

Research Report

Effects of alphabeticality, practice and type of instruction on reading an artificial script: An fMRI study

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Accepted 20 April 2005

Available online 6 June 2005

Abstract

In neuroimaging studies of word reading in natural scripts, the effect of alphabeticality is often confounded with the effect of practice. We used an artificial script to separately manipulate the effects of practice and alphabeticality following training with and without explicit letter instructions. Participants received multi-session training in reading nonsense words, written in an artificial script, wherein each phoneme was represented by 2 discrete symbols [7]. Three training conditions were compared: alphabetical whole words with letter decoding instruction (explicit); alphabetical whole-words (implicit) and non-alphabetical whole-words (arbitrary). Each participant was trained on the arbitrary condition and on one of the alphabetical conditions (explicit or implicit). fMRI scans were acquired after training during reading of trained words and relatively novel words in the alphabetical and arbitrary conditions. Our results showed greater activation in the explicit compared to the arbitrary conditions, but only for relatively-novel words, in the left posterior inferior frontal gyrus (IFG). In the implicit condition, the left posterior IFG was active in both trained and relatively novel words. These results indicate the involvement of the left posterior IFG in letter decoding, and suggest that reading of explicitly well-trained words did not rely on letter decoding, while in implicitly trained words letter decoding persisted into later stages. The superior parietal lobules showed reduced activation for items that received more practice, across all training conditions. Altogether, our results suggest that the alphabeticality of the word, the amount of practice and type of instructions have independent and interacting effects on brain activation during reading.

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Theme: Neural basis of behavior

Topic: Cognition

Keywords: Reading acquisition; fMRI; Skill learning; Alphabetical reading; Implicit; Transfer

1. Introduction

Reading acquisition is associated with a change in the cognitive processes involved in reading. In most reading acquisition models, the evolution of skilled reading is related to the distinction between alphabetical and non-alphabetical reading, and the application of letter decoding knowledge [23,67,79,80,89]. While reading of alphabetical

words may involve letter decoding (i.e., letter segmentation and grapheme–phoneme conversion), non-alphabetical words can only be read by the retrieval of word specific representations, consisting of either the whole word or based on salient features within the word. The dual route models consider these to be distinct mechanisms for reading [20–23], while connectionist models consider them as aspects of a single mechanism [47,70,79]. However, regardless of the question of whether letter decoding involves an abstract rule mechanism [20–23] or is a rule-like behavior based on the statistical regularities of the experienced script [47,70,79], most models of reading acquisition agree that the reliance

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on letter decoding changes in the course of training. Specifically, it has been suggested that in reading alphabetical words, the reliance on segmentation and letter decoding decreases with experience, and that reading familiar words becomes dependent on lexical non-alphabetical processes [23,80]¹. On the basis of this assumption, neuroimaging studies that aimed to examine the difference between alphabetical and non-alphabetical reading often compared words and pseudo-words, or high and low frequency words [4,31,32,59,63]. The logic of these studies was that while high frequency words are expected to rely on direct retrieval of lexical representations, pseudo-words and low frequency words would rely on letter decoding since they have no effective lexical representation. One should note, however, that the design of natural script studies under this assumption confounds alphabetical reading with low amounts of practice and precludes the separate testing of each effect.

Neuroimaging studies that compared alphabetical and non-alphabetical reading in languages with two script systems (i.e., Japanese and Chinese) lead to conflicting conclusions, showing both similarities [58] and differences [59,77,78] between the script systems. Furthermore, even the comparison of Kana and Kanji (in Japanese) and of traditional Chinese characters with Pinyin (the alphabetical script) is confounded with morpho-semantic differences [17], as well as differences in word frequency and familiarity [41]. In addition, reading of traditional Chinese characters may not rely entirely on word-specific recognition processes due to the use of phonological cues in many of the characters. The aim of the current study is to use an artificial script in a functional imaging study to examine the separate effects of alphabetality and the amount of experience and to test the hypothesis that the reliance on letter decoding decreases in the course of training on reading alphabetical words.

Another factor that may interact with the effects of alphabetality and practice is the type of instruction given during training, and specifically whether explicit instruction on letter decoding is afforded [51]. There is an ongoing debate about the critical necessity of explicit instruction of phonological decoding rules for the acquisition of reading skills [35]. Previous reading acquisition studies have shown that explicit instruction on phonological decoding enhanced reading acquisition [3,5,14,36,37,40,66,80,91] and see [23] for review. Moreover, mere exposure to alphabetical orthography was, in many cases, insufficient for inducing the discovery of the alphabetic principle in children [12,13,15,29,53,87]. However, other studies suggest that training on whole word reading may elicit learning of grapheme–phoneme correspondences by young beginning

readers [30,67,86,87,89] and may even be advantageous compared to explicit instruction of letter decoding [40].

In two recent studies [6,7], we directly addressed the question of whether whole word training results in the formation of letter representations and phonological decoding skills in literate adults. Participants received multi-session training in reading nonsense words, written in an artificial script, in which each phoneme was represented by 2 discrete symbols. Three training conditions were compared in terms of the time-course of learning and the ability to generalize the acquired knowledge (transfer): alphabetical whole words with letter decoding instruction (Explicit); alphabetical whole words without letter instruction (Implicit), and non-alphabetical whole words, with no consistent correspondence of letters to sounds (Arbitrary).

Our results [6,7] showed that training in the explicit and arbitrary conditions resulted in distinctive learning processes. The pattern of transfer results suggested that training in the explicit condition resulted mainly in learning to recognize the individual letters, but also in some word-specific recognition. Training in the arbitrary condition resulted in word-specific recognition that was based on recognition of the internal structure of symbols in the word. Furthermore, performance in the explicit condition was more accurate, but slower than performance in the arbitrary condition, presumably because it involved letter decoding. Training in the implicit condition, resulted in word-specific recognition in all participants, in addition to non-declarative letter decoding knowledge in some participants. However, letter knowledge in the implicit condition was lower than in the explicit condition, and evolved only under specific facilitating conditions. The three training conditions did not differ only in terms of the type of knowledge that was acquired, but also in terms of preservation of learning gains. The acquired knowledge was better preserved in the explicit compared to the arbitrary and implicit conditions both between sessions, and in terms of long-term testing. This finding suggests that training in the explicit condition reached a higher, more progressed, level of skilled performance [7].

In the current study, we used the Morse-like artificial script, studied in Bitan and Karni [7], to test the interaction between the effects of the alphabetality and the amount of experience following training in either explicit letter instruction or whole word training conditions on brain activation during reading. The separate manipulation of alphabetality and the amount of practice enabled the examination of the hypothesis that reading of familiar (well practiced) alphabetical words does not necessarily involve letter decoding. The use of an artificial script enabled us to control the amount of practice participants received on specific words (alphabetical and non-alphabetical) by comparing trained words to less trained words. Furthermore, the inclusion of arbitrary items afforded a condition wherein the script was devoid of any alphabetical or phonological

¹ Although different studies have shown greater involvement of phonological representations in word recognition in skilled reading [8,60,68], these studies did not differentiate between the level of the individual letters and the level of the word.

cues, which is not the case in high frequency words in natural scripts. Finally, the use of non-sense words in a phonological “translation” task eliminated the effect of semantic processes, which is confounded in the comparison of words and pseudo-words.

Our results showed that alphabeticality, the amount of practice and the type of instruction, may each (independently) affect the patterns of brain activation evoked by reading. Our results suggest that explicit training on alphabetical words relied more on letter decoding in initial as compared to later stages of reading, with the reading of highly familiar, well-trained alphabetical words much less dependent on word segmentation and letter decoding. Nevertheless, explicitly well-trained alphabetical words elicited a different pattern of activation compared to the one elicited by non-alphabetical words in the arbitrary condition, even though both of them presumably resulted in reading that did not rely on letter decoding. The pattern of activation following the implicit training on alphabetical words suggests that the reliance on letter decoding persisted to later stages of training, as compared to the explicit condition.

2. Method

2.1. Subjects

16 right-handed female volunteers, ages 22–26, native Hebrew speakers with normal linguistic and reading skills participated in the experiment and were paid for their time. Each subject participated in two training conditions: an alphabetical condition and an arbitrary condition, serially.

2.2. Behavioral phase

2.2.1. Stimuli

The stimuli and the procedure of the behavioral phase were identical to those used in Bitan and Karni [7]. The training stimuli consisted of two sets of 12 nonsense words written in an artificial Morse-like script. Four

consonants and two vowels were used to compose all non-words in a given set, with each element repeating six times in a set, e.g.:

Set 1: LOP, PNO, APL, TOL, TPO, NAL, NLO, LAT, ONT, PNA, APT, TNA.

Set 2: RUB, BMU, MUR, BRI, UMK, MIR, BKU, KRU, IRK, KMI, IMB, BKI.

We used a Morse-like artificial script in which a sequence of 2 symbols represented one letter, and 4 symbols, in different orders, were used to compose all letters. Each symbol appeared in 3 out of the 6 letters. (e.g., P: * < L: < * T: □ □ A: □ □ N: * □ O: < □). Two different transformations were used to represent the non-word in the novel script: an alphabetical transformation, in which each phoneme consistently corresponded to a letter (e.g., PNO: * < * □ < □ LOP: < * < □ * <), and an arbitrary transformation, in which phoneme to letter correspondence differed across words (e.g., PNO: □ □ □ * < LOP: * < < * * □). Thus, the symbol strings in the arbitrary condition could only be read as logographs (in similarity to Japanese Kanji).

For each set of training stimuli, four transfer tests were composed, 12 non-words in each test (Table 1). The word-transfer test consisted of new non-words composed of the original letters, and written with the same set of symbols (see examples in Table 1). The letter-transfer test consisted of new non-words composed of new letters written with the same set of symbols. A comparison of word transfer to letter-transfer served as the indication for the acquisition of letter decoding knowledge. A third transfer test was the symbol-transfer test in which the original non-words were written using a new set of symbols, with consistent mapping between the sets of symbols. Thus, the pattern of symbol repetitions and internal symmetries within each string was preserved. The fourth transfer test was the grapheme-transfer test, in which the original non-words were written using a still new set of symbols, in a completely new sequence. A difference between symbol-transfer and grapheme-transfer would indicate learning of the pattern of symmetries and repetitions in the sequence of symbols.

