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Research Report

Polysyllabic pseudo-word processing in reading and lexical decision: Converging evidence from behavioral data, connectionist simulations and functional MRI

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ABSTRACT

The cognitive mechanisms involved in polysyllabic pseudo-word processing—and their neurobiological correlates—were studied through the analysis of length effects on French words and pseudo-words in reading and lexical decision. Connectionist simulations conducted on the ACV98 network (Ans, B., Carbonnel, S., Valdois, S., 1998. A connectionist multiple-trace memory model for polysyllabic word reading. Psychol. Rev. 105, 678–723) paralleled the behavioral data in showing a strong length effect on naming latencies for pseudo-words only and the absence of length effect for both words and pseudo-words in lexical decision. Length effects in reading were characterized at the neurobiological level by a significant and specific activity increase for pseudo-words as compared to words in the right lingual gyrus (BA 19), the left superior parietal lobule and precuneus (BA7), the left middle temporal gyrus (BA21) and the left cerebellum. The behavioral results suggest that polysyllabic pseudo-word reading mainly relies on an analytic procedure. At the biological level, additional activations in visual and visual attentional brain areas during long pseudo-word reading emphasize the role of visual and visual attentional processes in pseudo-word reading. The present findings place important constraints on theories of reading in suggesting the involvement of a serial mechanism based on visual attentional processing in pseudo-word reading.

1. Introduction

The cognitive mechanisms underlying word recognition and reading have been intensively studied in recent years together with their cerebral correlates. A number of theoretical models—as the dual-route model (Coltheart et al., 1993, 2001), the PDP connectionist models (Harm and Seidenberg, 1999; Plaut et al., 1996; Seidenberg and McClelland, 1989) or the multitrace memory model (Ans et al., 1998)—based on distinct hypotheses about the structure of the cognitive reading system have been proposed to account for reading performance. However, most neuro-imaging data have been carried

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out within the dual-route framework (Jobard et al., 2003; Price et al., 2003). Through the analysis of length effects in reading and lexical decision, the current paper show evidence that, apart from dual-route models, connectionist models also provide a theoretical framework for the investigation of the neurological correlates of the reading system.

Our aim in the present paper was to study the cognitive mechanisms specifically involved in the processing of polysyllabic pseudo-words and to identify their neurobiological correlates. Length effects on words and pseudo-words in reading and lexical decision were studied for this purpose. Several experimental studies have investigated length effects in reading and/or lexical decision (Balota et al., 2004; Forster and Chambers, 1973; Hudson and Bergman, 1985; Klapp et al., 1973; Plaut, 1998; Spieler and Balota, 1997; Spoehr and Smith, 1973; Ziegler et al., 2001). In reading, length effect seems to be modulated by word frequency and varies according to the lexicality of the item to be read: an effect of number of syllables has been reported for low frequency words but not for high frequency words (Content and Peereman, 1993; Ferrand, 2000; Ferrand and New, 2003; Jared and Seidenberg, 1990; Mason, 1978). Strong length effects on naming latencies were consistently reported for pseudo-words (Ans et al., 1998; Mason, 1978; Ferrand, 2000; Ferrand and New, 2003; Weekes, 1997). A few data further suggest that length effects differentially affect brain activity during word and pseudo-word processing in reading (Baciu et al., 2001). With respect to lexical decision, no syllable length effect was reported for either words or pseudo-words (Ferrand and New, 2003; Frederiksen and Kroll, 1976; Richardson, 1976; see however New et al., submitted for publication).

The study was conducted within the framework of the connectionist multitrace memory model for polysyllabic word reading (Ans et al., 1998). The model postulates that two types of reading procedures, a global and an analytic procedure, are required for processing all kinds of letter strings. In contrast to the dual-route model, however, the two procedures operate according to a common set of computational principles and they do not work in parallel. Global processing always proceeds first, the analytic procedure applying only secondarily when global processing has failed. An orthographic and a phonological output are simultaneously generated following global processing. The phonological output is accepted as the global pronunciation of the input string if the orthographic output generated during processing is strictly identical to the orthographic input. When the two orthographic patterns differ, then the phonological output is inhibited and the system shifts in analytic mode. The system then processes the initial part of the input string which has been accurately recreated in output and processing is sequentially reiterated until the end of the sequence.

The two procedures mainly differ in the kind of visual attentional processing they involve. The whole orthographic object forms the focal window in global processing, whereas the visual attentional window is reduced to parts of the orthographic sequence, typically syllables, in analytic processing. Although the two procedures are not a priori dedicated to the processing of a particular type of letter string (real word or pseudo-word), it happens that most familiar words are processed as a whole, whereas global processing typically fails for pseudo-words. The system then shifts in the analytic mode and the pseudo-word is sequentially processed. The model thus does not predict any syllable length effect in familiar word naming, but a strong syllable length effect is expected in pseudo-word naming.

As all cognitive models, the ACV98 theoretical framework does not make clear-cut predictions at the neural level. However, one might expect that a similar network of cerebral regions should be activated during word naming whatever their length, if all familiar words were read globally. In contrast, cerebral activation should differ as a function of pseudo-word length. In the analytic processing of polysyllabic pseudo-words, each new syllable requires a new visual attentional capture for its pronunciation to be computed. Accordingly, the higher the number of syllables of a pseudo-word, the stronger should be the brain activation in the cerebral regions involved in visual and visual attentional processing.

