The Impact of Iconic Gestures on Foreign Language Word Learning and Its Neural Substrate

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Abstract: Vocabulary acquisition represents a major challenge in foreign language learning. Research has demonstrated that gestures accompanying speech have an impact on memory for verbal information in the speakers' mother tongue and, as recently shown, also in foreign language learning. However, the neural basis of this effect remains unclear. In a within-subjects design, we compared learning of novel words coupled with iconic and meaningless gestures. Iconic gestures helped learners to significantly better retain the verbal material over time. After the training, participants' brain activity was registered by means of fMRI while performing a word recognition task. Brain activations to words learned with iconic and with meaningless gestures were contrasted. We found activity in the premotor cortices for words encoded with iconic gestures. In contrast, words encoded with meaningless gestures elicited a network associated with cognitive control. These findings suggest that memory performance for newly learned words is not driven by the motor component as such, but by the motor image that matches an underlying representation of the word's semantics. *Hum Brain Mapp 00:000–000, 2010.* © 2010 Wiley-Liss, Inc.

Key words: gestures; foreign language learning; memory; premotor cortex; cognitive control; vocabulary acquisition

INTRODUCTION

In spite of progress made in cognitive sciences, language learning still follows traditional methods such as learning vocabulary using bilingual lists. Often foreign language learners are confronted with the fact that the information that they have tediously learned decays within a short time. Therefore, there is an urgent need to improve the longevity of acquired vocabulary through new multimodal learning strategies [Shams and Seitz, 2008]. Here, we investigate the use of gestures performed during the encoding of words in a foreign language. A long tradition in laboratory research has demonstrated that verbal information is better recognized and recalled if subjects encode it by performing gestures. In the early 1980s, the first experiments compared the "verbal task" (VT), in which subjects read or listened to words or phrases, with the "self-performed task" (SPT). In the SPT, subjects were instructed to produce a gesture illustrating the word or the phrase [Cohen, 1981; Engelkamp and Krumnacker, 1980; Saltz and Donnenwerthnolan, 1981]. The SPT induced a superior effect on memory, which was referred to as the "enactment effect" [Engelkamp and Krumnacker, 1980] or the "SPT effect" [Cohen, 1981].

The enactment effect is consistent throughout the literature. It has been assessed on different verbal materials [Saltz and Donnenwerthnolan, 1981], with different paradigms [Helstrup, 1984], on different populations [Bäckman and Nilsson, 1984; Cohen and Stewart, 1982; Feyereisen, 2009;

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Kausler et al., 1986] and in different research groups. Similarly, recent studies have also demonstrated that iconic cospeech gestures enhance foreign language learning. In fact, the use of gestures during word learning facilitates new vocabulary retrieval in children [Tellier, 2008] and in adults [Kelly et al., 2009]. Interestingly, memory enhancement is not only reported for action words and phrases (e.g., roll the ball) or for concrete nouns but also for function and abstract words. Being nondepictable, the latter must be paired with an arbitrary symbolic cospeech gesture [Macedonia, 2003]. Thus, accompanying a word with an iconic or symbolic gesture and thereby inducing the enactment effect is a reliable way of enhancing memory for verbal information in the mother tongue as well as in a foreign language.

Three theoretical approaches have been put forward to explain the enactment effect. The first approach suggests that the crucial factor for the enactment effect is the physical component of the gesture leaving a motor trace in memory [Engelkamp and Zimmer, 1984, 1985]. The second approach considers the enactment effect to be related to motor imagery [Denis et al., 1991; Masumoto et al., 2006; Saltz and Donnenwerthnolan, 1981], that is, to a mental representation of the action associated with the word during encoding.

The third theoretical approach denies the importance of the physical motor information and proposes instead that the enactment effect is driven by increased self-involvement of the subject when producing a gesture accompanying the word [Helstrup, 1987]. Self-involvement through planning of the action [Knopf, 1992] is assumed to lead to deep semantic and conceptual processing [Kormi-Nouri, 1995, 2000] and, thus, to cause better integration of relational information at the word, phrase, and sentence level [Helstrup, 1993; Knopf et al., 2005].

Thus, these three approaches differ with respect to whether the enhancing effect on verbal memory when performing a speech gesture during word learning is caused by the physical performance of the action itself, by the reactivation of a mental image, or possibly both.

We reason that if the enhancement only depends on motor activity or on multimodality of the stimulus as suggested in the early years [Bäckman and Nilsson, 1984, 1985], any kind of movement could have an enhancing effect on memory. There seems to be some evidence in favor of this view. In fact, in experiments on a tip-of-the-tongue lexical paradigm, it has been shown that not only iconic gestures but also meaningless gestures enhance verbal memory [Beattie and Coughlan, 1999; Beattie and Shovelton, 1999]. Furthermore, simple tapping can significantly increase word retrieval [Ravizza, 2003]. Children allowed to gesture were also significantly better in resolving tip-of-the-tongue and naming tasks than when they were not [Pine et al., 2007].

Such results have often been related to spreading activation [Anderson, 1983] in brain areas common to speech and gesture [Gentilucci and Dalla Volta, 2008]. Altogether, these studies are in accordance with the general view that moving while learning benefits memory [Ruscheweyh et al., in press; van Praag, 2009]. If, however, the enhancement effect depends on the specific type of gesture, only iconic or symbolic gestures should lead to an enhancement of memory for words. Iconic gestures are not mere physical movements but are actions being defined by goal and expectancy [Rizzolatti et al., 2000]. They may draw a precise kinematic image of a word's semantics. Performing an action referring to a word like "cut" requires the activation of a mental motor image of the word before its execution. Such iconic gestures are voluntary and may thus have a different status than automatically produced cospeech gestures. Previous behavioral studies that compared simple verbal encoding with encoding through a self-performed gesture could not elucidate this issue, as the factor inducing the enactment effect was confounded by motor activity, multimodality, and higher self-involvement.

Recent neuroscientific research opens up the idea that the enactment effect may be reconducted to the motor component contained in the representation of the verbal information. In fact, these studies have shown activity in motor brain regions during explicit memory for objects and actions [Leynes and Bink, 2002; Leynes et al., 2006; Nilsson et al., 2000; Nyberg et al., 2001; Senkfor, 2008; Senkfor et al., 2002; Van Mier, 2000]. So far, however, it is still not clear to which extent the behaviorally observed enhancement of verbal memory is related to activity in motor-related areas, and if so whether this reflects a motor trace of the physical action or a motor image connected to the words' semantics or possibly both.

In this study, we investigate the impact of enacted iconic when compared with meaningless gestures on memory for foreign language nouns. The learning experiment aims to dissociate the two aspects contained in the motor performance of the iconic gesture, namely, mere motor activity and specific motor imagery. If the enactment effect depends on mere motor activity, both kinds of gesture (i.e., iconic and meaningless) should lead to equal behavioral results. If, on the other hand, the enactment effect is supported by specific mental motor images, iconic gestures compared with meaningless gestures should induce superior memory performance. The brain imaging experiment contrasting whole brain activity evoked by iconic and meaningless gestures aims to identify cortical areas specifically involved in superior memory performance.

Considering the results of previous studies on iconic and meaningless gestures coupled with verbal information, we hypothesize first, that iconic gestures lead to superior memory performance, and second, that the use of a motor image may neurophysiologically be reflected in activity in particular areas of the motor cortices.

MATERIAL AND METHODS

Behavioral Experiment

Participants

Thirty-three native German-speaking subjects (mean age 23.17, M = 25, SD = 1.61, 17 females, 16 males)

TABLE I. Item list (Vimmi, German, and translation into English)

No.	Vimmi	German	English translation
1	fo	Reißverschluss	zip
2	dra	Ohrring	earring
3	bae	Pfeffermühle	pepper mill
4	lefu	Petersilie	parsley
5	bati	Besen	broom
6	zude	Becher	mug
7	paltra	Treppe	stair
8	pewo	Föhn	hairdryer
9	geloro	Gießkanne	ewer
10	kabida	Taschentuch	handkerchief
11	lamube	Seife	soap
12	denule	Regal	shelf
13	urabe	Geige	violin
14	kiale	Stempel	stamp
15	boreda	Faden	thread
16	wobeki	Tempel	temple
17	fesuti	Stuhl	chair
18	pigemola	Kaffee	coffee
19	ruzanego	Brücke	bridge
20	saluzafo	Erde	earth
21	loeke	Blume	flower
22	keme	Shampoo	shampoo
23	bikute	Pullover	pullover
24	ri	Kirsche	cherry
25	lun	Autowaschanlage	car wash site
26	ean	Nagellack	nail polish
27	tola	Baumstamm	(tree) trunk
28	gosa	Spitzer	(pencil) sharpener
29	kudi	Fächer	fan
30	mogra	Sekt	(sparkling) wine
31	wari	Streichholz	match
32	dalefi	Zange	pincer
33	furome	Handschuh	hand glove
34	nobani	Gabel	fork
35	pabezi	Kopfhörer	headset
36	esepo	Würfel	die
37	zuowe	Socken	sock
38	lenope	Brille	eyeglasses
39	deschoga	Hammer	hammer
40	nokaschu	Koffer	suitcase
41	dikemori	Flugzeug	airplaine
42	lodefawi	Boot	boat
43	beropuga	Fenster	window
44	toari	Antenne	antenna
45	tizo	Lippenstift	lipstick
46	tofita	Bürgersteig	sidewalk
47	wa	Serviette	napkin
48	rel	Halskette	necklace
49	iol	Wattestäbchen	cotton bud
50	doba	Zahnpasta	tooth paste
51	nado	Zweig	twig
52	seza	Deckel	lid
53	fapro	Butter	butter
54	piba	Bohrmaschine	drill
55	pukoni	Wasserhahn	water tap
56	ratube	Klebeband	tape
57	wepuda	Gebirge	mountain
58	fukepa	Mütze	bonnet
59	ilado	Schere	scissors
60	foine	Schale	bowl
61	zagido	Seil	rope
62	zobako	Käse	cheese
63	koneru	Schlüssel	key
64	wubonige	Kreuz	cross
65	mulogite	Regen	rain
66	miresado	Dach	roof
67	peabe	Käfig	cage
68	detu	Birne	pear
69	rowite	Wiege	cradle
70	gu	Spülmittel	dish liquid
71	nen	Kürbis	pumpkin
72	gao	Radiergummi	eraser
73	gitu	Briefmarke	(postage) stamp
74	tedo	Flöte	flute
75	lasi	Blech	plate
76	brido	Handtuch	towel
77	fola	Krücke	crutch
78	renobe	Säge	saw
79	mofire	Gebiss	denture
80	koludi	Parfüm	perfume
81	lofuse	Krawatte	necktie
82	uteli	Knopf	button
83	woade	Schwamm	sponge
84	dirube	Zettel	slip (of paper)
85	sabelo	Thermometer	thermometer
86	ganuma	Messer	knife
87	tanedila	Welle	wave
88	mapusebo	Telefon	telephone
89	kadonega	Spiegel	mirror
90	raone	Fernbedienung	remote control
91	kewo	Banane	banana
92	nukile	Poster	poster

participated in the experiment. They were right handed as assessed with the Edinburgh Handedness Inventory. All subjects were recruited from our participant database and were paid for their participation. Participants were randomly assigned to two training groups (Group 1 and Group 2) to counterbalance training conditions and items.