Table 1
Summary of conditions presented at the behavioral phase

	Trained items ≈200 repetitions	Word transfer ≈30 repetitions	Symbol transfer ≈30 repetitions	Letter transfer	Grapheme transfer
Explicit N=8	PNO: * < * □ < □ LOP: < * < □ * <	NOP: * □ < □ * < POL: * < < □ < * <	PNO: -π- ^π(LOP: π-π(-π	DUF: □ * < □ < □ < SFU: □ □ < < □ <	PNO: □] □] □ < LOP:] □ < □ < □ <
Implicit N=8	PNO: * < * □ < □ LOP: < * < □ * <	NOP: * □ < □ * < POL: * < < □ < * <	PNO: -π- ^π(LOP: π-π(-π	DUF: □ * < □ < □ < SFU: □ □ < < □ <	PNO: □] □] □ < LOP:] □ < □ < □ <
Arbitrary N=16	PNO: □ □ □ □ * < LOP: * < < * * □ <	NOP: * < * □ < □ POL: * < □ □ □ □	PNO: -ππ- (^ LOP: (^ (^ (π	DUF: □ < □ * < □ < SFU: □ < □ □ < □ <	PNO: □] □] □ < LOP: □ < □] □ <

Conditions administered during scanning are displayed in bold lines, with the amount of experience afforded prior to scanning indicated in terms of the number of repetitions per item. Two out of a total of 12 items are presented as an example in each condition. For convenience of comparison, all examples are presented from a single set of stimuli. In practice, a different set was used in the alphabetical and in the arbitrary condition in each subject.

2.2.2. Apparatus

The stimuli were presented on a 17-in. 60 Hz. PC screen, with each item subtending 1° viewing angle, from a viewing distance of 60 cm. Stimulus presentation as well as the recording of responses (using a standard three button mouse), was controlled by ‘Psy’, a psychophysical measurements program, operating on Linux environment (Bonneh, 1998).

2.2.3. Experimental procedure

Each subject was trained in two training conditions successively: an alphabetical condition—training on alphabetical non-words, and an arbitrary condition—training on non-alphabetical non-words with no consistent mapping of graphemes to phonemes. In the alphabetical condition, half of the subjects were trained in the ‘explicit’ condition—given instruction on the grapheme–phoneme correspondence prior to training, and half of the subjects were trained in the ‘implicit’ condition—with no instruction of grapheme–phoneme correspondence. In each group, half of the subjects were trained on the arbitrary condition before the alphabetical condition, and half of the subjects were trained on the alphabetical condition before the arbitrary condition. The two sets of trained non-words were written using a different set of symbols and were balanced across training conditions.

Fig. 1 shows that the first session of each training condition started with a ‘whole-word instruction’ block, in which the subject was presented with each target non-word in novel script with its corresponding translation to Latin letters below. Each stimulus was presented for 2000 ms and subjects were instructed to read it aloud and memorize the association. A ‘letter-instruction’ block was given prior to the ‘whole-word instruction’ block only in the explicit training condition. The ‘letter-instruction’ block consisted of 30 trials in which the individual letter patterns in the new script were presented together with their corresponding Latin letter translation, each pair for 2000 ms. Subjects were required to pronounce the related phoneme and memorize the association. The letters appeared in a fixed order that repeated for 5 times (total of 30 trials).

After the instruction block(s) 6 training blocks was administered. In each trial, a target word appeared for 800 ms with a Latin-letter-string presented below. Half of the trials in each block contained correct pairs, and half of the trials were incorrect pairs. The subject’s task was to indicate, for each test item, whether the Latin-letter-string was the correct translation, by pressing one of two keys (two alternative forced choice). Auditory feedback was given for errors. Each block consisted of 48 trials. In each training

condition, subjects were given training on 5 daily sessions, spaced 1–3 days apart. In sessions 2–5, only the training blocks were administered, and the training procedure was identical in all conditions.

At the end of the 5 training sessions, the transfer of learning gains to novel stimuli was tested (Fig. 1). Each of the four transfer tests was administered in a separate session with the order of transfer tests fixed for all subjects (i.e., word-transfer, symbol-transfer, letter-transfer and grapheme-transfer). In each of the 4 transfer session subjects first performed 3 blocks of the task using the originally trained non-words. The level of performance of the task with the trained stimuli served as the reference for calculating the transfer of performance gains to the transfer stimuli. Subjects then performed a ‘whole-word instruction’ block in which the transfer stimuli and their Latin letter equivalents were presented. No ‘letter-instruction’ was given during the transfer sessions. Finally, subjects performed 6 blocks of the task using the transfer stimuli. A transfer ratio was calculated for each subject in each transfer condition in the following manner. The difference between the mean performance in the transfer blocks and mean performance in the first training session was divided by the difference between the last performance of the original stimuli (in the transfer session) and performance in the first training session.

$$\text{Transfer ratio} = \frac{(\text{Transfer} - \text{Trained 1st session})}{(\text{Trained last session} - \text{Trained 1st session})}$$

All data were analyzed using the General Linear Model (GLM). 1 outlier of more than 2 standard deviations from the mean was excluded from the analysis of the behavioral results in the explicit-letter-transfer, and explicit-grapheme-transfer conditions. This subject was included in the analysis of the fMRI results since these conditions were not performed during scanning.

2.3. fMRI phase

2.3.1. Stimuli

Non-words from six of the conditions presented in the behavioral phase were examined during scanning: alphabetical trained words, alphabetical word-transfer, alphabetical symbol-transfer, arbitrary trained words, arbitrary word-transfer and arbitrary symbol-transfer (see Table 1). 12 items in each of the six conditions were presented twice, making a total of 144 trials per subject. Prior to scanning each trained item has been repeated for 230 times, and each transfer-test

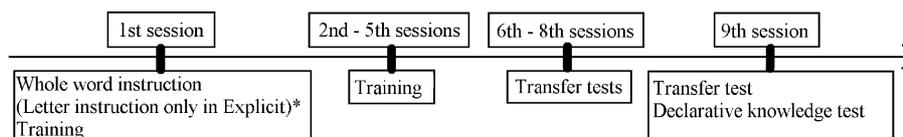


Fig. 1. Design of the behavioral phase. (*) Letter instruction was given only in the 1st session of the explicit training condition.

item has been repeated for only 30 times. Hence, the difference between trained and transfer items represents the changes that depend on the amount of practice.

2.3.2. Experimental procedure

The event-related fMRI scans were acquired on average 20 weeks after training. A previous study [7] showed that learning gains were preserved even 13 months after training. However, to ensure participants' high level of accuracy during scanning two refreshing sessions were performed during the preceding week. In the first refreshing session, participants performed 6 blocks of training in each training condition (i.e., alphabetical and arbitrary), and 2 blocks of each transfer condition (i.e., alphabetical word-transfer, alphabetical symbol-transfer, arbitrary word-transfer, and arbitrary symbol-transfer). In the second refreshing session, participants performed 4 practice blocks in which all 6 conditions were mixed in a pseudo-random order, with presentation procedure and duration matched to the presentation in the scanner (see below).

In the scanner, 144 trials were presented in four sets of 36 trials each. In each set, half of the items (six) from each of the six conditions were presented in a mixed pseudo-randomized order. Each trial began with a 400-ms fixation circle, followed after 300 ms by the target word presented for 2000 ms. The Latin letters string was presented 6800 ms after the target word for 400 ms, followed by an interval of 6100 ms before the beginning of the subsequent trial. Altogether, each trial lasted 16 s (Fig. 2). In similarity to the behavioral phase, subjects were required to judge whether the translation was correct and indicate their decision by a hand movement to one of two directions. Trials with incorrect responses were excluded from the analysis. In addition to the experimental task, a verb-generation task was administered in 2 sets of scans to determine the subjects' hemispheric dominance.

2.3.3. Data acquisition and analysis

fMRI scans were acquired in a 3T GE Signa scanner, equipped with a birdcage head coil. Subjects' heads were immobilized using foam pads. Visual stimuli were back-

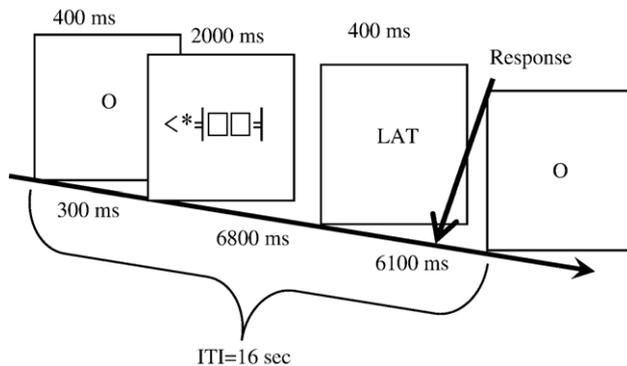


Fig. 2. The temporal sequence of displays in a single trial (16 s) during scanning.

projected by an RF-shielded projector system and viewed through a mirror device. The functional data were acquired using gradient echo planar imaging (GEPI) sequence, with TR = 3 s, TE = 35 ms and flip angle = 90°. 24 slices, 5 mm thick, were acquired parallel to the AC-PC plane, and covered the whole brain. Field of view (FOV) was 24 × 24 cm, and in plane resolution was 3.75 × 3.75 mm. For each subject, 4 MRI sessions of 196 volumes were acquired, while the first 4 volumes were discarded to allow for T1 equilibrium effects. T1-weighted anatomical images were obtained with TR = 400 ms, TE = 14 ms, flip angle = 80°, resulting in a data matrix of 256 × 256 voxels of 0.94 × 0.94 mm.

Data were analyzed with the Statistical Parametric Mapping software (SPM2, Wellcome Department of Imaging Neuroscience, London). The images were synchronized to the middle slice to correct for differences in slice acquisition time, spatially realigned to the first volume to correct for head movements, and normalized to the standard EPI template volume (MNI). The data were then smoothed with a Gaussian kernel of 10 mm.

At a first stage, data were analyzed individually for each subject and condition. Conditions were convoluted with the canonical hemodynamic response function (HRF) and high-pass filtered with a cutoff period of 128 s. Each of the six conditions, and each of the two stimuli presented in a trial (i.e., artificial script and Latin letters string) modeled separately. The *t* value contrasts, for each condition contrasted against the overall mean from the individual subjects were ultimately imported into a second level analysis (random effect). In order to contrast the various group effects, the following tests and comparisons were applied: (1) Group main effect for each condition was tested using the one-sample *t* test. (2) The effect of alphabetality (alphabetical vs. non-alphabetical) for each condition (i.e., trained words, word-transfer and symbol-transfer), and the effect of practice (i.e., trained vs. transfer conditions) were tested using a paired *t* test. (3) The differences between the explicit and implicit conditions were tested by using a two-sample *t* test.

In addition, the correlation between brain activation and the accuracy of performance in the behavioral phase was tested. A 'multiple regression with constant' analysis was performed, with the individual's mean accuracy in the transfer session (or in the 9th session for trained items) serving as the covariate. The performance during scanning was not used as a covariate since it was at ceiling level and had less variance. Moreover, the performance during the training and transfer test may better represent the individuals' learning ability. Finally, the correlation of activation with the behavioral index for letter knowledge (word-transfer minus letter-transfer) was tested for alphabetical trained and word-transfer items.

