-4515	870	912
P3	213	237	237	237	4405	4415	4288	4525	565	562	-3920	-3903	1025	1006
P4	181	187	182	191	2366	2066	2051	2080	495	497	-1569	-1678	1348	1392
P5	137	139	136	141	3883	3814	3842	3788	458	502	-2304	-2467	1036	1041
P6	138	151	170	134	3575	3506	3441	3567	493	486	-3123	-2837	1205	1173
P7	173	187	192	181	4262	4148	4255	4090	601	615	-5848	-2674	1060	1106
P8	174	200	205	195	3282	3069	2869	3280	669	653	-3597	-3784	1332	1038
P9	146	210	223	196	2576	2556	2540	2573	470	491	-1943	-1696	1214	1211
MEAN	160	177	181	173	3994	3871	3795	3946	526	532	-3450	-3062	1105	1080
<i>SD</i>	27	36	38	36	1250	1279	1205	1358	73	66	1367	1035	182	165
ANOVA	<i>F</i>(1.8) = 6.12; <i>p</i> = .038				<i>F</i>(1.8) = 8.77; <i>p</i> = .018				<i>ns</i>		<i>ns</i>		<i>ns</i>	
<i>b) Experiment 2</i>														
P1	161	141	127	154	8508	8905	9114	8705	443	424	-8201	-7893	625	632
P2	178	143	146	139	4018	4126	4178	4082	658	641	-3259	-3397	1007	1000
P3	287	245	208	282	3769	3572	3521	3623	654	662	-4695	-4586	847	866
P4	140	129	127	131	7839	8192	8158	8220	432	431	-9380	-9348	661	677
P5	135	132	135	130	5378	5321	5315	5326	498	493	-3855	-4023	1071	1078
P6	205	208	209	207	5001	4866	4912	4824	496	498	-5815	-5591	774	788
P7	165	156	165	147	4117	4104	3917	4272	568	563	-3787	-3662	866	871
P8	193	193	198	189	4337	4297	4306	4289	677	689	-3013	-2755	1114	1174
P9	171	171	171	172	4632	4624	4586	4657	553	561	-4029	-4113	928	882
MEAN	182	169	165	172	5289	5334	5334	5333	553	551	-5145	-5041	171	177
<i>SD</i>	45	39	34	49	1717	1897	1959	1841	93	98	2356	2286	877	885
ANOVA	<i>F</i>(1.8) = 5.8276; <i>p</i> = .0422				<i>ns</i>				<i>ns</i>		<i>ns</i>		<i>ns</i>	

For verbs, data are given averaged over all items (total) as well as for items that describe arm actions (arm) and nonarm actions (others). These latter data should be interpreted with caution though, because lexical parameters for nouns and verbs were equated over the entire set of verbs but not for the subsets. Last three rows: Mean overall participants, standard deviation, and repeated measures ANOVA. Gray fields indicate performance that deviated from the tendency suggested by the mean.

Values in *italics* correspond to the values obtained for the two subcategories of verbs (referring to arm actions, and leg or mouth actions = others). The values in **boldface** highlight the mean of the kinematic parameters overall participants and results of the repeated measures ANOVA.