Stimulus material

The training material comprised 92 nouns in "Vimmi," an artificial corpus (Table I) created to avoid associations and to control for different factors that, in natural languages, can favor the learning of particular vocabulary items. The artificial words were created according to Italian phonotactic rules, first being randomly generated by a Perl script and thereafter adjusted to avoid tautological occurrence of syllables, high frequency of particular consonants or vowels, the appearance of strings sounding unusual to German-speaking subjects, association with words

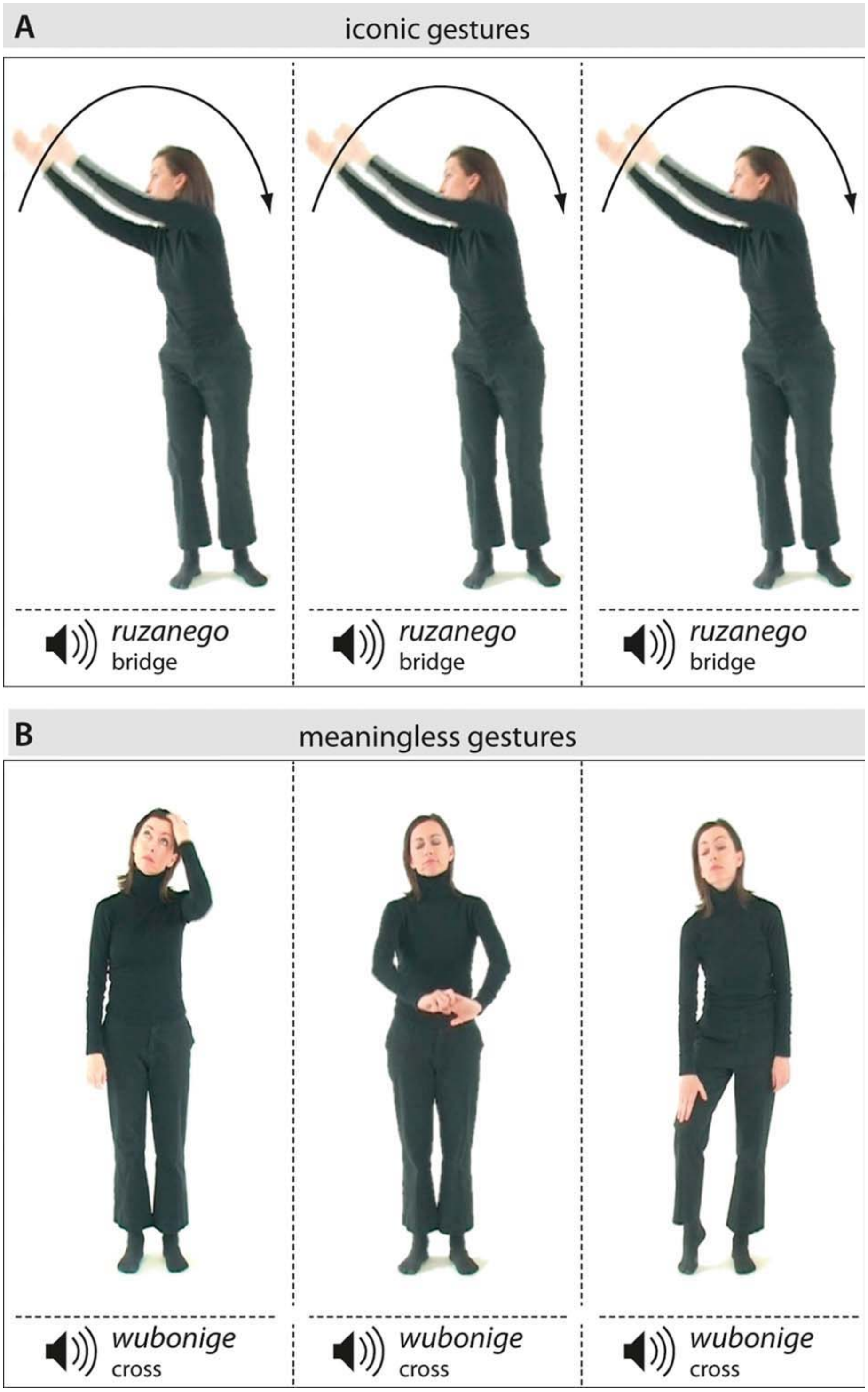

Figure 1.
Training materials. Images from the videos used for the two training conditions: (**A**) iconic and (**B**) meaningless gestures. The videos showed an actress performing the gestures to be imitated. The word appeared at the bottom of the screen in Vimmi, the artificial language, with its German translation and was played aloud. Participants were instructed to perform the gesture as they said the word.

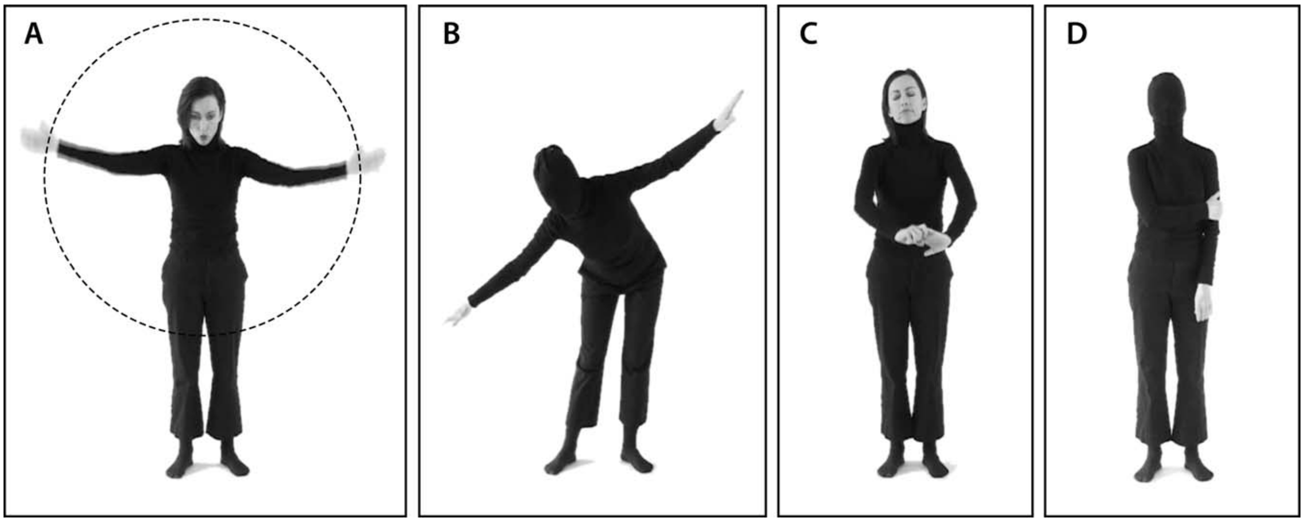

Figure 2.
Video shots illustrating the four training conditions. (**A**) Iconic gesture with visible face (ICO_FACE), with the actress showing a bimanual gesture mimicking a circle for the word earth, Vimmi saluzafo; (**B**) iconic gesture with masked face (ICO_NOFACE), with the actress performing the gesture for the word aeroplane, Vimmi dikemori; (**C**) meaningless gesture with visible face (MEANL_FACE); and (**D**) meaningless gesture with concealed face (MEANL_NOFACE).

from European languages taught at school (English, French, Italian, and Spanish), and with proper nouns comprising names of products available on the German market. The artificial words were assigned common meanings like bridge and suitcase. Familiarity of the semantics of the items was controlled for using the word frequency counter of German provided by the University of Leipzig (http://Wortschatz.Uni-Leipzig.de). The mean frequency of all items was 13.35, ranging from 9 to 16. Items were equally distributed in all training conditions in a counterbalanced way considering phonotactics (length, phoneme distribution, and syllabic structure), semantics, and frequency. The 92 words were recorded and cut in 92 single audio files, with each file having a length of ~0.8 s.

The gestures presented together with the words were of two kinds: iconic gestures and meaningless gestures. Iconic gestures [McNeill, 1992], also referred to as representational gestures [Kendon, 1981; Morris et al., 1979], depicted some aspect of the word's semantics. For instance, for the word *ruzanego* (English "bridge"), the gesture was an arch performed with both hands (Fig. 1A), whereas for the word *nokaschu* (English "suitcase") the actor lifted an imaginary suitcase. These gestures enriched the foreign word with a plausible sensory motor connotation.

Meaningless gestures were chosen to test for the effect of mere motor activity during encoding. Words were accompanied by mere physical activity which was bare of any iconic or symbolic image that could be associated with the word's semantics. These meaningless gestures could be small (touching one's own head) or larger (touching one's own knee) (see Fig. 1B). We did not consider using iconic gestures that were not semantically related, being aware that they would negatively affect information processing [Kelly et al., 2004] and probably hinder recall [Feyereisen, 2006]. A few previous experiments used mismatching gestures and have, in fact, reported interference effects [Bernardis et al., 2008; Holle and Gunter, 2007; Reynolds et al., 2004]. We therefore wanted to avoid this. Hence, we deliberately chose gestures that did not convey any meaning and could not be associated with the words they accompanied. Participants were cued to stretch their arms in front of themselves, to rub their legs, and turn their heads, for example. Moreover, for each word, the meaningless gestures were randomly interchanged at every single trial during the training sessions. By doing this, our aim was to prevent these gestures becoming symbolic and possibly supporting associations through consistency of use.