Our focus of interest was primarily on the classical language and reading areas, i.e., left inferior frontal gyrus (BA 44/45) and the left inferior parietal lobule (BA 40). Hence, a small volume correction (SVC) was applied to the *P* values of activated voxels in these anatomically predefined

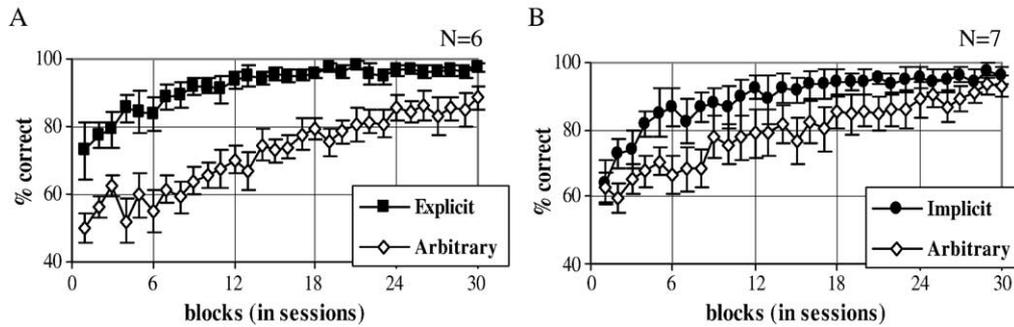


Fig. 3. Learning curves for the explicit group (A) and the implicit group (B). Accuracy of performance is shown for the alphabetic and the arbitrary conditions. Vertical lines indicate final blocks of each training session.

ROIs. Other regions of activation are interpreted if they survived a threshold of whole-brain corrected $P < 0.05$. The figures and tables present clusters larger than 15 voxels at a threshold of uncorrected $P < 0.001$, for descriptive purposes. Correlation with behavior is reported with a threshold of uncorrected $P < 0.001$ within our regions of interest, and whole-brain corrected $P < 0.05$ outside our region of interest. Results are reported based on the WFU atlas [61,62].

Two subjects were excluded from the analysis due to hardware malfunction during scanning. An additional subject was excluded due to right-hemispheric activation patterns as observed in the verb generation task. This results in 6 subjects for the ‘explicit’ group and 7 subjects for the ‘implicit’ group. The behavioral results are shown only for subjects included in the fMRI analysis.

3. Results

3.1. Behavioral

All training conditions induced significant improvement in the translation task, both in terms of accuracy and in

terms of reaction time (RT), with no speed-accuracy tradeoffs. The GLM analyses with group and condition order as between-subject variables, and training-condition, session and block as within subject variables, showed significant effect of session ($F(4,40) = 135.9$ and $F(4,40) = 49.5$, $P < 0.001$, for accuracy and RT, respectively) and block ($F(5,50) = 30.1$ and $F(5,50) = 27.1$, $P < 0.001$ for accuracy and RT, respectively). However the time-course of learning was different in the different training conditions. Figs. 3A, B show that the performance in both alphabetical conditions was more accurate compared to the performance in the arbitrary condition throughout the entire training process. A GLM analysis of the two groups revealed a significant difference between alphabetical and arbitrary conditions ($F(1,10) = 32.7$, $P < 0.001$). Within group analyses revealed a significant difference between the explicit and arbitrary conditions ($F(1,4) = 193.1$, $P < 0.001$) (Fig. 3A), and a non-significant trend for higher accuracy in the implicit compared to the arbitrary condition ($F(1,5) = 6.0$, $P = 0.06$) (Fig. 3B).

Between group analysis of the accuracy showed no significant difference between the explicit and implicit conditions ($F(1,10) < 1$). However, analysis of RTs

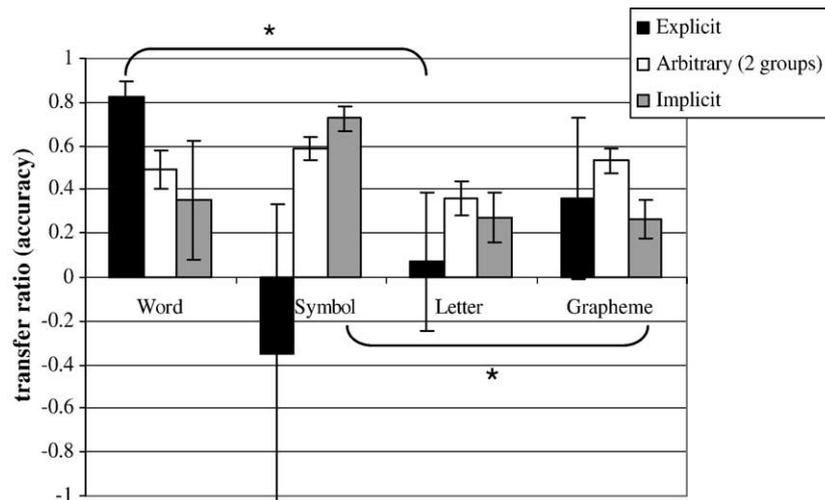


Fig. 4. Transfer results in the Explicit (one group), Implicit (one group) and Arbitrary (two groups) conditions. The measure for transfer was calculated as: (mean performance in the transfer session – first training session)/(last training session – first training session), with transfer ratio of 1.0 indicating full transfer. (*) Significant difference $P < 0.05$.

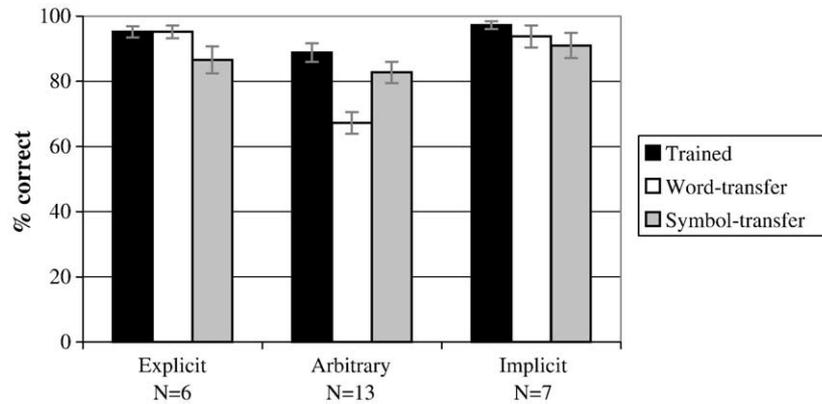


Fig. 5. Accuracy of performance during scanning, mean percent correct and standard errors are shown.

showed significantly faster responses in the implicit compared to the explicit condition throughout training ($F(1,10) = 17.9, P < 0.01$).

The results of the transfer tests indicate that the ability to transfer the acquired knowledge to untrained stimuli was markedly different following training in the explicit and arbitrary conditions (Fig. 4). Performance in the word-transfer test in the explicit condition was significantly higher than performance in the letter-transfer test ($t(4) = 2.8, P < 0.05$) (Fig. 4). The advantage of words composed of the original letters compared to words composed of new letters suggests that the letter knowledge was acquired in the explicit conditions. Nevertheless, accuracy of performance in explicit-word-transfer items, was lower than in trained

items (word-transfer ratio < 1). Although the significance of this difference may not be tested statistically, it may suggest that participants in the explicit condition have acquired some word-specific knowledge in addition to the letter-knowledge. As expected, there was no advantage of word-transfer over letter-transfer in the arbitrary condition ($t(5) < 1$). Moreover, in the explicit group, performance in the word-transfer test was significantly higher in the explicit condition than in the corresponding arbitrary condition ($t(5) = 2.5, P < 0.05$) (Fig. 4).

Fig. 4 shows that both the arbitrary and the implicit conditions resulted in a highest degree of transfer in the symbol-transfer test compared to the word and letter transfer tests (non-significant trend). In contrast to the explicit

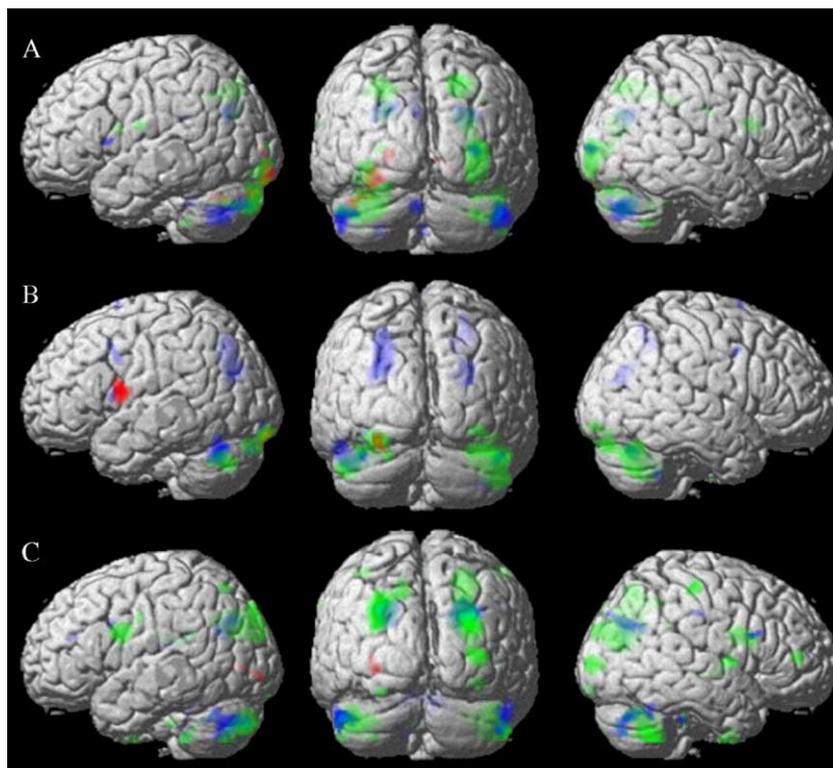


Fig. 6. Brain regions showing activation in the Explicit (red) Arbitrary (green) and Implicit (blue) conditions, in trained words (A), word-transfer (B) and symbol-transfer (C) items.