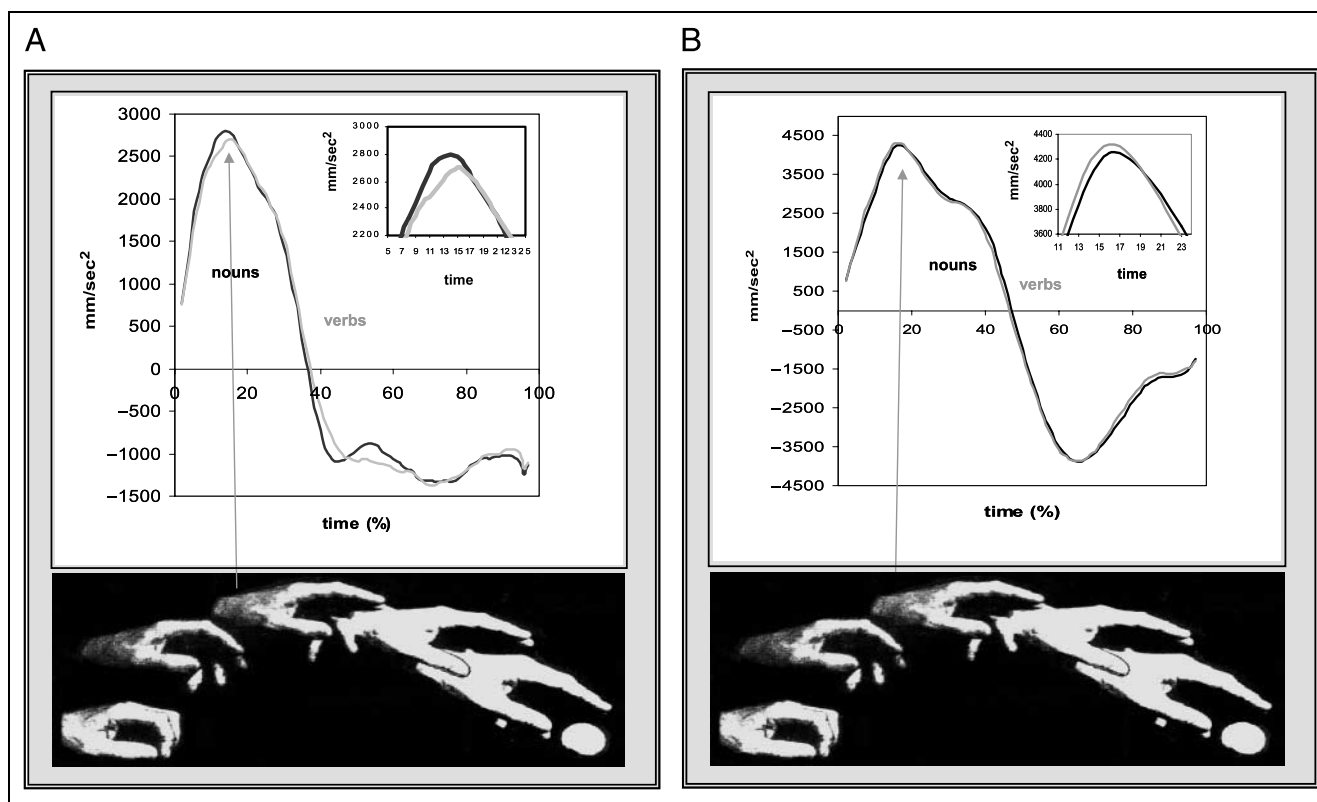


Figure 1. Averaged wrist acceleration/deceleration profiles of all participants (normalized between 0% and 100% of time) during processing of nouns (black) and verbs (gray) for (A) Experiment 1 and (B) Experiment 2. Note that by normalizing the data, real-time information is lost. One time unit in the graph corresponds approximately to 10 msec. The inset magnifies the wrist acceleration peak profile. The gray bar indicates the time window within which paired *t* tests (per time unit) revealed a significant difference between the two conditions.

analysis showed no significant difference between action verbs (386 msec, $SD = 56$; including items referring to actions performed with arm, 385 msec, and other body parts, 386 msec) and concrete nouns (400 msec, $SD = 73$), $F(1,8) = 2.5674$, $p = .1478$.

In contrast to Experiment 1, individual wrist acceleration peaks appeared earlier for action verbs than for concrete nouns in 6 of 9 participants (two participants had identical latencies for the two word categories; Table 1b). The ANOVA with repeated measures confirmed the effect of word category (182 msec for nouns vs. 169 msec for verbs), $F(1,8) = 5.8276$, $p = .0422$, thus indicating that processing action words before movement execution assists the reaching movement. In contrast to Experiment 1, however, the difference in amplitude of wrist acceleration peaks between the two groups did not reach significance. None of the other kinematic landmarks showed significant effects of word group. Figure 1B plots wrist acceleration profiles, normalized between 0% and 100% of time and averaged over items and participants.