Considering that the facial expression of the actor could also have an impact on memory [Sueyoshi Ayano, 2005], we conducted the experiment with the factor face controlled. In half of the video stimuli, the actress showed her face, in the other half, it was concealed by a mask. As a result, we had four training conditions comprising:

1. Iconic gesture with face (ICO_FACE). Here, the actress performed an iconic gesture representing some feature of the item to be trained with her face visible (Fig. 2A).
2. Iconic gesture without face (ICO_NOFACE). Here, the actress performed an iconic gesture representing some feature of the items to be trained with her face obscured by a mask (Fig. 2B).
3. Meaningless gestures with face (MEANL_FACE). Here, the actress performed meaningless gestures with her face visible (Fig. 2C).

4. Meaningless gestures without face (MEANL_NOFACE). Here, the actress performed meaningless gestures with her face obscured by a mask (Fig. 2D).

Four sets of videos were therefore recorded according to the training conditions described above. Each video clip had an average duration of 4.7 s.

Training procedure and memory assessment

For each item to be learned, the training consisted of four components: the video, the Vimmi audio file, the word written in Vimmi, and its written translation into German. During the presentation stage, the video first appeared on the screen, with the word written in Vimmi as a subtitle, followed by its translation into German after 3,500 ms (Fig. 1). The start of the audio file was separately timed for each item. It coincided with the start of the movement in the video. The presentation of each item lasted a total of 5 s. The participants were informed that the goal of the training was to remember as many words as possible and that their performance would be assessed every day. Participants were randomly subdivided into two groups and training according to the following scheme:

Group 1

- iconic gestures with face (ICO_FACE) (items 1–23),
- meaningless gestures with face (MEANL_FACE) (items 24–46),
- iconic gestures without face (ICO_NOFACE) (items 47–69), and
- meaningless gestures without face (MEANL_NOFACE) (items 70–92).

Group 2

- meaningless gestures without face (MEANL_NOFACE) (items 1–23),
- iconic gestures without face (ICO_NOFACE) (items 24–46),
- meaningless gestures with face (MEANL_FACE) (items 47–69), and
- iconic gestures with face (ICO_FACE) (items 70–92).

Each training session of 29 min contained 23 items. The items were randomly subdivided into four smaller blocks (6 + 6 + 6 + 5 items). A block was first shown and participants were instructed to watch it. Thereafter, the block was played again and the participants were cued to imitate the gesture and to repeat the word in Vimmi after seeing and hearing it. Each block was shown six times, with every word again randomized within the block itself. In a second round of training, all four small blocks were repeated another six times, with all the words being randomized again within the blocks. In total, every vocabulary item was presented 13 times every day. The order of the training sessions (Fig. 3A,B) changed every day, alternating and counterbalancing iconic and meaningless gestures. The daily training consisted of four sessions, with a 15-min break between the second and third session and 10-min breaks after the first and third sessions. Participants were trained for 4 days. The software used for the training was Presentation (version 12).

Memory performance was assessed starting from the second experiment day. Participants had to perform a written translation task. Before starting the training session, they were given a randomized list of the 92 previously trained words to be translated from German into Vimmi (duration 7.5 min) and then a further randomized list of the same terms to be translated from Vimmi into German (duration 7.5 min).

fMRI Experiment

Participants

To investigate neural activity and to relate it to the two different kinds of cospeech gestures provided during encoding, we recorded fMRI data from 18 of the 33 subjects who participated in the behavioral experiment (mean age 23.44, $M = 25$, SD = 1.38, 10 females, 8 males). Subjects were randomly selected and gave written consent. None of the subjects had a prior history of neurological and/or psychiatric diseases. The experiment was approved by the local Ethics Committee.

Experimental design and procedure

Participants were trained 1 additional day to ensure that they had reached a ceiling in both training conditions. Before scanning, they were assessed through a written translation test from Vimmi into German (mean performance 96.56%, F (1, 17) = 3.20, $P = 0.91$). The critical stimuli consisted of the 92 trained Vimmi words (Table I) and 23 unknown filler words (Table II). The filler words were constructed in the same way as the trained items and were unknown to the participants. Participants lay on their backs in the scanner. Written Vimmi words were shown with an LCD projector onto a back-projection screen mounted in the bore of the magnet behind the subject's head. The audio file, with an approximate duration of 1 s, was played coinciding with the start of the visual stimulus (i.e., the written word). Each trial presented a single item. Participants held a response box in their left hand and were instructed to press a key if they detected an unknown word. The stimulus was introduced with a fixation cross for 300 ms. The Vimmi word followed and remained on the screen for 1,000 ms. The interstimulus interval lasted 8,000 ms. All training conditions were balanced across the presentation blocks. The entire scanning session comprised 138 trials. It included the 92 trained items, 23 fillers, and 23 null events (low-level baseline). During the null event trials, participants saw a black screen for 10 s. All items were presented in pseudo-

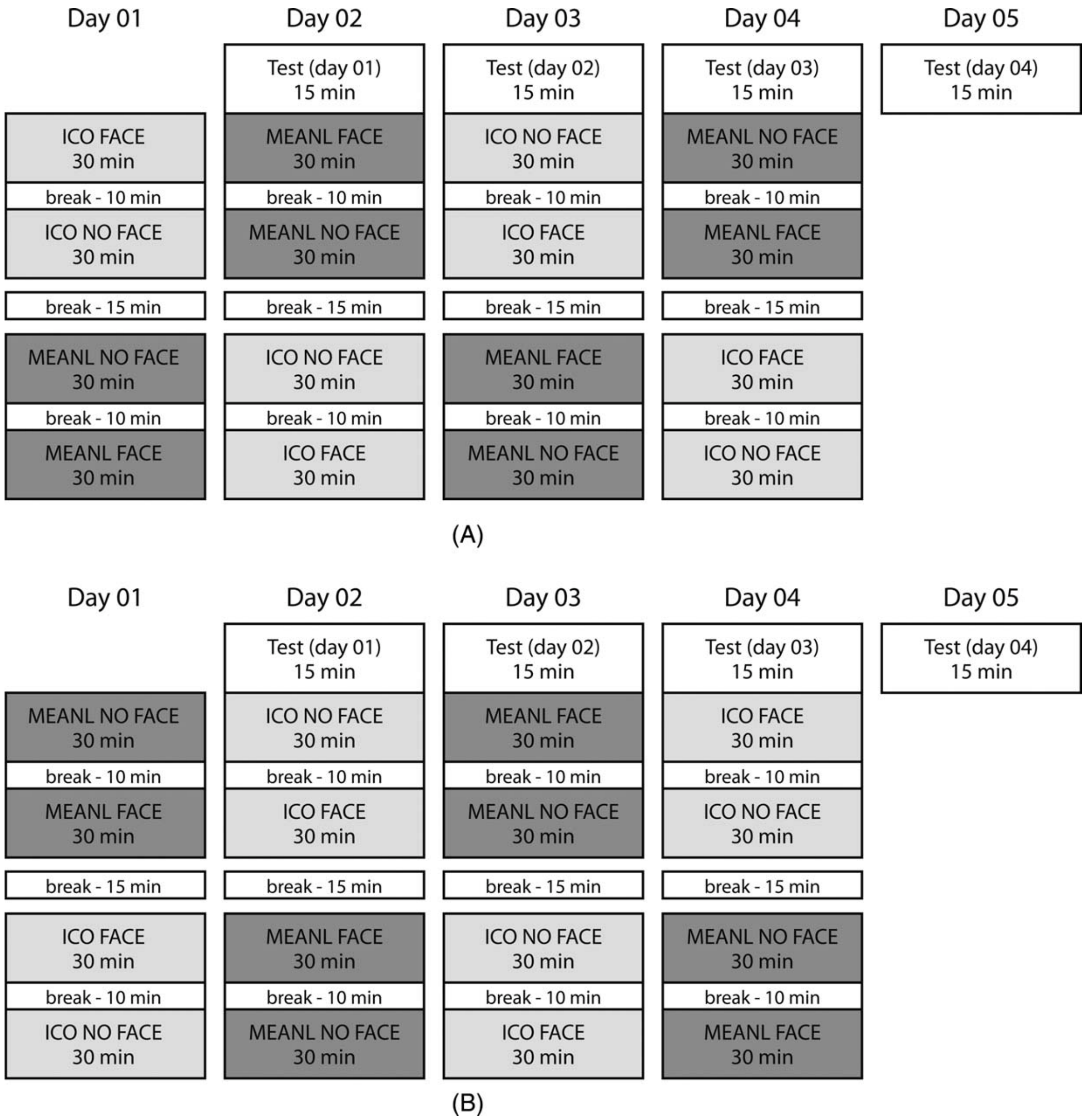

Figure 3.
(**A**) Training schedule for Group 1 and (**B**) training schedule for Group 2.

randomized order in a single block lasting 23 min. An event-related paradigm was used with 10-s epochs to measure the BOLD response.

fMRI data acquisition

A 3-T Bruker (Ettlingen, Germany) Medspec 30/100 system acquired 20 axial slices (4-mm thick, 1-mm interslice distance, FOV 19.2 cm, data matrix of 64 × 64 voxels, in-plane resolution of 3 mm × 3 mm) every 2 s during functional measurements (BOLD-sensitive gradient EPI sequence, TR = 2 s, TE = 30 ms, flip angle = 90°, acquisition bandwidth = 100 Hz). Before functional imaging, T1-weighted modified driven equilibrium Fourier transform (MDEFT) images (data matrix 256 × 256, TR = 1.3 s, TE = 10 ms) were obtained with a nonslice-selective inversion pulse followed by a single excitation of each slice [Norris, 2000]. These images were used to coregister functional scans with previously obtained high-resolution whole-head 3D brain scans: 128 sagittal slices, 1.5-mm thickness, FOV 25.0 cm × 25.0 cm × 19.2 cm, data matrix of 256 × 156 voxels.