Table 2
Regions of activation in individual conditions compared to the overall mean

Condition	Region	Broadman area	Hemisphere	z score	Voxels	x	y	z
<i>Explicit trained</i>								
	Inferior occipital gyrus/cuneus	17/18	L	4.54	215	−36	−96	−18
	Lingual gyrus	18	R	3.61	41	14	−72	−4
<i>Explicit word-transfer</i>								
	Inferior occipital gyrus/fusiform gyri	18/19	L	4.06	68	−26	−94	−22
	Inferior frontal gyrus/insula	44/13	L	4.02	325	−46	0	12
<i>Explicit symbol-transfer</i>								
	Middle occipital gyrus	18/19	L	4.22	53	−32	−76	2
<i>Arbitrary trained</i>								
Occipital:	Inferior occipital gyrus/cerebellum	18	L	4.07	1043	−36	−94	−8
	Middle occipital gyrus	18	L	3.38	28	−26	−96	6
	Inferior occipital/middle occipital gyri	18/19	R	4.43	994	32	−98	−8
Parietal:	Precuneus/inferior parietal lobule	7/40	L	4.48	703	−22	−70	40
	Superior parietal lobule/precuneus/supramarginal gyrus	7/40	R	4.32	843	22	−68	48
	Postcentral gyrus	43	L	3.88	49	−64	−10	20
Frontal:	Insula	13	L	3.84	98	−40	4	16
	Insula/inferior frontal gyrus	13/44	R	3.83	257	42	16	20
	Precentral gyrus	3	R	3.58	41	52	−16	30
	Medial frontal gyrus	6	L	3.39	15	−8	14	48
<i>Arbitrary word-transfer</i>								
	Inferior occipital/fusiform gyri/cerebellum	17/18	L	4.03	472	−26	−98	−18
	Inferior occipital/fusiform gyri	18	R	3.62	173	34	−94	−10
	Fusiform gyrus	37	R	3.59	18	48	−62	−24
<i>Arbitrary symbol-transfer</i>								
Occipital:	Fusiform gyrus	20	R	3.33	20	42	−30	−32
	Inferior occipital gyrus	17	L	3.43	24	−24	−98	−20
	Inferior occipital gyrus	18	R	3.56	46	36	−96	−18
	Middle occipital gyrus	19	R	3.96	199	34	−96	4
	Precuneus/superior occipital gyrus	7/19	L	4.1	1267	−20	−70	34
Parietal:	Cuneus/superior parietal gyrus	19/7	R	4.78	1842	30	−74	20
	Inferior parietal lobule	40	R	3.49	48	36	−42	28
	Superior parietal lobule	7	L	3.56	46	−40	−66	58
	Postcentral gyrus	3	R	3.69	145	48	−26	56
Frontal:	Precentral gyrus	6	L	3.36	25	−64	−10	36
	Precentral gyrus/basal ganglia	6	R	4.27	258	54	−2	6
	Insula	13	L	4.03	298	−34	−42	20
	Inferior frontal gyrus	9/44	L	4.77	429	−46	2	24
	Inferior frontal gyrus	46	R	4.05	59	54	46	8
	Inferior frontal gyrus	9/44	R	3.69	331	52	4	26
	Medial frontal gyrus	6	R	3.36	29	4	−28	60
<i>Implicit trained</i>								
Occipital:	Middle occipital gyrus	19	R	4.08	50	32	−96	4
	Precuneus	7	L	5.75	235	−18	−68	30
	Cuneus/precuneus	7	L	4.22	70	−4	−76	30
	Precuneus	7	R	4.46	238	26	−70	28
Frontal:	Precentral/inferior frontal gyrus	44	L	3.97	50	−54	14	8
<i>Implicit word-transfer</i>								
Occipital:	Inferior occipital gyrus	19	L	3.35	35	−46	−90	−12
	Cuneus/precuneus/superior occipital gyrus	7/19	L	4.55	646	−28	−72	24
Parietal:	Cuneus/superior parietal gyrus	19/7	R	3.65	399	28	−72	28
Frontal:	Precentral gyrus	44	L	3.43	26	−58	10	8
	Precentral gyrus	6/9	R	3.33	18	58	4	40
	Inferior frontal/middle frontal gyri	44/8	L	3.61	71	−46	6	36

(continued on next page)

Table 2 (continued)

Condition	Region	Broadman area	Hemisphere	z score	Voxels	x	y	z
<i>Implicit symbol-transfer</i>								
Occipital:	Precuneus	7	L	4.3	367	-22	-66	24
	Cuneus/precuneus	19	R	4.98	440	24	-70	28
Frontal:	Precentral gyrus	6	R	4.09	33	50	-22	38
	Middle frontal gyrus	46	L	3.57	16	-40	38	20
	Inferior frontal gyrus	45	R	3.84	43	56	18	24
	Inferior frontal gyrus	9	L	3.34	20	-48	10	32

Clusters larger than 15 voxels are presented at a threshold of uncorrected $P < 0.001$. Clusters significant at a threshold of small volume corrected $P < 0.05$ are indicated in bold.

condition, following training in the implicit condition, there was no significant difference between word-transfer and letter-transfer (transfer ratios were 0.35 and 0.27, respectively, $t(6) < 1$).

Participants' mean accuracy of performance within the scanner was 0.86 across all conditions (Fig. 5). A GLM analysis, with training condition (alphabetical vs. arbitrary) and test-type (trained, word-transfer, symbol-transfer) as within subject variables, and group (explicit vs. implicit) as a between subject variable was conducted on the accuracy of performance in the scanner. A significant main effect was found for the training condition ($F(1,11) = 36.0$, $P < 0.01$) and test-type ($F(2,10) = 14.8$, $P < 0.01$) and a significant interaction between training condition and test-type ($F(2,10) = 11.2$, $P < 0.01$). Paired t tests found that the arbitrary-word-transfer condition a significantly lower accuracy compared to the alphabetical-word-transfer in both the explicit group ($t(5) = 8.3$, $P < 0.01$) and implicit group ($t(6) = 3.4$, $P < 0.05$). Accuracy in the arbitrary-word-transfer condition was significantly lower compared to the arbitrary-trained condition in both the explicit group ($t(5) = 3.7$, $P < 0.05$) and the implicit group ($t(6) = 3.9$, $P < 0.01$).

3.2. fMRI

3.2.1. Comparison of the explicit and arbitrary conditions

Fig. 6 and Table 2 show the patterns of activation evoked by reading in each of the single conditions. Reading of trained words in the explicit condition activated bilaterally the occipital cortex, with a larger cluster on the left including the calcarine and extending into the inferior

occipital gyrus. Reading of trained words in the arbitrary condition activated much broader areas, again bilaterally, in the occipital cortices (including the inferior and middle occipital gyri), in parietal regions (the banks of the intra-parietal sulci, inferior and superior parietal lobules), in the precentral gyri and in the insula. No clusters of activation exceeded the 15 voxels threshold in the direct comparison of explicit-trained and arbitrary-trained items (Table 3).

Reading of word-transfer items in the explicit condition showed robust activation in the posterior left inferior frontal gyrus (LIFG) including the pars opercularis of the left inferior frontal gyrus (BA 44). This cluster survived small volume correction for the anatomically predefined ROI (Table 2). Reading of explicit-word-transfer items also activated the left occipital cortex (inferior-occipital/posterior-fusiform gyrus). Word-transfer items in the arbitrary condition activated only bilateral occipital regions. Fig. 7 and Table 3 show the results of a direct comparison between explicit and arbitrary word transfer, with significantly greater activation in the explicit-word-transfer compared to the arbitrary-word-transfer items in the posterior part of the left inferior frontal gyrus, and in bilateral occipital regions.

Reading of symbol-transfer items in the explicit condition showed activation only in the left occipital cortex (Fig. 6). However, the arbitrary-symbol-transfer items activated a robust cluster of voxels in the posterior left inferior frontal gyrus (LIFG), and its right homologue. The left side cluster survived small volume correction for the anatomically predefined ROI (Table 2). In addition, the arbitrary-symbol-transfer items activated bilateral occipital, parietal and frontal regions. No clusters of activation

Table 3
Regions of activation in a direct comparison between the explicit and arbitrary conditions

Condition	Region	Broadman area	Hemisphere	z score	voxels	x	y	z
<i>Explicit-Arbitrary</i>								
Trained:	no clusters							
Word-transfer:	Inferior frontal gyrus	9	L	3.51	27	-64	6	28
	Middle occipital gyrus	18	L	3.5	59	-32	-92	0
	Middle occipital gyrus	37	R	3.31	34	50	-70	2
Symbol-transfer:	no clusters							
<i>Arbitrary-Explicit</i>								
no clusters								

Clusters larger than 15 voxels are presented at a threshold of uncorrected $P < 0.001$. Clusters significant at a threshold of small volume corrected $P < 0.05$ are indicated in bold.

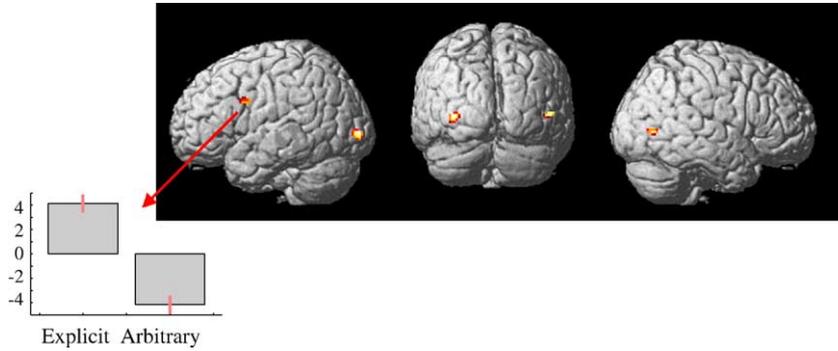


Fig. 7. Brain regions showing more activation in the explicit-word-transfer compared to the arbitrary-word-transfer condition, with the signal change in the posterior LIFG.

exceeded the threshold in the direct comparison of explicit-symbol-transfer and arbitrary-symbol-transfer items (Table 3).

3.2.2. The implicit condition

In the implicit condition both trained and word-transfer items activated the posterior part of the left inferior frontal gyrus (LIFG), in clusters that survived small volume correction for the anatomically predefined ROI (Fig. 6, Table 2). In the implicit-trained condition, activation in the posterior LIFG [-58, 8, 14] was correlated with the behavioral index for letter knowledge (word-transfer minus letter-transfer) ($Z = 3.39$, uncorrected $P < 0.001$) (Fig. 8). Such correlation with letter knowledge was not found in the explicit or arbitrary training condition. However, in contrast to the explicit group, no significant difference was found in the left inferior frontal gyrus between the implicit-word-transfer and the arbitrary-word-transfer conditions. (The difference between the findings in the explicit and implicit condition may be a result of either the difference between training conditions or differences between groups). In

addition, the implicit-trained items activated bilateral parietal and right occipital cortices. Implicit word transfer items activated the left occipital and right parietal cortices, and bilateral precentral gyri. Reading the symbol-transfer words in the implicit condition activated bilateral frontal gyri, and bilateral occipital regions (Fig. 6 and Table 2).