A comparison of the two experiments revealed that movement time was significantly shorter in Experiment 2 (see Table 1a and b), $F(1,16) = 6.9750$, $p = .0178$, which suggests that the motor task was easier

when lexical decision was made before movement execution. The percentage of errors did not differ between the two experiments.

Figure 2 plots latency of wrist acceleration peak for nouns and verbs in the two experiments. Performance for action verbs is also shown split by items referring to actions performed with the arm and those performed with other body parts. These data show that interference (Experiment 1) and facilitation (Experiment 2) were more pronounced for verbs designating actions performed with the arm, which was the effector used in the motor task. However, given that relevant word parameters were controlled only over the entire set of words, these latter results have to be interpreted with caution.

DISCUSSION

Cross-talk between Language and Motor Tasks

Our results thus show that processing action words can interfere with or facilitate overt motor behavior, depending on the temporal relation between language and motor tasks. When performed in parallel (Experiment 1), processing action verbs seems to transiently

action recognition can be dissociated from imitation and execution (Halsband et al., 2001; Rumiati, Zanini, Vorano, & Shallice, 2001). Intact conceptual knowledge about graspable objects can also persist together with impairment in using these objects (Rosci, Valentina, Laiacona, & Capitani, 2003). Similarly, lesions over left motor cortex do not predictably lead to impairment in processing action words (Saygin, Wilson, Dronkers, & Bates, 2004; De Renzi & di Pellegrino, 1995), suggesting that motor processes alone are not sufficient to represent all that we know about action concepts. However, although language-related activity in motor and premotor cortex might not be necessary for understanding, it might potentially help action word recognition. Brain-damaged patients with left motor lesion but no obvious deficit in action word (verb) processing might thus turn out to perform poorer than healthy participants when tested with more subtle measures.

APPENDIX 1

Mean values of word frequency, length in letters, number of syllabic groups, bigram frequency, trigram frequency, number and cumulative frequency of orthographic neighbors, age of acquisition, and imageability are reported for nouns, verbs, and pseudowords. Word age of acquisition was controlled with empirical ratings of 20 subjects on a seven-point scale (according to Gilhooly & Logie, 1980; 1 = 0–2 years; 7 = older than 13 years). Word im-

Concluding Remarks

The present behavioral study supports previous findings, which showed that processing of action words involves cortical motor regions. We highlight that perceiving action verbs can interfere with or prime a reaching movement depending on the temporal relation between the two tasks. The arguments that we shortly developed above favor the view that language-related activity in cortical motor regions contributes to the understanding of action words, although we point out limits of this hypothesis given the currently available data. For a better understanding of the nature of the link between action word processing and motor activity, we need to better capture the rule that governs the switch from interference to priming between language and motor tasks and to measure in parallel motor performance and action word understanding.

ageability was evaluated in the same way by 18 other subjects (with 0 = impossible; 6 = very easy to generate a mental image of the word). ANOVAs are reported for nouns and verbs and words and pseudowords. Verbs and pseudoverbs were also carefully matched for endings, such that as many verbs as pseudoverbs (32/42) ended with “er,” which is a frequent ending for verbs in French.

	<i>Nouns</i>	<i>Verbs</i>	<i>ANOVA (by Item)</i>	<i>Pseudonouns</i>	<i>Pseudoverbs</i>	<i>ANOVA (by Item)</i>
FQ	18.64	19.41	$F(1,82) = .009, p = .9253$	–	–	–
LETT	6.57	6.57	*****	6.57	6.57	*****
SYLL	1.98	2.16	$F(1,82) = 3, p = .0869$	2.32	2.07	$F(1,166) = 1.396, p = .2390$
BIGR	4554.23	4826.52	$F(1,82) = .287, p = .5935$	4559.84	5161.68	$F(1,166) = .192, p = .6615$
TRIG	754.49	662.09	$F(1,82) = .449, p = .5048$	667.32	601.94	$F(1,166) = .558, p = .4560$
NB NEIGH	2.28	2.83	$F(1,82) = 3.016, p = .0861$	2	2.39	$F(1,166) = 2.279, p = .1330$
FQ NEIGH	10.53	10.26	$F(1,82) = .009, p = .9248$	11.86	13.89	$F(1,166) = 1.939, p = .1656$
AoA	3.79	3.94	$F(1,82) = .332, p = .5662$	–	–	–
IMAG	4.31	4.07	$F(1,82) = 1.763, p = .1879$	–	–	–