TABLE II. List of unknown words for the scanning procedure

No.	Unknown words	German	English translation
93	pe	—	—
94	tro	—	—
95	oem	—	—
96	fale	—	—
97	sago	—	—
98	fenu	—	—
99	grema	—	—
100	loni	—	—
101	dakalo	—	—
102	turone	—	—
103	neludo	—	—
104	zefako	—	—
105	ameda	—	—
106	doiku	—	—
107	menako	—	—
108	schaboki	—	—
109	paramo	—	—
110	madimoke	—	—
111	wozalefu	—	—
112	rifupoge	—	—
113	laimo	—	—
114	luto	—	—
115	kelasi	—	—

fMRI data analysis

A 2 $\times$ 2 factorial design was used with the factors training (ICO = iconic gestures, MEANL = meaningless gestures) and face (FACE = visible face, NOFACE = masked face). The fMRI data were analyzed using the Lipsia software package [Lohmann et al., 2001]. Functional data were corrected for motion and the temporal offset between the slices. Thereafter, functional slices were aligned with a 3D stereotactic coordinate reference system using a rigid linear registration. The registration parameters were acquired on the basis of the MDEFT slices to achieve an optimal match between these slices and the individual 3D reference data set, which was standardized to the Talairach stereotactic space [Talairach and Tournoux, 1988]. The registration parameters were further used to transform the functional slices by using trilinear interpolation, so that the resulting functional slices were aligned with the stereotactic coordinate system. In the last step of preprocessing, the data were smoothed with a Gaussian filter of 10-mm FWHM. A temporal high-pass filter with a cutoff frequency of 1/100 Hz was applied for baseline correction. The statistical evaluation was based on a general linear regression with prewhitening [Worsley et al., 2002]. Specifically, autocorrelation parameters were estimated from the least squares residuals using the Yule-Walker equations. These parameters were subsequently used to whiten both data and design matrix. Finally, the linear model was re-estimated using least squares on the whitened data to produce estimates of effects and their standard errors. Subsequently, parameter (contrast-) images were calculated for each participant and entered into a second-level Bayesian analysis. This analysis, compared with null hypothesis significance, is highly reliable in small-group statistics with high within-subject variability caused by outliers [Friston and Penny, 2003; Friston et al., 2008; Neumann and Lohmann, 2003; Penny et al., 2005]. Given the high anatomical and physiological variability of the subjects, robustness against outliers is of basic importance for tools analyzing fMRI data.

RESULTS

Behavioral Results

To assess the influence of the training and the effect of facial cues on retrieval, a repeated measures ANOVA was performed with the factors training (ICO = iconic gestures, MEANL = meaningless gestures), face (FACE = visible face, NOFACE = masked face), and time (DAY 01, DAY 02, DAY 03, and DAY 04).

For the translation test from German into Vimmi (Fig. 4A), encoding through iconic gestures proved to be significantly superior, F (1,32) = 22.86, $P < 0.001$. The ANOVA revealed significant effects also for the factors face F (1,32) = 13.98, $P = 0.001$ and time F (3,96) = 307.047, $P < 0.001$.

In the translation test from Vimmi into German (Fig. 4B), encoding through iconic gestures again was significantly superior, F (1,32) = 15.20, $P < 0.001$. Likewise, time was significant again, F (3,96) = 486.21, $P < 0.001$. The factor face did not play a role above chance, F (1,32) = 1.89, $P = 0.179$.

Approximately 60 days after the last training day, the participants' retrieval performance was assessed through a free recall test. The results of the free recall test were split into two sections: first, items recalled in both languages, and second, items recalled loosely (i.e., only German or only Vimmi). The first section of the free recall test mirrors the memory performance, which is relevant for foreign language use: The learner must be able to recall an item and its correspondent in the other language (Fig. 5A). The second section reflects more an overall verbal memory performance (Fig. 5B). In both sections of the free recall, the factor training was highly significant, respectively F (1,28) = 80.11, $< P$ 0.001 and F (1,28) = 122.18, $P < 0.001$. A further analysis in the long-term range showed that the effect for the factor face was below chance in both sections. In sum, the behavioral results clearly demonstrate that performing iconic gestures during learning has a positive impact on memory for new nouns.

fMRI Results

The factor face

The contrast between all words learned seeing the face of the actress and all words learned seeing the mask, that is ([ICO_FACE–MEANL_FACE] versus [ICO_NOFACE–MEANL_NOFACE], revealed that during word recognition,

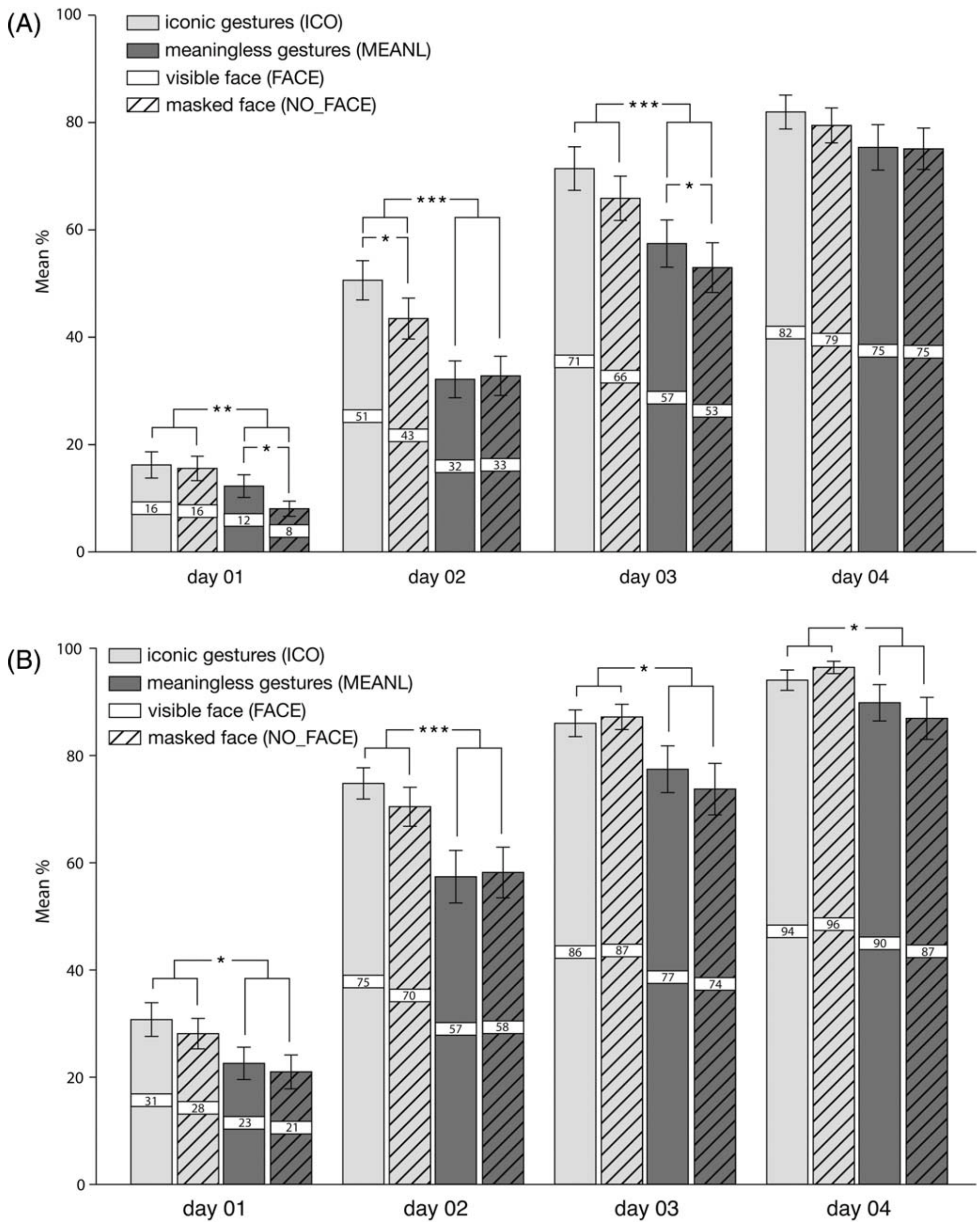

Figure 4.

(**A**) Training results for the written translation test from German into Vimmi. Words encoded through iconic gestures are significantly superior in retrieval for the first three time points. The factor FACE plays a significant role on Days 01–03. The factor face seems to be more helpful if the sensory motor cues are meaningless, as shown in Day 01 and Day 03. Figure error bars represent ± 1 SE. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. (**B**) Training results for the written translation test from Vimmi into German. This translation direction can be considered less demanding. The data show higher retrieval compared with the translation task from German into Vimmi. Words encoded through iconic gestures are superior in retrieval at all time points. The factor FACE does not play a significant role at any time. Figure error bars represent ± 1 SE. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

no brain region responded to the factor face encoded during learning. Note, however, that the subjects saw the same facial expressions hundreds of times during the training. This might have lead to habituation to the stimulus.

Iconic gestures and the premotor cortex

The whole brain analysis of the main contrast between iconic and meaningless gestures ([ICO_FACE–ICO_NOFACE] versus [MEANL_FACE–MEANL_NOFACE]) showed differences in the BOLD response in a number of regions as listed in Table III. Specifically, the most striking difference was the bilateral activation in the premotor cortex for iconic gestures.

We also performed an analysis of percent signal change within the voxels surrounding the peaks of activation in the premotor cortices, respectively, Talairach coordinates left −23, −12, 48 (126 voxels) and right 22, −12, 51 (40 voxels). We averaged the group time series of all the subjects who participated in the study. The means were entered in a repeated measures ANOVA considering the mean percent signal change between 4 and 8 s as dependent variable with the factor GESTURE_TYPE (iconic, meaningless). The main effect GESTURE_TYPE was significant in both motor cortices, respectively, left $F(1,16) = 159.620$, $P < 0.0001$ and right $F(1,16) = 87.667$, $P < 0.0001$ (Fig. 6).