3.2.3. Effects of practice across conditions

The presentation of the Latin letter-string (for which the matching response was required) was modeled separately in the analysis. Fig. 9 and Table 4 show regions activated in a comparison of the artificial script to Latin letter-strings. Greater activation for artificial script compared to Latin letter-strings was found in the bilateral superior parietal lobules (SPL), as well as bilateral fusiform and inferior occipital gyri, right paracentral and left precentral gyri. Fig. 10B shows that activation in the right SPL for Latin letter-strings was decreased even compared to baseline.

The comparison of trained and transfer items, across training conditions (alphabetical and arbitrary), revealed greater activation for the transfer as compared to the trained

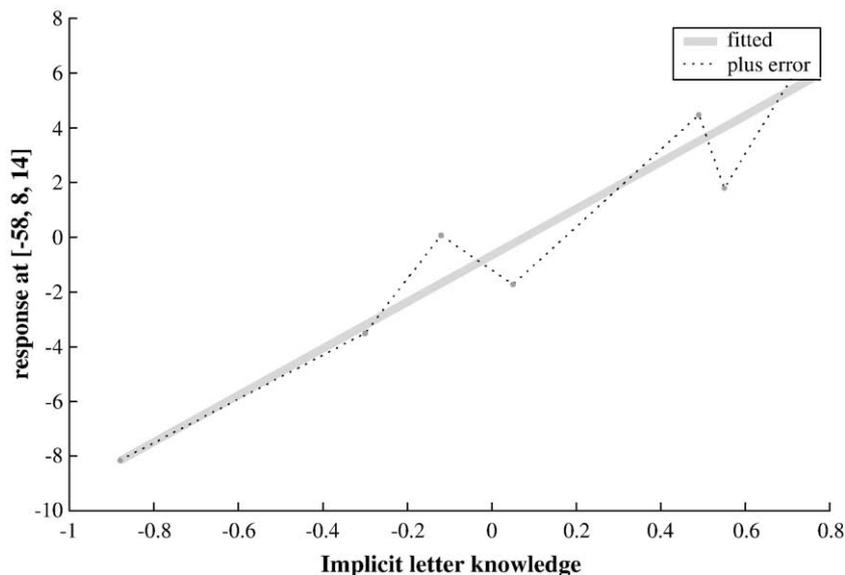


Fig. 8. The correlation of activation in the posterior LIFG during reading of Implicit-trained-words, with the individual's level of letter knowledge in the implicit condition (measured by the difference: word-transfer-letter-transfer).

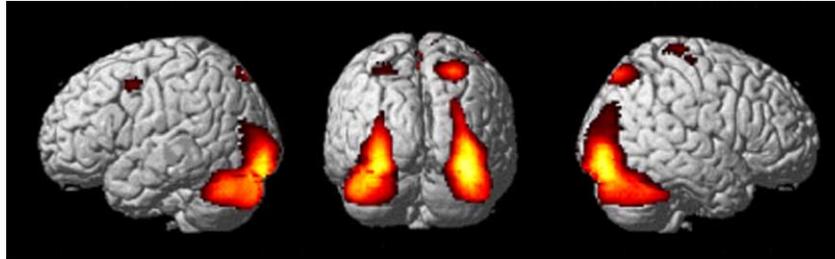


Fig. 9. Brain region showing more activation during the presentation of the artificial script as compared to Latin-letter-string.

items in the right SPL (Figs. 10A, B), however, this cluster did not survive the threshold of corrected $P < 0.05$. Nevertheless, the activation in the bilateral SPL [28, –58, 58] and [–20, –64, 54] during the reading of the transfer items was correlated with performance in the transfer conditions ($Z = 4.51$ and 4.91 , respectively, whole-brain corrected $P < 0.05$, Fig. 11). Performance of trained items was not correlated with the activation in the SPL.

4. Discussion

The results of the current study show that the amount of experience afforded for a specific set of stimuli is an important factor, interacting with the type of script (alphabetical vs. non-alphabetical) and the type of instructions (explicit vs. implicit) in determining the involvement of different cortical regions in reading. More experience resulted in lesser recruitment of the right SPL in: (a) all transfer conditions compared to the trained conditions, and (b) in the artificial script compared to Latin letter strings. Activation in the posterior left inferior frontal gyrus (LIFG) was affected by experience in interaction with the type of script and the type of instruction. The posterior LIFG was more active in the explicit-word-transfer compared to the arbitrary-word-transfer conditions, suggesting it is involved in segmentation and letter decoding. Our results further show that while the posterior LIFG was not active in

explicitly trained words, activation was evident in the implicit condition, in both trained and word-transfer items. Moreover, the posterior LIFG and its right homologue were also activated in the arbitrary-symbol-transfer condition.

4.1. Practice effects in the SPL

Previous studies suggest that the SPL is involved in coordination of spatial attention [90]. The right SPL was depicted in studies of mirror reading in English [2,54,72] and Japanese [28], suggesting its involvement in the visuo-spatial processing of new words. These findings are consistent with the activation of the SPL in reading our Morse-like script, which presumably relies mainly on the identification of the spatial sequencing of symbols.

The reduction in activation in the right SPL in trained items compared to transfer items, and in Latin letter-strings compared to artificial script, suggests that activation in the SPL decreased with the familiarity of the stimulus. Activation in the bilateral SPL was correlated with the individual's accuracy of performance only in transfer items, supporting the hypothesis that the SPL was required for processing transfer items more than for processing trained items. Previous studies showed decreased activation in the right SPL following training on a mirror reading task [54,72]. Two studies that compared brain activation patterns during the reading of Chinese alphabetical script (Pinyin) and Chinese non-alphabetical characters [17,41] found more

Table 4
Regions of activation in comparisons across conditions

Condition	Region	Broadman area	Hemisphere	z score	Voxels	x	y	z
Artificial script-Latin letter-strings:	*Inferior/middle occipital gyri/fusiform gyrus/cerebellum	17/19/37	L	Inf	5060	–28	–96	–18
	*Inferior/middle occipital gyri/fusiform gyrus/cerebellum	19/37	R	Inf	5693	36	–90	–16
	*Superior parietal lobule	7	R	6.97	608	22	–82	54
	*Paracentral lobule/postcentral gyrus	6/3	R	6.06	878	4	–34	60
	*Precentral gyrus	6	L	5.15	97	–58	2	48
	*Superior parietal lobule	7	L	4.7	114	–24	–80	56
	Insula	13	R	3.89	46	38	–14	8
	Precentral gyrus	4	R	3.71	39	48	–22	66
Trained-transfer:	No clusters of activation							
Transfer-trained:	Precuneus/superior parietal lobule	7	R	3.47	32	16	–84	52
	cerebellum	–	R	3.59	47	50	–44	–34

Clusters larger than 15 voxels are presented at a threshold of uncorrected $P < 0.001$. Clusters significant at a threshold of whole-brain corrected $P < 0.05$ are indicated in bold and a star.

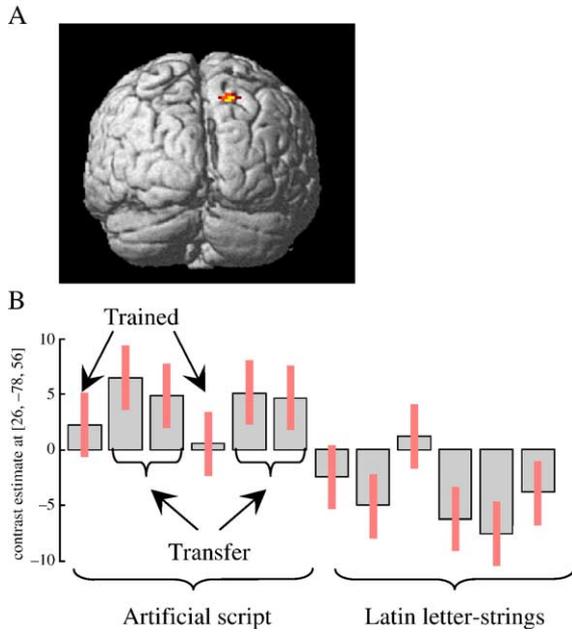


Fig. 10. (A) Brain regions showing more activation in the transfer compared to the trained items across all training conditions. (B) Signal change in the right superior parietal lobule.

activation in the right SPL for reading the less experienced Pinyin script. One may reasonably speculate that in the current study, less familiar items required the allocation of more attention to the visual search for the distinctive features compared to more familiar items. An alternative interpretation for the difference between Latin letter-strings and the artificial script in the SPL may be the difference in the visual characteristics of the stimuli, or the fact that the artificial script stimuli were presented before the Latin-letter-string, and may have activated working memory

processes. However, these interpretations cannot account for the differential activation in the SPL between trained and transfer items.

Altogether the pattern of activation in the right SPL represents two apparently conflicting trends. While activation in transfer items increased with the individual's accuracy of performance, activation in trained items decreased in spite of the higher accuracy of performance in trained compared to transfer items. These results suggest that training may have induced unique qualitative changes in task performance, and presumably a reliance on different processes, which could not be achieved without practice, even in highly competent individuals. Similar notions of switching in processing modes during different stages of experience have recently been posited in a number of tasks [56,73,82].

4.2. The LIFG in the explicit and arbitrary conditions

The explicit and arbitrary training conditions resulted in distinct patterns of brain activation, consistent with our behavioral findings in the current and previous studies [6,7]. The behavioral findings showed that training in the explicit condition resulted the acquisition of letter decoding knowledge (as suggested by the advantage for word-transfer over the letter-transfer test), while training in the arbitrary condition resulted in learning of word-specific patterns of symbol repetitions and symmetries (as indicated by a high level of performance in the symbol-transfer condition and an advantage of symbol-transfer over grapheme-transfer, in a previous experiment with a larger sample [7]). The fMRI results show that while the explicitly trained items activated a limited left-lateralized region in the occipital cortex, arbitrary trained items activated broad bilateral regions,

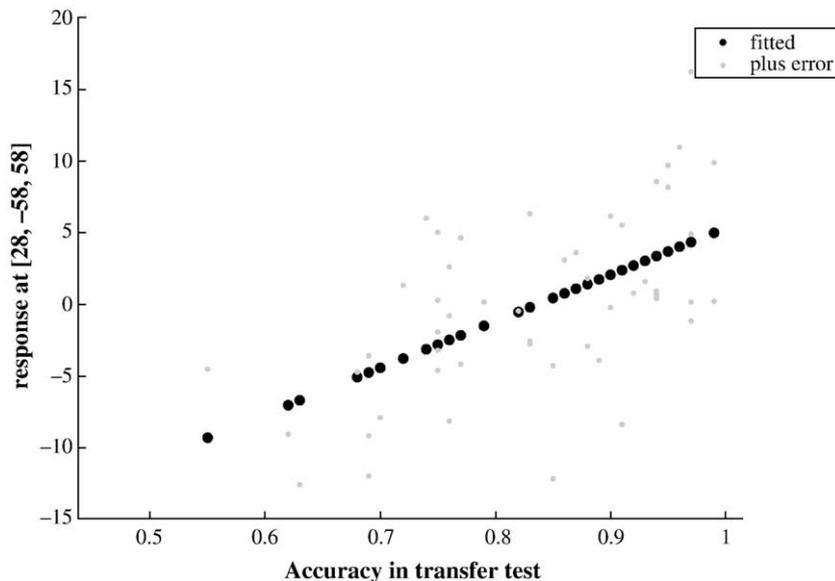


Fig. 11. The correlation of activation in the right SPL during reading of transfer items, with the individual's performance level in the transfer test.

mainly in the parietal lobes. These findings are consistent with previous studies showing left lateralized activation in alphabetical scripts, compared to right and bilateral activation in the non-alphabetical Chinese script [17,83], and with studies showing bilateral parietal activation in visuo-spatial working memory [28,54,57,72,88,90]. Our findings are also consistent with previous neuroimaging studies showing differential activation for alphabetical and non-alphabetical reading in natural script [4,31,32,63].