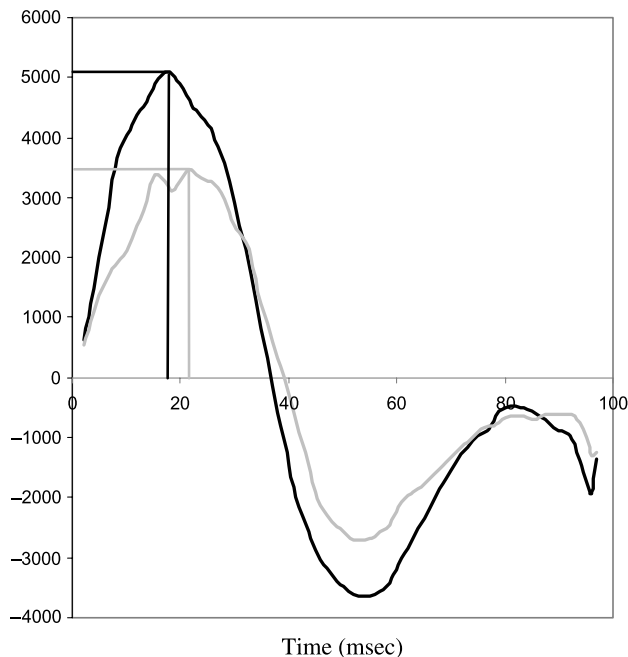
FQ = word frequency; LETT = length in letters; SYLL = number of syllabic groups; BIGR = bigram frequency; TRIG = trigram frequency; NB NEIGH = number of orthographic neighbors; FQ NEIGH = cumulative frequency of orthographic neighbors; AoA = age of acquisition; IMAG = imageability.

APPENDIX 2

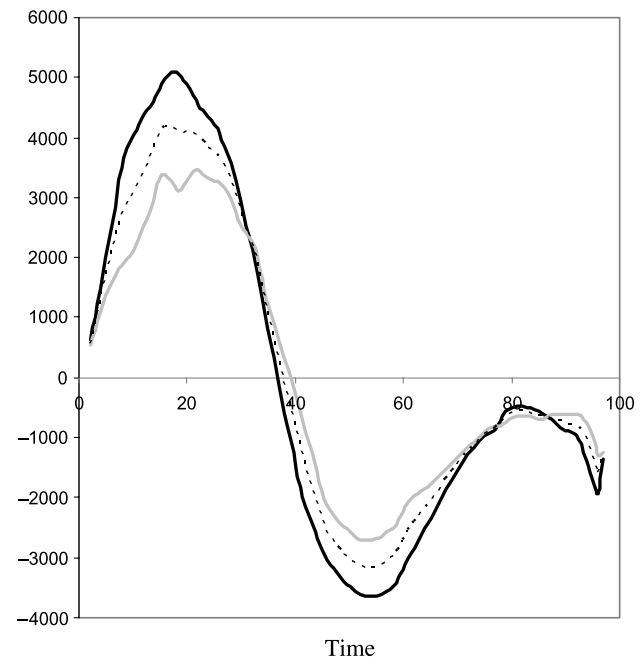
To obtain the results presented Table 1, latencies and amplitudes of wrist acceleration/deceleration peaks were determined for each individual trial as illustrated below (left) and means were calculated only for peak values. The kinematic profiles in Figure 1, by contrast,

were obtained by averaging profiles of normalized individual trials (between 0% and 100%) such that across trials, peak values were averaged with nonpeak values (red curve; right). Note that this latter procedure weakens the observed effects.