The network for meaningless gestures

Words learned with meaningless gestures elicited activity in a vast brain network in both hemispheres during their recognition. Within this, the most extensive activation peaked in the left cuneus BA 19 (−6, −90, 30). Activity was also observed in its right counterpart. The network further comprised activity in the left posterior cingulate gyrus, BA 30 (−27, −66, 15) and in BA 9 (−45, 9, 30), the left inferior frontal junction area. Other areas involved in the network were the right anterior cingulate gyrus, BA 32 (3, 30, 33) and the right rostrolateral prefrontal cortex, BA 10 (24, 57, 24).

DISCUSSION

Performing iconic gestures when learning verbal information has an impact on memory. Here, we investigated the impact of iconic gestures and meaningless gestures on nouns of a foreign language. Behavioral measurements and an event-related fMRI experiment were used. We will first discuss the behavioral results and then the brain imaging results.

Behavioral Study

Behavioral data showed that iconic gestures lead to significantly better memory performance than meaningless gestures. Our data clearly challenge the view that the effect of iconic gestures depends exclusively on multimodality, as both training methods were multimodal [Bäckman and Nilsson, 1984, 1985]. The enhancing effect through enactment, moreover, cannot only be driven by self-involvement as such [Helstrup, 1987], as participants were equally involved in performing iconic and meaningless gestures. The observed difference must thus be explained by the difference in the specific motor activity performed together with the word to be learned [Engelkamp and Zimmer, 1984, 1985].

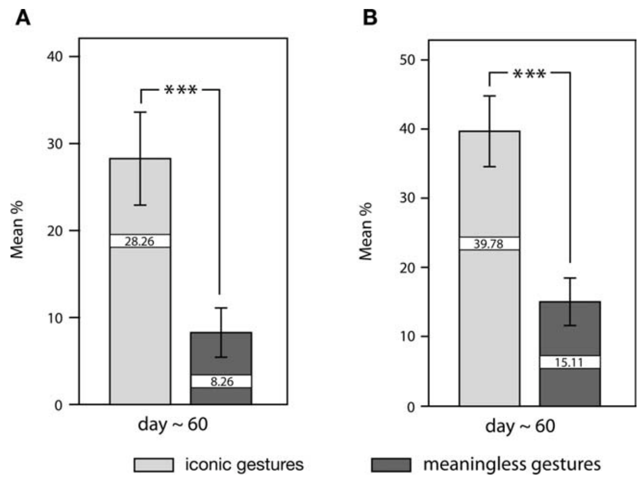

Figure 5.
(**A**) Free recall test results of paired items (Vimmi and German) after ∼60 days. The ability to retrieve a word paired with its correspondent in the other language is essential in foreign language use. Items encoded with iconic gestures are vastly superior in their retrieval. (**B**) Free recall test results of loose items in Vimmi or German after ∼60 days. This task mirrors the faculty to retrieve acquired verbal information but not the necessary word inventory needed to make active use of the foreign language. Again iconic gestures help to achieve significantly better results in retrieval. Figure error bars represent ±1 SE. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

The major difference between the two types of training with cospeech gestures and with iconic gestures resides in the fact that iconic gestures create a "meaningful" kinetic image reflecting some aspects of the word's semantics. Meaningless gestures by definition are neither iconic nor symbolic. They completely lack a motor image that can be integrated with the word's semantics. By contrast, iconic gestures can possibly be understood as actions producing an image of the word conveying its semantic content. The present data show that gestures must be iconic to support memory for concrete nouns. Also, Pavio's dual code theory [Paivio, 1986; Paivio and Csapo, 1969] focused on the idea that most concepts can be expressed through a word and through a mental image. Mental images are composed of analog codes, perceptual, physical features, and can enrich the symbolic code (i.e., language). In Paivio's view, words in a foreign language can be better memorized if presented as pictures or enriched through them. This is due to the "picture superiority effect" [Paivio, 1971], a memory effect that has been well documented in the last 4 decades [Hockley, 2008]. The better retrieval of words encoded through iconic gestures observed in this experiment is possibly based on enriched representations involving images.

In recent years, the general relation between gesture and language has been the focus of discussion. From an evolutionary point of view, language has been claimed to have

TABLE III. Results of fMRI main contrast (Iconic, gestures – meaningless gestures)

	Left hemisphere					Right hemisphere				
Lobe	BA	x	y	z	mm^3	BA	x	y	z	mm^3
Frontal										
Middle frontal gyrus	6	−24	−9	48	1971	6	18	−9	51	216
Inferior frontal gyrus	9	−45	9	30	1107					
Superior frontal gyrus						10	24	57	24	837
Occipital										
Cuneus	19	−6	−90	30	2835					
Limbic										
Cingulate gyrus						32	3	30	33	243
Posterior cingulate gyrus	30	−27	−66	15	135					
Temporal										
Superior temporal gyrus						22	60	−3	3	108

evolved from iconic and symbolic gestures [Arbib, 2006; Gentilucci and Corballis, 2006; Gentilucci and Dalla Volta, 2008; Gentilucci et al., 2008; Rizzolatti and Arbib, 1998; Tomasello, 2008]. From a developmental point of view, gestures appear spontaneously during infancy [Goldin-Meadow, 2005; Tomasello, 2005]; they support first language learning [Gliga and Csibra, 2009] and cognition [Goldin-Meadow, 1999, 2003].

It has been shown that iconic cospeech gestures enhance communication [Dick et al., 2009; Wu and Coulson, 2007a,b] and can serve to disambiguate ambiguous words in sentences [Holle and Gunter, 2007]. Furthermore, mismatching information between a word's semantics and gestural shape can lead to incongruity effects during communication [Barbieri et al., 2009; Bernardis and Gentilucci, 2006; Bernardis et al., 2008; Chieffi et al., 2009; Kircher et al., 2009]. Our findings confirm the close relationship between gesture and language and extend it to word learning in a foreign language.

fMRI Study

The fMRI experiment reveals the neural basis underlying the impact of gestures on memory for nouns. The brain activation patterns observed for words learned in the context of iconic gestures and in the context of meaningless gestures differ strikingly. The former activation pattern suggests a superior memory performance because

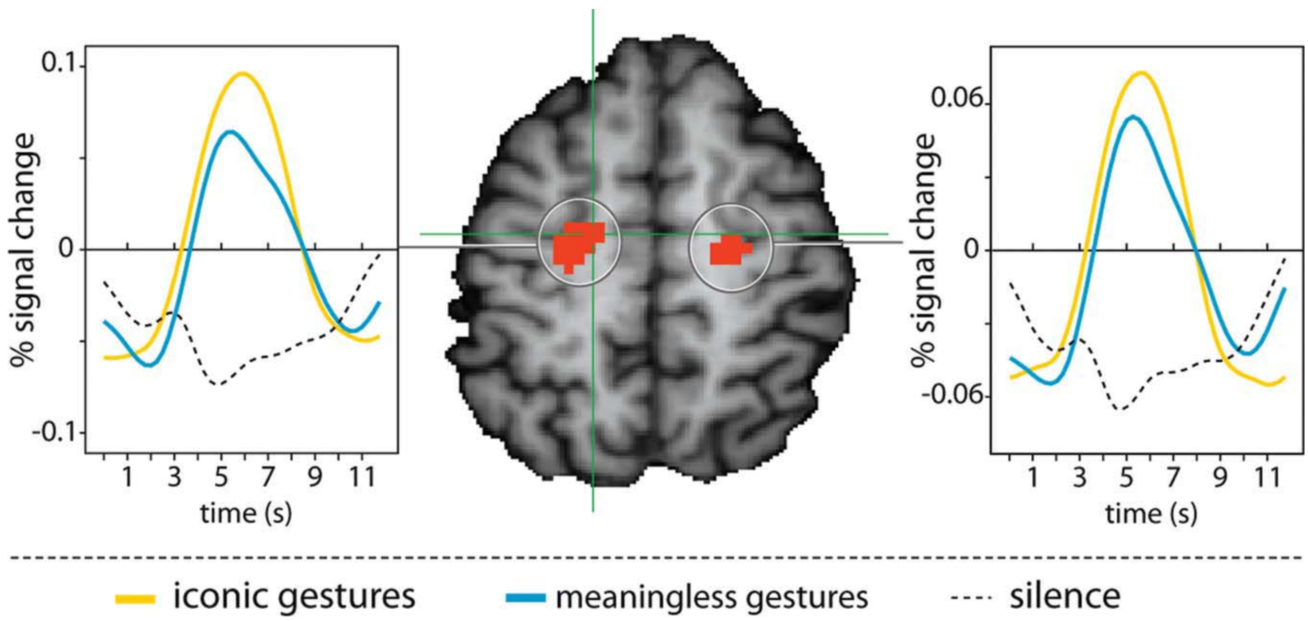

Figure 6.
Areas in the motor cortices of significant signal intensity changes (in red). Time courses are given for the most significant voxel of each cluster.