To differentiate alphabetical from non-alphabetical reading, we specifically focused on the comparison of the explicit-word-transfer and the arbitrary-word-transfer conditions, which reflected the contribution of letter decoding to reading in the behavioral studies. The stronger activation of the posterior LIFG in the explicit-word-transfer compared to the arbitrary-word-transfer condition suggests that this region is involved in letter decoding. A number of previous studies reported the involvement of the posterior LIFG in phonological processes [10,17,32,38,46,49,50,52,76,82,85], and specifically in tasks that require grapheme–phoneme conversion [18,27,31,41,63,72]. However, the complete absence of posterior LIFG activation in reading alphabetical words, given fully available letter knowledge, suggests that the reading of explicitly trained words did not rely on letter decoding in the same way that relatively new words did. Rather, our results are compatible with the proposal that sufficiently familiar alphabetical words were presumably identified mainly through word-specific recognition processes [80]. This interpretation is consistent with our behavioral evidence for some degree of word-specific knowledge in the explicit condition in addition to letter knowledge.

The activation in the posterior LIFG (and its right homologue) was also evident in the arbitrary-symbol-transfer condition, suggesting that the function of the posterior LIFG may be broader than the above notion of phonological decoding. Behaviorally, both the word-transfer in the explicit condition, and the symbol-transfer in the arbitrary condition showed an intermediate level of skilled performance (with higher performance in trained items, and lower performance in the other transfer conditions). This level of performance suggests that subjects were able to analyze and decode the symbol-strings, presumably according to their knowledge about regularities within the trained items. Thus, we propose that the posterior LIFG was activated in these conditions, perhaps, because they required the segmentation of the symbol-string into familiar subunits (either letters or clusters of symbol patterns). In addition, both conditions may have involved the mapping of the segmented subunits onto other representations—either letters onto phonemes in the explicit-word-transfer condition, or new symbols onto trained symbols in the arbitrary-symbol-transfer condition.

Previous studies have shown learning related changes in the activation of the posterior LIFG in the artificial-grammar-learning paradigm [34], that presumably requires learning of the mapping of untrained letters onto trained

letters [11,19,65,69,75]. Moreover, the posterior LIFG was found to be involved in the acquisition of grammar rules of an artificial language [85] as well as in processing syntax and grammar in patients with Broca's aphasia [39,45,55,81,84]. These findings are consistent with our proposal that the posterior LIFG (and probably its right hemisphere homologue) is involved in the analysis, segmentation and decoding of regularities within a sequence, and mapping of one type of subunits to another. Phonological segmentation and grapheme–phoneme mapping may, therefore, constitute just one aspect of this broader function.

Although the greater activation in the posterior LIFG in the explicit-word-transfer compared to the arbitrary-word transfer is associated with a higher level of accuracy in the scanner, the pattern of activation in other conditions suggest that activation in the posterior LIFG does not reflect a general effect of low task difficulty. For example, high accuracy in explicit-trained items (comparable to the explicit-word-transfer) was not associated with activation in the LIFG. Moreover, despite comparable levels of accuracy in the arbitrary-symbol transfer and explicit-symbol-transfer conditions, only the former showed activation of the posterior LIFG. An alternative interpretation for the activation of the posterior LIFG in the explicit-word-transfer and arbitrary-symbol-transfer conditions is that the phonological/articulatory representation of the target word was retrieved as a preparation for production [24]. However, this interpretation must assume that the articulatory representation was retrieved although voiced response was not required, but only in some conditions.

4.3. Interaction of alphabeticality and skill in trained items

Despite the lack of activation in the LIFG in explicit-trained items, our results show a different pattern of activation in explicitly trained words and in arbitrary trained words. In addition to the differential reading process (letter decoding vs. word-specific recognition), the distinct pattern of activation may be the result of different levels of skill in the reading process in the explicit and arbitrary trained items. Despite the equivalent amount of training and equivalent level of accuracy achieved by the end of training, our behavioral results suggest that reading in the explicit condition has reached a more advanced level of skilled reading, as reflected in higher preservation of learning gains in the explicit condition compared to the arbitrary condition, both in the long-term and between the training sessions [7]. The higher skill level in the explicit condition resulted, presumably, from the different number of repetitions on letters compared to words in the trained stimuli (each letter appears in 6 different words). We proposed that training in both conditions resulted in the formation of proceduralized routines for reading, with, however, the word recognition routine evolving at a slower rate compared to the letter-decoding routine. The less extensive activation in posterior visual and perceptual regions, in explicit-trained compared

to the arbitrary-trained items, may be the result of the more “automatic” routine in the explicit condition. This interpretation is consistent with findings of more extensive activation in reading a less skilled script, regardless of the alphabeticality of the language [16].

4.4. *Implicit vs. explicit instructions*

The pattern of activation in the implicit condition showed similarities to the patterns of activation evoked by both the arbitrary and explicit conditions. The implicit condition was similar to the arbitrary condition in showing robust bilateral activation. Furthermore, in similarity to the arbitrary condition, all types of items in the implicit condition showed activation in parietal regions along the intraparietal sulci, suggesting the involvement of visuo-spatial processing [54,57,72,88]. In addition, both the arbitrary and implicit conditions showed robust cerebellar activation. This finding is consistent with previous studies showing cerebellar involvement in mirror reading [71] as well as in orthographic, phonological and semantic processing in natural script [33,42,92].

In similarity to the explicit condition, the implicit word-transfer condition showed activation in the left posterior IFG, suggesting some reliance on letter decoding in reading (in light of the above interpretation of the explicit vs. arbitrary comparison). However, in contrast to the explicit condition, activation in the left posterior IFG was evident also in implicit-trained items, suggesting that letter decoding in the implicit condition persisted even in reading trained words. Moreover, activation in the left posterior IFG during reading of implicit-trained items was correlated with the individual’s effective letter knowledge (measured behaviorally as the difference between word-transfer and letter-transfer ratios). This finding supports the interpretation that the activation in the left posterior IFG in reading alphabetical words is associated with letter knowledge, and the conclusion that reading implicit-trained items involved letter decoding. Altogether, the pattern of activation in the implicit condition suggests that learning involved word-specific pattern recognition, as well as letter decoding. However, the acquisition of letter knowledge may have been less effective in the implicit compared to the explicit condition, resulting in the reliance on letter decoding, even for reading implicit-trained items.

In the current study, no significant difference in accuracy was found between word-transfer and letter-transfer in the implicit condition, however, in similarity to the explicit condition, performance in the implicit condition was more accurate than in the arbitrary condition. This mixed pattern of results may suggest the acquisition of letter knowledge in a small number of participants or a minimal level of letter knowledge in the entire group. The small sample and large variability among individuals prevent a clear conclusion. However, the mixed pattern of activation in the implicit condition is consistent with the behavioral findings of our

previous study [7]. The implicit condition resulted in word-specific recognition knowledge in all participants, in addition to letter knowledge in some individuals, that was, however, less effective than the explicitly instructed letter knowledge [7]. It may be hypothesized that the mixed learning of both word and letter units in the implicit condition resulted in less intensive practice on the letters, and less effective letter knowledge. Thus, our behavioral as well as our brain activation findings suggest that letter decoding acquired in the implicit condition was less effective than that acquired in the explicit condition. Previous studies have also found different patterns of brain activation in explicit and implicit training conditions [1,44,48,74]. However, rather than reflecting the difference in “awareness”, we propose that the different patterns of activation in explicit and implicit training in the current study reflect the differential amounts of practice on the relevant units (letters).

4.5. *Fusiform and supramarginal gyri*

Many studies that investigated single word reading reported activation in the fusiform gyrus, which was associated with the recognition of the orthographic pattern of familiar words prior to lexical access [4,9,17,25,26,31,64,77]. In the current study, we did not observe any consistent activation in the fusiform gyrus area. This lack of activation may be the result of insufficient training received in the current study, which is presumably required to induce a representation in this part of the cortex, typically associated with visual processing of highly familiar object categories in experts [26,31,43].

A number of word reading studies showed activation in the left angular and supramarginal gyri (SMG), claimed to be associated with mapping of orthography to phonology [9,32,41,59,76]. In the current study, these regions were not activated in the explicit-word-transfer condition that presumably entailed grapheme–phoneme conversion. Rather, the angular gyrus and SMG were activated bilaterally in the arbitrary-trained and arbitrary-symbol-transfer conditions, which do not afford letter decoding. An alternative interpretation of the results, that may account for the activation of the SMG in the arbitrary rather than in the explicit condition, is that letter decoding in the explicit condition involved mapping from the artificial letters to Latin letters, rather than mapping of letters to phonemes. In spite of the efforts to enhance the association of letters to phonemes by requiring the pronunciation of the target words and letters, participants may have reverted to mapping artificial letters to familiar Latin letters in the explicit condition. This shortcut may have been too demanding in the arbitrary condition due to the higher visual complexity of whole words, resulting in mapping of orthography to phonology in the arbitrary condition. Hence, it may be suggested that the SMG was activated in the arbitrary and not in the explicit condition since it is involved in the

conversion of orthography to phonology regardless of the size of the units (i.e., letters or words). The posterior LIFG, on the other hand, may be involved in the segmentation and mapping of units, regardless of their modality, and hence it was activated in the explicit-word-transfer and arbitrary-symbol-transfer conditions.