Analyses underlying the results in Table 1



Analyses underlying data in Figure 1



Acknowledgments

We thank Alfonso Caramazza and one anonymous reviewer for helpful comments on an earlier version of this article. T. A. N. is a member of the Marie Curie Research and Training Network: Language and Brain (RTN: LAB) funded by the European Commission (MRTN-CT-2004-512141) as part of its Sixth Framework Program.

Reprint requests should be sent to Véronique Boulenger, CNRS UMR, 5015 Institut des Sciences Cognitives, 67 bd Pinel, 69675 Bron Cedex, France, or via e-mail: boulenger@isc.cnrs.fr.

REFERENCES

- Alkhadhi, H., Brugger, P., Boendermaker, S. H., Crelier, G., Curt, A., Hepp-Reymond, M. C., & Kollias, S. S. (2005). What disconnection tells about motor imagery: Evidence from paraplegic patients. *Cerebral Cortex*, *15*, 131–140.
- Bak, T. H., O'Donovan, D. G., Xuereb, J. H., Boniface, S., & Hodges, J. R. (2001). Selective impairment of verb processing associated with pathological changes in Brodmann areas 44 and 45 in the motor neurone disease–dementia–aphasia syndrome. *Brain*, *124*, 103–120.
- Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica*, *106*, 3–22.
- Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: Comparing symbolic, spatial and imitative cues. *Brain and Cognition*, *44*, 124–143.
- Buccino, G., Binkofski, G., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, G., Rizzolatti, G., & Freund, H. J. (2001). Action observation activates the premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*, 400–404.
- Buccino, G., Lui, F., Canessa, N., Patteri, L., Lagravinese, G., Benuzzi, F., Porro, C. A., & Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study. *Journal of Cognitive Neuroscience*, *16*, 114–126.
- Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study. *Cognitive Brain Research*, *24*, 355–363.
- Castiello, U., Lusher, D., Mari, M., Edwards, M. G., & Humphreys, G. W. (2002). Observing a human or a robotic hand grasping an object: Differential motor priming effects. In V. Prinz & B. Hommel (Eds.), *Attention and Performance XIX* (pp. 314–334). Cambridge: MIT Press.
- Damasio, A. R., & Tranel, D. (1993). Nouns and verbs are retrieved with differently neural systems. *Proceedings of the National Academy of Sciences, U.S.A.*, *90*, 4957–4960.
- De Renzi, E., & di Pellegrino, G. (1995). Sparing of verbs and preserved, but ineffectual reading in a patient with impaired word production. *Cortex*, *31*, 619–636.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, *91*, 176–180.
- Edwards, M. G., Humphreys, G. W., & Castiello, U. (2003). Motor facilitation following action observation: A behavioural study in prehensile action. *Brain and Cognition*, *53*, 495–502.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*, 2608–2611.
- Ferrari, P. F., Gallese, V., Rizzolatti, G., & Fogassi, L. (2003). Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *European Journal of Neuroscience*, *17*, 1703–1714.

- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.
- Gallese, V., & Lakoff, G. (2005). The brain's concepts: The role of the sensory–motor system in conceptual knowledge. *Cognitive Neuropsychology*, *22*, 455–479.
- Gilhooly, K. J., & Logie, R. H. (1980). Methods and designs: Age of acquisition, imagery, concreteness, familiarity, and ambiguity measures for 1,944 words. *Behaviour Research Methods and Instrumentation*, *12*, 395–427.
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, *41*, 301–307.
- Halsband, U., Schmitt, J., Weyers, M., Binkofski, F., Grützner, G., & Freund, H. J. (2001). Recognition and imitation of pantomimed motor acts after unilateral parietal and premotor lesions: A perspective on apraxia. *Neuropsychologia*, *39*, 200–216.
- Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, *17*, 187–524.
- Jeannerod, M., & Frak, V. (1999). Mental imaging of motor activity in humans. *Current Opinion in Neurobiology*, *9*, 735–739.
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, *297*, 846–848.
- Mahon, B. Z., & Caramazza, A. (2005). The orchestration of the sensory–motor systems: Clues from neuropsychology. *Cognitive Neuropsychology*, *22*, 480–494.
- Mason, M. F., Banfield, J. F., & Macrae, C. N. (2004). Thinking about actions: The neural substrates of person knowledge. *Cerebral Cortex*, *14*, 209–214.
- Meister, I. G., Boroojerdi, B., Foltys, H., Sparing, R., Huber, W., & Topper, R. (2003). Motor cortex hand area and speech: Implications for the development of language. *Neuropsychologia*, *41*, 401–406.
- New, B., Pallier, C., Ferrand, L., & Matos, R. (2001). Une base de données lexicales du français contemporain sur Internet: LEXIQUE. *L'Année Psychologique*, *101*, 417–462.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, *9*, 97–113.
- Oliveri, M., Finocchiaro, C., Shapiro, K., Gangitano, M., Caramazza, A., & Pascual-Leone, A. (2004). All talk and no action: A transcranial magnetic stimulation study of motor cortex activation during action word production. *Journal of Cognitive Neuroscience*, *16*, 374–381.
- Pulvermüller, F. (1996). Hebb's concept of cell assemblies and the psychophysiology of word processing. *Psychophysiology*, *33*, 317–333.
- Pulvermüller, F. (1999). Words in the brain's language. *Behavioral and Brain Sciences*, *22*, 253–279.
- Pulvermüller, F. (2001). Brain reflections of words and their meaning. *Trends in Cognitive Sciences*, *5*, 517–525.
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, *6*, 576–582.
- Pulvermüller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *European Journal of Neuroscience*, *21*, 793–797.
- Pulvermüller, F., Lutzenberger, W., & Preissl, H. (1999). Nouns and verbs in the intact brain: Evidence from event-related potentials and high-frequency cortical responses. *Cerebral Cortex*, *9*, 497–506.
- Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience*, *17*, 1–9.
- Preissl, H., Pulvermüller, F., Lutzenberger, W., & Birbaumer, N. (1995). Evoked potentials distinguish between nouns and verbs. *Neuroscience Letters*, *197*, 81–83.
- Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in Neurosciences*, *21*, 188–194.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Research, Cognitive Brain Research*, *3*, 131–141.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, *2*, 661–670.
- Rosci, C., Valentina, C., Laiacona, M., & Capitani, E. (2003). Apraxia is not associated to a disproportionate naming impairment for manipulable objects. *Brain and Cognition*, *53*, 412–415.
- Rumiati, R. I., Zanini, S., Vorano, L., & Shallice, T. (2001). A form of ideational apraxia as a selective deficit of contention scheduling. *Cognitive Neuropsychology*, *18*, 617–642.
- Sauseng, P., Bergmann, J., & Wimmer, H. (2004). When does the brain register deviances from standard word spellings? An ERP study. *Brain Research, Cognitive Brain Research*, *20*, 529–532.
- Saygin, A. P., Wilson, S. M., Dronkers, N. F., & Bates, E. (2004). Action comprehension in aphasia: Linguistic and non linguistic deficits and their lesion correlates. *Neuropsychologia*, *42*, 1788–1804.
- Sereno, S. C., & Rayner, K. (2003). Measuring word recognition in reading: Eye movements and event-related potentials. *Trends in Cognitive Sciences*, *7*, 489–493.
- Sereno, S. C., Rayner, K., & Posner, M. I. (1998). Establishing a time-line of word recognition: Evidence from eye movements and event-related potentials. *NeuroReport*, *9*, 2195–2200.
- Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., Fazio, F., Rizzolatti, G., Cappa, S. F., & Perani, D. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, *17*, 273–281.
- Thevenet, M., Paulignan, Y., & Prablanc, C. (2001). OPTODISP Program. License INSERM-CNRS-UCBL.