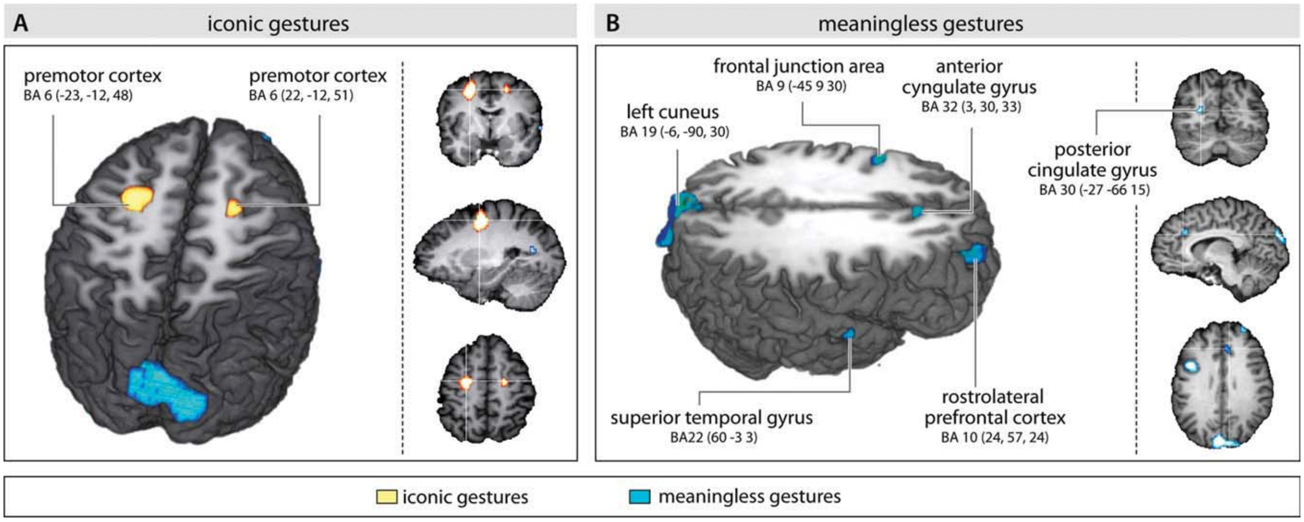

Figure 7.

fMRI study results. (**A**) Main contrast for iconic gestures versus meaningless gestures. Areas of signal intensity change relative to words encoded according to the training conditions, that is, iconic gestures versus meaningless gestures. Motor encoding through iconic gestures elicits activity in the dorsal right and in the left premotor cortices (BA6). (**B**) Meaningless gestures create a bilateral large-scale network mirroring cognitive control. The color-coded regions in both figures show clusters with high Bayesian posterior probability of condition.

of the support of motor representations. The latter activation pattern, in contrast, rather indicates the involvement of metacognitive processes dealing with the difficult task of learning novel words while producing meaningless gestures.

For the recognition of words encoded through iconic gestures, we observed brain activation in the premotor cortex, confirming the hypothesis that the representations of words encoded with this kind of gestures are coupled with motor images. The dimension of activation in the left precentral gyrus was larger compared with the right hemisphere, with 1971 and 216 mm^3, respectively (Fig. 7A,B). This may reflect the fact that the iconic gestures were performed by right-handed subjects with their dominant limbs and is consistent with results of an experiment investigating the processing of sentences containing action verbs [Tettamanti et al., 2005]. Note that the right limbs have a more active role in the execution of the gestures even if the target movement is bimanual [Schubotz and von Cramon, 2001].

The present activation is found in the dorsal part of the premotor cortex. This may be due to the fact that the action performed during the training mainly involved hand, arm, and shoulder movements [Hlustík et al., 2002] and is in accordance with the finding that motor verbs are mapped onto the topography of motor cortices in a somatotopic way [Hauk et al., 2004]. Given that during the scanning procedure our subjects only saw the written words and heard the audio file, the activity in the premotor cortex appears to be induced by internal motor simulation processes. These occur upon word input even without the visual cue of the action, suggesting that participants activated motor images they had created during word encoding [Gallese et al., 1996; Porro et al., 1996]. Thus, we assume that activity in the premotor cortex results from the resonance of the network established during learning. In our study, the behavioral training linked the different sensorial components of a word (i.e., sound and written form) with the word's semantics and a specific motor pattern [Emmorey, 2006].

The present brain imaging results may be put into the larger context of recent discussions on the role of motor representation in cognition. Activations in the premotor cortex have been shown to be induced by visual stimulation [Blakemore and Frith, 2005; Grezes and Decety, 2001; Keysers et al., 2003; Longcamp et al., 2006; Rizzolatti and Craighero, 2004] and/or acoustic stimulation [Kaplan and Iacoboni, 2007; Schubotz et al., 2003] both in humans and animals [Gallese et al., 1996]. These activations in the premotor cortex were taken into account for the existence of shared motor representations. They interconnect many aspects of action, i.e., perception, encoding, simulation, preparation, and execution [Calvo-Merino et al., 2006], as well as action verbalization [Grezes and Decety, 2001]. The present finding of activations in the premotor cortex upon recognition of words learned in the context of iconic gestures provides further evidence for the existence of word representations that are enriched by motor aspects. Thereby, it supports the original proposal by Engelkamp and Zimmer [1984, 1985] which holds that verbal information is better retained once enriched with a motor trace created through enactment. Our results show that foreign language words learned through enactment produce activity in the premotor cortices and are thus the first to indicate the neural basis of the enactment effect long discussed in behavioral psychology.

Processing Meaningless Gestures: A Case of Conflict

The set of items encoded with meaningless gestures showed an entirely different neural pattern during recognition reflecting mechanisms of cognitive control [Cole and Schneider, 2007]. The brain activity pattern suggests that in the present experiment, participants evaluated the usefulness of the gestures and their possible congruence with the word's semantics even for the meaningless gestures. In fact, we find activation in the anterior cingulate gyrus, BA 32 (3, 30, 33), an area often related to conflicting information processing [Roberts and Hall, 2008]. Previous studies have seen this brain region as engaged in error detection [Carter et al., 1998] and conflict monitoring [Botvinick, 2007; Botvinick et al., 2001; Russ et al., 2003]. Depending on the experimental task, the anterior cingulate gyrus cooperates with other brain areas mediating error monitoring [Ullsperger and von Cramon, 2004; Wittfoth et al., 2008]. Thus, it is possible that in our experiment, the anterior cingulate gyrus became active because of incongruence detection between a word's semantics and the interchanging meaningless movements.

The posterior cingulate gyrus, BA 30 (−27, −66, 15), a portion of the retrosplenium, is also involved in the network for meaningless gestures. Functional studies of the retrosplenial cortex point to an array of cognitive abilities [Vann et al., 2009], with a role in memory for spatial navigation [Maguire, 2001] and for visual and verbal information, with the latter being reported in patient studies [Kim et al., 2007; McDonald et al., 2001]. Recent findings highlight the importance of the posterior cingulate gyrus in retrieval processes for images, with it being more active for poor imagers [Guillot et al., 2008]. In our experiment, encoding through meaningless gestures did not provide the learners with a consistent gestural image for a word's semantics; instead, the image was fuzzy and, hence, poor. The posterior cingulate cortex might have reacted to this aspect of the information engaging in body and space-related integration processes.

The largest activation observed for meaningless gestures was located in the cunei bilaterally, with a focus in the left cuneus BA 19 (−6, −90, 30), however. The cuneus is a higher visual association area shown to be involved in reading tasks [Joubert et al., 2004], object and picture processing, and also in responding to visual fuzziness as shown in studies on imitation of meaningless gestures [Hermsdörfer et al., 2001; Peigneux et al., 2000]. Given that in both learning conditions participants read the stimuli, we doubt that the present activation in the cunei reflects reading in general. Rather, participants may have adopted a cognitive strategy, concentrating more on the written form to memorize the words once they realized that the meaningless gestures were not helpful cues. Here, we attribute the modulation of activity in the cunei to integration and association effort the brain deployed to connect the words semantics with the meaningless motor images.

Recognizing words learned through meaningless gestures elicited activity in BA 9 (−45, 9, 30), the frontolateral region located around the junction of the inferior frontal sulcus and the inferior precentral sulcus, also called the inferior frontal junction. This area has been associated with cognitive control tested in task-switching and set-shifting paradigms [Brass et al., 2005a; Derrfuss et al., 2004]. The inferior frontal junction is known to integrate information coming from working memory, the language, and premotor domains [Brass et al., 2005b]. Activity in this cortical area may again be due to the incongruence of the word–gesture combination, and hence the brain's effort to find a way integrating the two.

The involvement of the superior temporal gyrus in this network provides further support for an interpretation inclining toward integration effort. In a study on crossmodal binding of congruent and incongruent audiovisual speech, activity in the left superior temporal gyrus was found [Calvert et al., 2000]. In our data, the activity was located in the right superior temporal gyrus. We speculate that the right superior temporal gyrus might have mediated integration related to spatial, auditory, and visual integration processes of own body motion as described in a patient study [Karnath and Dieterich, 2006].

A further brain area involved is the right rostrolateral prefrontal cortex, BA 10 (24, 57, 24), a region known to be engaged in several aspects of higher cognition [Ramnani and Owen, 2004] including conflict resolution [Chen et al., 2006; Depue et al., 2007] and inhibition processes [Blasi et al., 2006].

Overall, the results for words learned in the context of meaningless gestures indicate that the brain puts considerable effort into trying to match and integrate verbal with meaningless gestural information perceived during learning.

Although there is evidence suggesting that activity in the network for meaningless gestures could be driven by cognitive control, it is important to note that the components of the described network are also known to modulate memory. In fact, the occipital visual areas and the posterior cingulate cortex have been repeatedly associated with episodic memory [Spaniol et al., 2009; von Zerssen et al., 2001; Wagner et al., 2005], whereas the anterior cingulate gyrus [Hazlett et al., 2010; Mensebach et al., 2009] and the parietal junction [Ziemus et al., 2007] have been found to be engaged in semantic and verbal memory tasks. Thus, the two functional roles connected to the network for meaningless gestures (i.e., cognitive control and memory) do not mutually exclude each other. Instead, we presume that they are complementary to each other and account for the complexity of the process.

CONCLUSIONS

This study on the impact of gestures on foreign language word learning indicates that iconic gestures compared with meaningless gestures significantly help to enhance the memorization of foreign language nouns. Brain imaging substantiated the neural basis of this effect by showing that recognition of words encoded with iconic gestures triggered an activation pattern involving premotor cortices, whereas recognition of words encoded in the presence of meaningless gestures activated a network for cognitive control. Our results reconcile different theoretical positions on the factors inducing the enactment effect. On the one hand, we were able to demonstrate that the enactment effect left a motor trace in the verbal representation of nouns, thereby supporting the theoretical view formulated in cognitive psychology by Engelkamp and Zimmer [1985]. This trace in motor cortices is empirically detectable upon audible and visual presentation of the word. On the other hand, our results also are in line with the mental imagery view proposed by Saltz and Donnenwerthnolan [1981] and Denis et al. [1991] in showing that a gesture leads to better memory performance only if it allows to create a motor image that matches with an internal representation of the concept's semantics.