5. Conclusions

Our results suggest that the posterior LIFG is involved in letter decoding as part of its broader function in segmentation and decoding of sequences. The results provide a neural support for the notion that reading of well-trained alphabetical words does not rely on letter decoding. Nevertheless, our results suggest that even when reading of trained alphabetical words is done with minimal recourse to letter decoding, it may still elicit a different pattern of activation from reading non-alphabetical words because of a difference in the evolution of the reading routine. Consistent with our behavioral findings, the fMRI results suggest that implicit training on alphabetical words resulted in less effective letter knowledge, with letter decoding persisting even to the reading of trained words.

The critical effect of the amount of practice was also demonstrated in the pattern of activation in the right superior parietal lobules. Our results showed that the individual's level of competence in reading relatively novel artificial script words, and their amount of experience with reading specific trained words, have independent and opposite effects on the activation in the right SPL. This finding further emphasizes the unique effect of experience, which continues to shape performance even in competent readers. Altogether, our findings suggest that the neural processes involved in reading a given word and the pattern of brain activation elicited by its presentation are determined by the interaction of the alphabeticality of the word, the type of instruction received by the reader during the acquisition of reading (explicit or implicit) and the amount of practice afforded for the specific word.

Acknowledgments

This research was conducted while the first author was affiliated with the Neurobiology department in Weizmann Institute, Israel. The authors would like to thank Dr. James Booth for his valuable comments on the manuscript.

References

- [1] H.J. Aizenstein, A.W. MacDonald, V.A. Stenger, R.D. Nebes, J.K. Larson, S. Ursu, C.S. Carter, Complementary category learning systems identified using event-related functional MRI, *J. Cogn. Neurosci.* 12 (2000) 977–987.
- [2] B. Alivisatos, M. Petrides, Functional activation of the human brain during mental rotation, *Neuropsychologia* 35 (1997) 111–118.
- [3] N.J. Benson, M.W. Lovett, C.L. Kroeber, Training and transfer-of-learning effects in disabled and normal readers: evidence of specific deficits, *J. Exp. Child Psychol.* 64 (1997) 343–366.
- [4] J.R. Binder, K.A. McKiernan, M.E. Parsons, C.F. Westbury, E.T. Possing, J.N. Kaufman, L. Buchanan, Neural correlates of lexical access during visual word recognition, *J. Cogn. Neurosci.* 15 (2003) 372–393.
- [5] C. Bishop, Transfer effects of word and letter training in reading, *J. Verbal Learn. Verbal Behav.* 3 (1964) 214–221.
- [6] T. Bitan, A. Karni, Alphabetical knowledge from whole words training: effects of explicit instruction and implicit experience on learning script segmentation, *Cogn. Brain Res.* 16 (2003) 323–337.
- [7] T. Bitan, A. Karni, Procedural and declarative knowledge of word recognition and letter decoding in reading an artificial script, *Cogn. Brain Res.* 19 (2004) 229–243.
- [8] J.R. Booth, C.A. Perfetti, B. MacWhinney, Quick, automatic, and general activation of orthographic and phonological representations in young readers, *Dev. Psychol.* 35 (1999) 3–19.
- [9] J.R. Booth, D.D. Burman, J.R. Meyer, D.R. Gitelman, T.B. Parrish, M.M. Mesulam, Relation between brain activation and lexical performance, *Hum. Brain Mapp.* 19 (2003) 155–169.
- [10] M.W. Burton, S.L. Small, S.E. Blumstein, The role of segmentation in phonological processing: an fMRI investigation, *J. Cogn. Neurosci.* 12 (2000) 679–690.
- [11] L.T. Butler, D.C. Berry, Implicit memory: intention and awareness revisited, *Trends Cogn. Sci.* 5 (2001) 192–197.
- [12] B. Byrne, Studies in the acquisition procedure: rationale, hypotheses and data, in: P.B. Gough, L.C. Ehri, R. Treiman, University of Texas at Austin. Center for Cognitive Science (Eds.), *Reading Acquisition*, L. Erlbaum Associates, Hillsdale, NJ, 1992, pp. 1–34.
- [13] B. Byrne, R. Fielding-Barnsley, Phonemic awareness and letter knowledge in the child's acquisition of the alphabetic principle, *J. Educ. Psychol.* 81 (1989) 313–321.
- [14] B. Byrne, R. Fielding-Barnsley, L. Ashley, Effects of preschool phoneme identity training after six years: outcome level distinguished from rate of response, *J. Educ. Psychol.* 92 (2000) 659–667.
- [15] D.W. Carnine, Phonics versus look–say: transfer to new words, *Read. Teach.* 30 (6) (1977) 636–640 (Mar 77).
- [16] M.W. Chee, N. Hon, H.L. Lee, C.S. Soon, Relative language proficiency modulates BOLD signal change when bilinguals perform semantic judgments, blood oxygen level dependent, *NeuroImage* 13 (2001) 1155–1163.
- [17] Y. Chen, S. Fu, S.D. Iversen, S.M. Smith, P.M. Matthews, Testing for dual brain processing routes in reading: a direct contrast of Chinese character and Pinyin Reading using fMRI, *J. Cogn. Neurosci.* 14 (2002) 1088–1098.
- [18] D. Clark, A.D. Wagner, Assembling and encoding word representations: fMRI subsequent memory effects implicate a role for phonological control, *Neuropsychologia* 41 (2003) 304–317.
- [19] A. Cleeremans, A. Destrebecqz, M. Boyer, Implicit learning: news from the front, *Trends Cogn. Sci.* 2 (1998) 406–416.
- [20] M. Coltheart, Lexical access in simple reading tasks, in: G. Underwood (Ed.), *Strategies of Information Processing*, Academic Press, London, 1978, pp. 151–216.
- [21] M. Coltheart, K. Rastle, Serial processing in reading aloud—evidence for dual-route models of reading, *J. Exp. Psychol. Hum.* 20 (1994) 1197–1211.
- [22] M. Coltheart, et al., Models of reading aloud: dual-route and parallel-distributed-processing approaches, *Psychol. Rev.* 100 (1993) 589–608.
- [23] M. Coltheart, K. Rastle, C. Perry, R. Langdon, J. Ziegler, DRC: a dual route cascaded model of visual word recognition and reading aloud, *Psychol. Rev.* 108 (2001) 204–256.
- [24] A.R. Damasio, N. Geschwind, The neural basis of language, *Annu. Rev. Neurosci.* 7 (1984) 127–147.

- [25] H. Damasio, T.J. Grabowski, D. Tranel, R.D. Hichwa, A.R. Damasio, A neural basis for lexical retrieval. [see comment] [erratum appears in *Nature* 1996 Jun 27;381(6595):810], *Nature* 380 (1996) 499–505.
- [26] S. Dehaene, H.G. Le Clec, J.B. Poline, D. Le Bihan, L. Cohen, The visual word form area: a prelexical representation of visual words in the fusiform gyrus, *NeuroReport* 13 (2002) 321–325.
- [27] J.F. Demonet, F. Chollet, S. Ramsay, D. Cardebat, J.L. Nespoulous, R. Wise, A. Rascol, R. Frackowiak, The anatomy of phonological and semantic processing in normal subjects, *Brain* 115 (1992) 1753–1768.
- [28] Y. Dong, H. Fukuyama, M. Honda, T. Okada, T. Hanakawa, K. Nakamura, Y. Nagahama, T. Nagamine, J. Konishi, H. Shibasaki, Essential role of the right superior parietal cortex in Japanese kana mirror reading: an fMRI study, *Brain* 123 (2000) 790–799.
- [29] L.C. Ehri, J. Sweet, Fingerpoint-reading of memorized text: what enables beginners to process the print? *Read. Res. Q.* 26 (1991) 442–462.
- [30] L.C. Ehri, L.S. Wilce, Movement into reading: is the first stage of printed word learning visual or phonetic? *Read. Res. Q.* 20 (1985) 163–179.
- [31] C.J. Fiebach, A.D. Friederici, K. Muller, D.Y. von Cramon, fMRI evidence for dual routes to the mental lexicon in visual word recognition, *J. Cogn. Neurosci.* 14 (2002) 11–23.
- [32] J.A. Fiez, S.E. Petersen, Neuroimaging studies of word reading, *Proc. Natl. Acad. Sci. U. S. A.* 95 (1998) 914–921.
- [33] J.A. Fiez, S.E. Petersen, M.K. Cheney, M.E. Raichle, Impaired nonmotor learning and error-detection associated with cerebellar damage—a single case-study, *Brain* 115 (1992) 155–178.
- [34] P. Fletcher, C. Buchel, O. Josephs, K. Friston, R. Dolan, Learning-related neuronal responses in prefrontal cortex studied with functional neuroimaging, *Cereb. Cortex* 9 (1999) 168–178.
- [35] B.R. Foorman, Research on “The Great Debate”: code-oriented versus whole language approaches to reading instruction, *Sch. Psychol. Rev.* 24 (1995) 376–392.
- [36] B.R. Foorman, et al., How letter–sound instruction mediates progress in first-grade reading and spelling, *J. Educ. Psychol.* 83 (1991) 456–469.
- [37] B.R. Foorman, D.J. Francis, J.M. Fletcher, P. Mehta, C. Schatschneider, The role of instruction in learning to read: preventing reading failure in at-risk children, *J. Educ. Psychol.* 90 (1998) 37–55.
- [38] A.D. Friederici, The neurobiology of language comprehension, in: A.D. Friederici (Ed.), *Language Comprehension: A Biological Perspective*, Springer, Berlin, 1998, pp. 263–301.
- [39] N. Friedmann, Agrammatism and the psychological reality of the syntactic tree, *J. Psycholinguist. Res.* 30 (2001) 71–90.
- [40] U. Frith, Beneath the surface of developmental dyslexia, in: K. Patterson, J.C. Marshall, M. Coltheart (Eds.), *Surface Dyslexia: Neuropsychological and Cognitive Studies of Phonological Reading*, Lawrence Erlbaum Associates, London, 1985, pp. 301–330.
- [41] S. Fu, Y. Chen, S. Smith, S. Iversen, P.M. Matthews, Effects of word form on brain processing of written Chinese, *NeuroImage* 17 (2002) 1538–1548.
- [42] R. Fulbright, The cerebellum’s role in reading: a functional MR imaging study, *AJNR, Am. J. Neuroradiol.* 20 (1999) 1925–1930.
- [43] I. Gauthier, P. Skudlarski, J.C. Gore, A.W. Anderson, Expertise for cars and birds recruits brain areas involved in face recognition, *Nat. Neurosci.* 3 (2000) 191–197.
- [44] S.T. Grafton, E. Hazeltine, R. Ivry, Functional mapping of sequence learning in normal humans, *J. Cogn. Neurosci.* 7 (1995) 497–510.
- [45] Y. Grodzinsky, The neurology of syntax: language use without Broca’s area, *Behav. Brain Sci.* 23 (2000) 1–21 (discussion 21–71).
- [46] P. Hagoort, P. Indefrey, C. Brown, H. Herzog, H. Steinmetz, R.J. Seitz, The neural circuitry involved in the reading of German words and pseudowords: a PET study, *J. Cogn. Neurosci.* 11 (1999) 383–398.
- [47] M.W. Harm, M.S. Seidenberg, Phonology, reading acquisition, and dyslexia: insights from connectionist models, *Psychol. Rev.* 106 (1999) 491–528.
- [48] E. Hazeltine, S.T. Grafton, R. Ivry, Attention and stimulus characteristics determine the locus of motor-sequence encoding. A PET study, *Brain* 120 (1997) 123–140.
- [49] S. Heim, B. Opitz, K. Muller, A.D. Friederici, Phonological processing during language production: fMRI evidence for a shared production–comprehension network, *Brain Res. Cogn. Brain Res.* 16 (2003) 285–296.
- [50] A.N. Herbster, M.A. Mintun, R.D. Nebes, J.T. Becker, Regional cerebral blood flow during word and nonword reading, *Hum. Brain Mapp.* 5 (1997) 84–92.
- [51] F. Hutzler, J.C. Ziegler, C. Perry, H. Wimmer, M. Zorzi, Do current connectionist learning models account for reading development in different languages? *Cognition* 91 (2004) 273–296.
- [52] P. Indefrey, W.J.M. Levelt, The neural correlates of language production, in: M.S. Gazzaniga (Ed.), *The New Cognitive Neuroscience*, MIT Press, Cambridge, MA, 2000, pp. 845–865.
- [53] W.E. Jeffrey, S.J. Samuels, Effect of Method of Reading Training on Initial Learning and Transfer, *J. Verbal Learn. Verbal Behav.* 6 (1967) 354–358.
- [54] J. Kassubek, K. Schmidtke, H. Kimmig, C.H. Lucking, M.W. Greenlee, Changes in cortical activation during mirror reading before and after training: an fMRI study of procedural learning, *Cogn. Brain Res.* 10 (2001) 207–217.
- [55] M.-L. Kean, *Agrammatism*, Academic Press, Orlando, 1985 (xiii, 266 pp.).
- [56] M. Korman, N. Raz, T. Flash, A. Karni, Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance, *Proc. Natl. Acad. Sci. U. S. A.* 100 (2003) 12492–12497.
- [57] S.M. Kosslyn, N.M. Alpert, W.L. Thompson, C.F. Chabris, S.L. Rauch, A.K. Anderson, Identifying objects seen from different viewpoints. A PET investigation, *Brain* 117 (1994) 1055–1071.
- [58] S. Koyama, R. Kakigi, M. Hoshiyama, Y. Kitamura, Reading of Japanese Kanji (morphograms) and Kana (syllabograms): a magnetoencephalographic study, *Neuropsychologia* 36 (1998) 83–98.
- [59] I. Law, I. Kannao, H. Fujita, N.A. Lassen, S. Miura, K. Uemura, Left supramarginal/angular gyri activation during reading of syllabograms in the Japanese language, *J. Neurolinguist.* 6 (1991) 243–251.
- [60] G. Lukatela, M.T. Turvey, Visual lexical access is initially phonological: 1. Evidence from associative priming by words, homophones, and pseudohomophones, *J. Exp. Psychol. Gen.* 123 (1994) 107–128.
- [61] J.A. Maldjian, P.J. Laurienti, R.A. Kraft, J.H. Burdette, An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets, *NeuroImage* 19 (2003) 1233–1239.
- [62] J.A. Maldjian, P.J. Laurienti, J.H. Burdette, Precentral gyrus discrepancy in electronic versions of the Talairach atlas, *NeuroImage* 21 (2004) 450–455.
- [63] A. Mechelli, M.L. Gorno-Tempini, C.J. Price, Neuroimaging studies of word and pseudoword reading: consistencies, inconsistencies, and limitations, *J. Cogn. Neurosci.* 15 (2003) 260–271.
- [64] A.C. Nobre, T. Allison, G. McCarthy, Word recognition in the human inferior temporal lobe, *Nature* 372 (1994) 260–263.
- [65] S. Pacton, P. Perruchet, M. Fayol, A. Cleeremans, Implicit learning out of the lab: the case of orthographic regularities, *J. Exp. Psychol.: General* 130 (2001) 401–426.
- [66] T.C. Papadopoulos, Phonological and cognitive correlates of word-reading acquisition under two different instructional approaches in Greek, *Eur. J. Psychol. Educ.* 16 (2001) 549–568.
- [67] C.A. Perfetti, The representation problem in reading acquisition, in: P.B. Gough, L.C. Ehri, R. Treiman, University of Texas at Austin. Center for Cognitive Science (Eds.), *Reading Acquisition*, L. Erlbaum Associates, Hillsdale, NJ, 1992, pp. 145–174.
- [68] C.A. Perfetti, L. Bell, Phonemic activation during the 1st 40 Ms of word identification—Evidence from backward-masking and priming, *J. Mem. Lang.* 30 (1991) 473–485.

- [69] P. Perruchet, C. Pacteau, Synthetic grammar learning—implicit rule abstraction or explicit fragmentary knowledge, *J. Exp. Psychol. Gen.* 119 (1990) 264–275.
- [70] D.C. Plaut, J.L. McClelland, M.S. Seidenberg, K. Patterson, Understanding normal and impaired word reading: computational principles in quasi-regular domains, *Psychol. Rev.* 103 (1996) 56–115.
- [71] R.A. Poldrack, J.D.E. Gabrieli, Characterizing the neural mechanisms of skill learning and repetition priming: evidence from mirror reading, *Brain* 124 (2001) 67–82.
- [72] R.A. Poldrack, J.E. Desmond, G.H. Glover, J.D. Gabrieli, The neural basis of visual skill learning: an fMRI study of mirror reading, *Cereb. Cortex* 8 (1998) 1–10.
- [73] M.E. Raichle, J.A. Fiez, T.O. Videen, A.M. MacLeod, J.V. Pardo, P.T. Fox, S.E. Petersen, Practice-related changes in human brain functional anatomy during nonmotor learning, *Cereb. Cortex* 4 (1994) 8–26.
- [74] P.J. Reber, D.R. Gitelman, T.B. Parrish, M.M. Mesulam, Dissociating explicit and implicit category knowledge with fMRI, *J. Cogn. Neurosci.* 15 (2003) 574–583.
- [75] M. Redington, N. Chater, Transfer in artificial grammar learning: a reevaluation, *J. Exp. Psychol. Gen.* 125 (1996) 123–138.
- [76] J.M. Rumsey, B. Horwitz, B.C. Donohue, K. Nace, J.M. Maisog, P. Andreason, Phonological and orthographic components of word recognition. A PET-rCBF study, *Brain* 120 (1997) 739–759.
- [77] Y. Sakurai, T. Momose, M. Iwata, Y. Sudo, K. Ohtomo, I. Kanazawa, Different cortical activity in reading of Kanji words, Kana words and Kana nonwords, *Cogn. Brain Res.* 9 (2000) 111–115.
- [78] Y. Sakurai, T. Momose, M. Iwata, Y. Sudo, Y. Kumakura, K. Ohtomo, I. Kanazawa, Cortical activation in reading assessed by region of interest-based analysis and statistical parametric mapping, *Brain Research, Brain Res. Protoc.* 6 (2001) 167–171.
- [79] M.S. Seidenberg, D.C. Plaut, A.S. Petersen, J.L. McClelland, K. McRae, Nonword pronunciation and models of word recognition, *J. Exp. Psychol. Hum. Percept. Perform.* 20 (1994) 1177–1196.
- [80] D.L. Share, Phonological recoding and self-teaching: sine qua non of reading acquisition, *Cognition* 55 (1995) 151–218 (discussion 219–226).
- [81] A. Sirigu, L. Cohen, T. Zalla, P. Pradat-Diehl, P. Van Eeckhout, J. Grafman, Y. Agid, Distinct frontal regions for processing sentence syntax and story grammar, *Cortex* 34 (1998) 771–778.
- [82] R. Sosnik, B. Hauptmann, T. Flash, A. Karni, The evolution of versatile but effector specific novel motor trajectories in adults, *Abstr. - Soc. Neurosci.* 27 (2001) (Program no. 939.7).
- [83] L.H. Tan, J.A. Spinks, C.M. Feng, W.T. Siok, C.A. Perfetti, J. Xiong, P.T. Fox, J.H. Gao, Neural systems of second language reading are shaped by native language, *Hum. Brain Mapp.* 18 (2003) 158–166.
- [84] R.W. Taubner, A.M. Raymer, K.M. Heilman, Frontal–opercular aphasia, *Brain Lang.* 70 (1999) 240–261.
- [85] M. Tettamanti, H. Alkadhi, A. Moro, D. Perani, S. Kollias, D. Weniger, Neural correlates for the acquisition of natural language syntax, *NeuroImage* 17 (2002) 700–709.
- [86] G.B. Thompson, D.S. Cottrell, C.M. Fletcher-Flinn, Sublexical orthographic–phonological relations early in the acquisition of reading: the knowledge sources account, *J. Exp. Child Psychol.* 62 (1996) 190–222.
- [87] G.B. Thompson, C.M. Fletcher-Flinn, D.S. Cottrell, Learning correspondences between letters and phonemes without explicit instruction, *Appl. Psycholinguist.* 20 (1999) 21–50.
- [88] L.G. Ungerleider, S.M. Courtney, J.V. Haxby, A neural system for human visual working memory, *Proc. Natl. Acad. Sci. U. S. A.* 95 (1998) 883–890.
- [89] G.C. Van Orden, B.F. Pennington, G.O. Stone, Word identification in reading and the promise of subsymbolic psycholinguistics, *Psychol. Rev.* 97 (1990) 488–522.
- [90] T.D. Wager, E.E. Smith, Neuroimaging studies of working memory: a meta-analysis, *Cogn. Affect. Behav. Neurosci.* 3 (2003) 255–274.
- [91] R. Wesseling, P. Reitsma, The transient role of explicit phonological recoding for reading acquisition, *Read. Writ.* 13 (2000) 313–336.
- [92] H.D. Xiang, C.Y. Lin, X.H. Ma, Z.Q. Zhang, J.M. Bower, X.C. Weng, J.H. Gao, Involvement of the cerebellum in semantic discrimination: an fMRI study, *Hum. Brain Mapp.* 18 (2003) 208–214.