Both behavioral and neural evidence converge to indicate that iconic gestures have an impact on the learning of new words in a foreign language, here, demonstrated for concrete nouns. Future research combining behavioral and neuroimaging studies must show whether similar evidence can be found for other word categories and for words presented in the context of sentences.

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REFERENCES

Anderson JR (1983): A spreading activation theory of memory. J Verb Learn Verb Behav 22:261–295.

Arbib MA (2006): Action to Language via the Mirror Neuron System, Vol. 13. Cambridge: Cambridge University Press. 552p.

Bäckman L, Nilsson LG (1984): Aging effects in free recall: An exception to the rule. Hum Learn: J Pract Res Appl 3:53–69.

Bäckman L, Nilsson LG (1985): Prerequisites for lack of age differences in memory performance. Exp Aging Res 11:67–73.

Barbieri F, Buonocore A, Dalla Volta R, Gentilucci M (2009): How symbolic gestures and words interact with each other. Brain Lang 110:1–11.

Beattie G, Coughlan J (1999): An experimental investigation of the role of iconic gestures in lexical access using the tip-of-the-tongue phenomenon. Br J Psychol 90:35–56.

Beattie G, Shovelton H (1999): Do iconic hand gestures really contribute anything to the semantic information conveyed by speech? An experimental investigation. Semiotica 123:1–30.

Bernardis P, Gentilucci M (2006): Speech and gesture share the same communication system. Neuropsychologia 44:178–190.

Bernardis P, Salillas E, Caramelli N (2008): Behavioural and neurophysiological evidence of semantic interaction between iconic gestures and words. Cogn Neuropsychol 25:1114–1128.

Blakemore S-J, Frith C (2005): The role of motor contagion in the prediction of action. Neuropsychologia 43:260–267.

Blasi G, Goldberg TE, Weickert T, Das S, Kohn P, Zoltick B, Bertolino A, Callicott JH, Weinberger DR, Mattay VS (2006): Brain regions underlying response inhibition and interference monitoring and suppression. Eur J Neurosci 23:1658–1664.

Botvinick MM (2007): Conflict monitoring and decision making: Reconciling two perspectives on anterior cingulate function. Cogn Affect Behav Neurosci 7:356–366.

Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD (2001): Conflict monitoring and cognitive control. Psychol Rev 108:624–652.

Brass M, Derrfuss J, Forstmann B, Cramon DYv (2005a): The role of the inferior frontal junction area in cognitive control. Trends Cogn Sci 9:314–316.

Brass M, Ullsperger M, Knoesche TR, von Cramon DY, Phillips NA (2005b): Who comes first? The role of the prefrontal and parietal cortex in cognitive control. J Cogn Neurosci 17:1367–1375.

Calvert GA, Campbell R, Brammer MJ (2000): Evidence from functional magnetic resonance imaging of crossmodal binding in the human heteromodal cortex. Curr Biol 10:649–657.

Calvo-Merino B, Grezes J, Glaser DE, Passingham RE, Haggard P (2006): Seeing or doing? Influence of visual and motor familiarity in action observation. Curr Biol 16:1905–1910.

Carter CS, Braver T, Barch DM, Botvinick M, Noll D, Cohen JD (1998): The role of the anterior cingulate cortex in error detection and the on-line monitoring of performance: An event related fMRI study. Biol Psychiatry 43:13s–13s.

Chen Q, Wei P, Zhou X (2006): Distinct neural correlates for resolving stroop conflict at inhibited and noninhibited locations in inhibition of return. J Cogn Neurosci 18:1937–1946.

Chieffi S, Secchi C, Gentilucci M (2009): Deictic word and gesture production: Their interaction. Behav Brain Res 203:200–206.

Cohen RL (1981): On the generality of some memory laws. Scand J Psychol 22:267–281.

Cohen RL, Stewart M (1982): How to avoid developmental effects in free-recall. Scand J Psychol 23:9–15.

Cole MW, Schneider W (2007): The cognitive control network: Integrated cortical regions with dissociable functions. Neuroimage 37:343–360.

Denis M, Engelkamp J, Mohr G (1991): Memory of imagined actions—Imagining oneself or another person. Psychol Res 53:246–250.

Depue BE, Curran T, Banich MT (2007): Memory suppression in PTSD treatment? Science 318:1722.

Derrfuss J, Brass M, von Cramon DY (2004): Cognitive control in the posterior frontolateral cortex: Evidence from common activations in task coordination, interference control, and working memory. Neuroimage 23:604–612.

Dick AS, Goldin-Meadow S, Hasson U, Skipper JI, Small SL (2009): Co-speech gestures influence neural activity in brain regions associated with processing semantic information. Hum Brain Mapp 30:3509–3526.

Emmorey K (2006): The signer as an embodied mirror neuron system: Neural mechanisms underlying sing language and action. In: Arbib MA, editor. Action to Language via the Mirror Neuron System. Cambridge: Cambridge University Press. pp 110–135.

Engelkamp J, Krumnacker H (1980a): Imaginale und motorische Prozesse beim Behalten verbalen Materials. Zeitschrift für Experimentelle und Angewandte Psychologie 27:511–533.

Engelkamp J, Zimmer HD (1984): Motor program information as a separable memory unit. Psychol Res 46:283–299.

Engelkamp J, Zimmer HD (1985): Motor programs and their relation to semantic memory. Ger J Psychol 9:239–254.

Feyereisen P (2006): Further investigation on the mnemonic effect of gestures: Their meaning matters. Eur J Cogn Psychol 18:185–205.

Feyereisen P (2009): Enactment effects and integration processes in younger and older adults' memory for actions. Memory 17:374–385.

Friston KJ, Penny W (2003): Posterior probability maps and SPMs. Neuroimage 19:1240–1249.

Friston K, Chu C, Mourão-Miranda J, Hulme O, Rees G, Penny W, Ashburner J (2008): Bayesian decoding of brain images. Neuroimage 39:181–205.

Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996): Action recognition in the premotor cortex. Brain 119:593–609.

Gentilucci M, Corballis MC (2006): From manual gesture to speech: A gradual transition. Neurosci Biobehav Rev 30:949–960.

Gentilucci M, Dalla Volta R (2008): Spoken language and arm gestures are controlled by the same motor control system. Q J Exp Psychol (Colchester) 61:944–957.

Gentilucci M, Dalla Volta R, Gianelli C (2008): When the hands speak. J Physiol Paris 102:21–30.

Gliga T, Csibra G (2009): One-year-old infants appreciate the referential nature of deictic gestures and words. Psychol Sci 20:347–353.

Goldin-Meadow S (1999): The role of gesture in communication and thinking. Trends Cogn Sci 3:419–429.

Goldin-Meadow S (2003): Hearing Gesture: How Our Hands Help Us Think, Vol. 14. Cambridge: Belknap Press of Harvard University Press. 280 p.

Goldin-Meadow S (2005): Watching language grow. Proc Natl Acad Sci USA 102:2271–2272.

Grezes J, Decety J (2001): Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. Hum Brain Mapp 12:1–19.

Guillot A, Collet C, Nguyen VA, Malouin F, Richards C, Doyon J (2008): Functional neuroanatomical networks associated with expertise in motor imagery. Neuroimage 41:1471–1483.

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

Hazlett EA, Byne W, Brickman AM, Mitsis EM, Newmark R, Haznedar MM, Knatz DT, Chen AD, Buchsbaum MS (2010): Effects of sex and normal aging on regional brain activation during verbal memory performance. Neurobiol Aging 31:826–838.

Helstrup T (1984): Serial position phenomena—Memory for acts, contents and spatial position patterns. Scand J Psychol 25:131–146.

Helstrup T (1987): One, two, or three memories—A problem-solving approach to memory for performed acts. Acta Psychol 66:37–68.

Helstrup T (1993): Actions, context, memory—What is the relation? Scand J Psychol 34:19–26.

Hermsdörfer J, Goldenberg G, Wachsmuth C, Conrad B, Ceballos-Baumann AO, Bartenstein P, Schwaiger M, Boecker H (2001): Cortical correlates of gesture processing: Clues to the cerebral mechanisms underlying apraxia during the imitation of meaningless gestures. Neuroimage 14:149–161.

Hlustík P, Solodkin A, Gullapalli RP, Noll DC, Small SL (2002): Functional lateralization of the human premotor cortex during sequential movements. Brain Cogn 49:54–62.

Hockley WE (2008): The picture superiority effect in associative recognition. Mem Cogn 36:1351–1359.

Holle H, Gunter TC (2007): The role of iconic gestures in speech disambiguation: ERP evidence. J Cogn Neurosci 19:1175–1192.

Joubert S, Beauregard M, Walter N, Bourgouin P, Beaudoin G, Leroux JM, Karama S, Lecours AR (2004): Neural correlates of lexical and sublexical processes in reading. Brain Lang 89:9–20.

Kaplan JT, Iacoboni M (2007): Multimodal action representation in human left ventral premotor cortex. Cogn Process 8:103–113.

Karnath HO, Dieterich M (2006): Spatial neglect—A vestibular disorder? Brain 129 (Part 2):293–305.

Kausler DH, Lichty W, Hakami MK, Freund JS (1986): Activity duration and adult age differences in memory for activity performance. Psychol Aging 1:80–81.

Kelly SD, Kravitz C, Hopkins M (2004): Neural correlates of bimodal speech and gesture comprehension. Brain Lang 89:253–260.

Kelly SD, McDevitt T, Esch M (2009): Brief training with co-speech gesture lends a hand to word learning in a foreign language. Lang Cogn Process 24:313–334.

Kendon A (1981): Gestures, Their Origins and Distribution. Semiotica 37:129–163.

Keysers C, Kohler E, Umilta MA, Nanetti L, Fogassi L, Gallese V (2003): Audiovisual mirror neurons and action recognition. Exp Brain Res 153:628–636.

Kim JH, Park KY, Seo SW, Na DL, Chung CS, Lee KH, Kim GM (2007): Reversible verbal and visual memory deficits after left retrosplenial infarction. J Clin Neurol 3:62–66.

Kircher T, Straube B, Leube D, Weis S, Sachs O, Willmes K, Konrad K, Green A (2009): Neural interaction of speech and gesture: Differential activations of metaphoric co-verbal gestures. Neuropsychologia 47:169–179.

Knopf M (1992): Gedächtnis für Handlungen. Funktionsweise und Entwicklung. Heidelberg: University of Heidelberg.

Knopf M, Mack W, Lenel A, Ferrante S (2005): Memory for action events: Findings in neurological patients. Scand J Psychol 46:11–19.

Kormi-Nouri R (1995): The nature of memory for action events: An episodic integration view. Eur J Cogn Psychol 7:337–363.

Kormi-Nouri R (2000): The role of movement and object in action memory. Int J Psychol 35:132.

Leynes PA, Bink ML (2002): Did I do that? An ERP study of memory for performed and planned actions. Int J Psychophysiol 45:197–210.

Leynes PA, Grey JA, Crawford JT (2006): Event-related potential (ERP) evidence for sensory-based action memories. Int J Psychophysiol 62:193–202.

Lohmann G, Muller K, Bosch V, Mentzel H, Hessler S, Chen L, Zysset S, von Cramon DY (2001): LIPSIA—A new software system for the evaluation of functional magnetic resonance images of the human brain. Comput Med Imaging Graph 25:449–457.

Longcamp M, Tanskanen T, Hari R (2006): The imprint of action: Motor cortex involvement in visual perception of handwritten letters. Neuroimage 33:681–688.

Macedonia M (2003): Sensorimotor enhancing of verbal memory through "Voice Movement Icons" during encoding of foreign language (German: Voice Movement Icons. Sensomotorische Encodierungsstrategie zur Steigerung der quantitativen und qualitativen Lerneffizienz bei Fremdsprachen) PhD Thesis. Salzburg: University of Salzburg.

Maguire EA (2001): The retrosplenial contribution to human navigation: A review of lesion and neuroimaging findings. Scand J Psychol 42:225–238.

Masumoto K, Yamaguchi M, Sutani K, Tsuneto S, Fujita A, Tonoike M (2006): Reactivation of physical motor information in the memory of action events. Brain Res 1101:102–109.

McDonald CR, Crosson B, Valenstein E, Bowers D (2001): Verbal encoding deficits in a patient with a left retrosplenial lesion. Neurocase: Neural Basis Cogn 7:407–417.

McNeill D (1992): Hand and mind: What gestures reveal about thought, Vol. 11. Chicago: University of Chicago Press. 416p.

Mensebach C, Beblo T, Driessen M, Wingenfeld K, Mertens M, Rullkoetter N, Lange W, Markowitsch HJ, Ollech I, Saveedra AS, et al. (2009): Neural correlates of episodic and semantic memory retrieval in borderline personality disorder: An fMRI study. Psychiatry Res: Neuroimaging 171:94–105.

Morris D, Collett P, Marsh P, Oshaughnessy M (1979): Gestures, Their Origins and Distribution. Stein and Day, NewYork.

Neumann J, Lohmann G (2003): Bayesian second-level analysis of functional magnetic resonance images. Neuroimage 20:1346–1355.

Nilsson L-G, Nyberg L, Klingberg T, Åberg C, Persson J, Roland PE (2000): Activity in motor areas while remembering action events. Neuroreport 11:2199–2201.

Norris DG (2000): Reduced power multislice MDEFT imaging. J Magn Reson Imaging 11:445–451.

Nyberg L, Petersson KM, Nilsson LG, Sandblom J, Aberg C, Ingvar M (2001): Reactivation of motor brain areas during explicit memory for actions. Neuroimage 14:521–528.

Paivio A (1971): Imagery and Verbal Processes, Vol. 11. New York: Holt. 596p.

Paivio A (1986): Mental Representations: A Dual Coding Approach, Vol 10. Oxford: Oxford University Press. 322p.

Paivio A, Csapo K (1969): Concrete image and verbal memory codes. J Exp Psychol 80:279.

Peigneux P, Salmon E, van der Linden M, Garraux G, Aerts J, Delfiore G, Degueldre C, Luxen A, Orban G, Franck G (2000): The role of lateral occipitotemporal junction and area MT/V5 in the visual analysis of upper-limb postures. Neuroimage 11:644–655.

Penny WD, Trujillo-Barreto NJ, Friston KJ (2005): Bayesian fMRI time series analysis with spatial priors. Neuroimage 24:350–362.

Pine KJ, Bird H, Kirk E (2007): The effects of prohibiting gestures on children's lexical retrieval ability. Dev Sci 10:747–754.

Porro CA, Francescato MP, Cettolo V, Diamond ME, Baraldi P, Zuiani C, Bazzocchi M, di Prampero PE (1996): Primary motor and sensory cortex activation during motor performance and motor imagery: A functional magnetic resonance imaging study. J Neurosci 16:7688–7698.

Ramnani N, Owen AM (2004): Anterior prefrontal cortex: Insights into function from anatomy and neuroimaging. Nat Rev Neurosci 5:184–194.

Ravizza S (2003): Movement and lexical access: Do noniconic gestures aid in retrieval? Psychon Bull Rev 10:610–615.

Reynolds JR, Donaldson DI, Wagner AD, Braver TS (2004): Item- and task-level processes in the left inferior prefrontal cortex: Positive and negative correlates of encoding. Neuroimage 21:1472–1483.

Rizzolatti G, Arbib MA (1998): Language within our grasp. Trends Neurosci 21:188–194.

Rizzolatti G, Craighero L (2004): The mirror-neuron system. Annu Rev Neurosci 27:169–192.

Rizzolatti G, Fogassi L, Gallese V (2000): Cortical mechanisms subserving object grasping and action recognition: A new view on the cortical motor functions. In: Gazzaniga MS, editor. The New Cognitive Neuroscience. Cambridge, MA: MIT Press. pp. 539–552.

Roberts KL, Hall DA (2008): Examining a supramodal network for conflict processing: A systematic review and novel functional magnetic resonance imaging data for related visual and auditory stroop tasks. J Cogn Neurosci 20:1063–1078.

Ruscheweyh R, Willemer C, Kruger K, Duning T, Warnecke T, Sommer J, Volker K, Ho HV, Mooren F, Knecht S, et al.: Physical activity and memory functions: An interventional study. Neurobiol Aging (in press). doi: 10.1016/j.neurobiolaging.2009.08.001

Russ MO, Mack W, Grama CR, Lanfermann H, Knopf M (2003): Enactment effect in memory: Evidence concerning the function of the supramarginal gyrus. Exp Brain Res 149:497–504.

Saltz E, Donnenwerthnolan S (1981): Does motoric imagery facilitate memory for sentences—A selective interference test. J Verb Learn Verb Behav 20:322–332.

Schubotz RI, von Cramon DY (2001): Functional organization of the lateral premotor cortex: fMRI reveals different regions activated by anticipation of object properties, location and speed. Brain Res Cogn Brain Res 11:97–112.

Schubotz RI, von Cramon DY, Lohmann G (2003): Auditory what, where, and when: A sensory somatotopy in lateral premotor cortex. Neuroimage 20:173–185.

Senkfor AJ (2008): Memory for pantomimed actions versus actions with real objects. Cortex 44:820–833.

Senkfor AJ, Van Petten C, Kutas M (2002): Episodic action memory for real objects: An ERP investigation with perform, watch, and imagine action encoding tasks versus a non-action encoding task. J Cogn Neurosci 14:402–419.

Shams L, Seitz AR (2008): Benefits of multisensory learning. Trends Cogn Sci 12:411–417.

Spaniol J, Davidson PSR, Kim ASN, Han H, Moscovitch M, Grady CL (2009): Event-related fMRI studies of episodic encoding and retrieval: Meta-analyses using activation likelihood estimation. Neuropsychologia 47:1765–1779.

Sueyoshi Ayano HDM (2005): The role of gestures and facial cues in second language listening comprehension. Lang Learn 55:661–699.

Talairach J, Tournoux P (1988): Co-planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System: An Approach to Cerebral Imaging. Stuttgart: Thieme.

Tellier M (2008): The effect of gestures on second language memorisation by young children. Gesture 8:219–235.

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

Tomasello M (2005): Constructing a Language: A Usage-Based Theory of Language Acquisition, Vol. 8. Cambridge, MA: Harvard University Press. 388p.

Tomasello M (2008): Origins of Human Communication, Vol. 13. Cambridge, MA: MIT. 393p.

Ullsperger M, von Cramon DY (2004): Neuroimaging of performance monitoring: Error detection and beyond. Cortex 40:593–604.

Van Mier H (2000): Human learning. In: Toga AW, Mazziotta JC, editors. Brain Mapping: The Systems. London: Academic Press. pp 605–620.

van Praag H (2009): Exercise and the brain: Something to chew on. Trends Neurosci 32:283–290.

Vann SD, Aggleton JP, Maguire EA (2009): What does the retrosplenial cortex do? Nat Rev Neurosci 10:792–802.

von Zerssen GC, Mecklinger A, Opitz B, von Cramon DY (2001): Conscious recollection and illusory recognition: An event-related fMRI study. Eur J Neurosci 13:2148–2156.

Wagner AD, Shannon BJ, Kahn I, Buckner RL (2005): Parietal lobe contributions to episodic memory retrieval. Trends Cogn Sci 9:445–453.

Wittfoth M, Kustermann E, Fahle M, Herrmann M (2008): The influence of response conflict on error processing: Evidence from event-related fMRI. Brain Res 1194:118–129.

Worsley KJ, Liao CH, Aston J, Petre V, Duncan GH, Morales F, Evans AC (2002): A general statistical analysis for fMRI data. Neuroimage 15:1–15.

Wu YC, Coulson S (2007a): How iconic gestures enhance communication: An ERP study. Brain Lang 101:234–245.

Wu YC, Coulson S (2007b): Iconic gestures prime related concepts: An ERP study. Psychon Bull Rev 14:57–63.

Ziemus B, Baumann O, Luerding R, Schlosser R, Schuierer G, Bogdahn U, Greenlee MW (2007): Impaired working-memory after cerebellar infarcts paralleled by changes in BOLD signal of a cortico-cerebellar circuit. Neuropsychologia 45:2016–2024.