The predictions are quite different with respect to lexical decision. Indeed, a decision about the familiarity of the input string is made on the basis of the orthographic output generated in global mode. If this orthographic output is strictly identical to the orthographic input, then a Yes response will follow. A No decision will be made when the orthographic output differs from the orthographic input. It follows that lexical decision only depends on processing in global mode, so that no syllable length effect should affect response latencies whatever the items' length or lexicality (words or pseudo-words). Thus, no additional brain regions should be activated when processing longer items as compared to shorter ones in lexical decision.

In the present study, the ACV98's predictions have been assessed using both behavioral and brain activation measures. Simulations were further conducted in order to check the theoretical predictions of the model. Experiment 1 used behavioral measures—reaction times (RTs) and error rates—to assess length effects in reading and lexical decision. The participants were presented with 72 words and 72 pseudo-words mixed with fillers. The experimental items varied in length from one to three syllables and from 4 to 11 letters. Two groups of young adults participated in the experiment: the first group was assessed in reading, the second in lexical decision. In reading, the participants were asked to read aloud the stimuli as quickly and as accurately as possible. In lexical decision, they had to judge whether or not each stimulus was a real French word. Reaction times and accuracy of response were recorded for each stimulus. Simulations of the reading and lexical decision performance were further conducted on the ACV98 network using the same set of items.

Experiment 2 assessed length effects using the event-related fMRI while participants performed the same reading and lexical decision tasks. Twenty healthy volunteers were examined: twelve during reading, eight during lexical decision. All were right-handed native French speakers with good reading level and normal or corrected to normal vision. The event-related fMRI paradigm (ER-fMRI) was used because this technique allows mixing several types of stimuli. Thus, it was possible to present within the same functional scan six types of stimuli (words and pseudo-words composed of one, two or three syllables). During the fMRI session, the participants belonging to the "reading" group were asked to read each item internally, without articulating or vocalizing.

2. Results

2.1. *Experiment 1 (behavioral data)*

2.1.1. *Reaction time analyses*

Reaction times (RTs) for the experimental words and pseudo-words were analyzed, and those for the items (7.7%) yielding erroneous responses or recording errors were discarded. Mean RTs were analyzed by participants (F1) and by items (F2). An ANOVA including Task (reading or lexical decision) as between-subject factor, and Lexicality (word or pseudo-word) and Length (1-, 2- or 3-syllables) as within-subject factors was used in the analysis. The mean RTs recorded in reading and lexical decision for words and pseudo-words of 1, 2 and 3 syllables are presented in Fig. 1A.

In reading, the analysis revealed a main lexicality effect on naming latencies. RTs were 162.1 ms longer on average for pseudo-words (F1(1,42) = 194.15, MSE = 4466.87, $P < 0.00001$; F2 (1,120) = 432.16, MSE = 1945.04, $P < 0.000001$). Length effect interacted with lexicality (F1(2.84) = 42.45, MSE = 1112.22, $P < 0.00001$; F2(2,120) = 22.9, MSE = 1945.04, $P < 0.00001$) showing that RTs were far more affected by length for pseudo-words than for words. A slight but significant length effect was found for words in the by-subjects analysis only (F1 (2,84) = 10.11, MSE = 516.6, $P < 0.0002$; F2(2,120) = 2.79, MSE = 1945.04, $P = 0.07$). For the pseudo-words, length effect was highly significant by subjects (F1(2,84) = 73.36, MSE = 1944.73, $P < 0.00001$) and by items (F2(2,120) = 70.76, MSE = 1945.04, $P < 0.00001$). A highly significant Length by Lexicality interaction was obtained when the analysis was restricted to 1- to 3-syllable items (F1(1,42) = 55.44, MSE = 1594.02, $P < 0.00001$; F2(1,120) = 43.08, MSE = 1945.04, $P < 0.00001$). Planned comparisons revealed that naming RTs were slightly longer for 3-syllable words than for 1-syllable words (diff = 30.82 ms; F1(1,42) = 21.38, MSE = 488.52, $P < 0.00004$; F2(1,120) = 5.56, MSE = 1945.04, $P < 0.03$). In contrast, 3-syllable pseudo-word naming yielded far longer latencies than 1-syllable pseudo-word naming (diff = 157.58 ms; F1 (1,42) = 89.84, MSE = 3040.14, $P < 0.00001$; F2(1,120) = 135.48, MSE = 1945.04, $P < 0.00001$). Overall, the present findings show far stronger length effects on naming latency for pseudo-words than for words.

In lexical decision, the analysis revealed a main lexicality effect of 84.6 ms (F1(1,42) = 52.84, MSE = 4466.87, $P < 0.00001$; F2(1,120) = 96.55, MSE = 2227.32, $P < 0.00001$). A marginally significant interaction was found between length and lexicality when the analysis included the three length levels (F1(2,84) = 3.2, MSE = 1112.22, $P < 0.05$; F2(2,120) = 1.58, MSE = 2227.32, $P = 0.21$). As for words, length effect was significant by subjects only (F1(2,84) = 9.6, MSE = 516.6, $P < 0.0002$; F2(2,120) = 2.69, MSE = 2227.32, $P = 0.08$); the effect was significant by subjects and by items for the pseudo-words

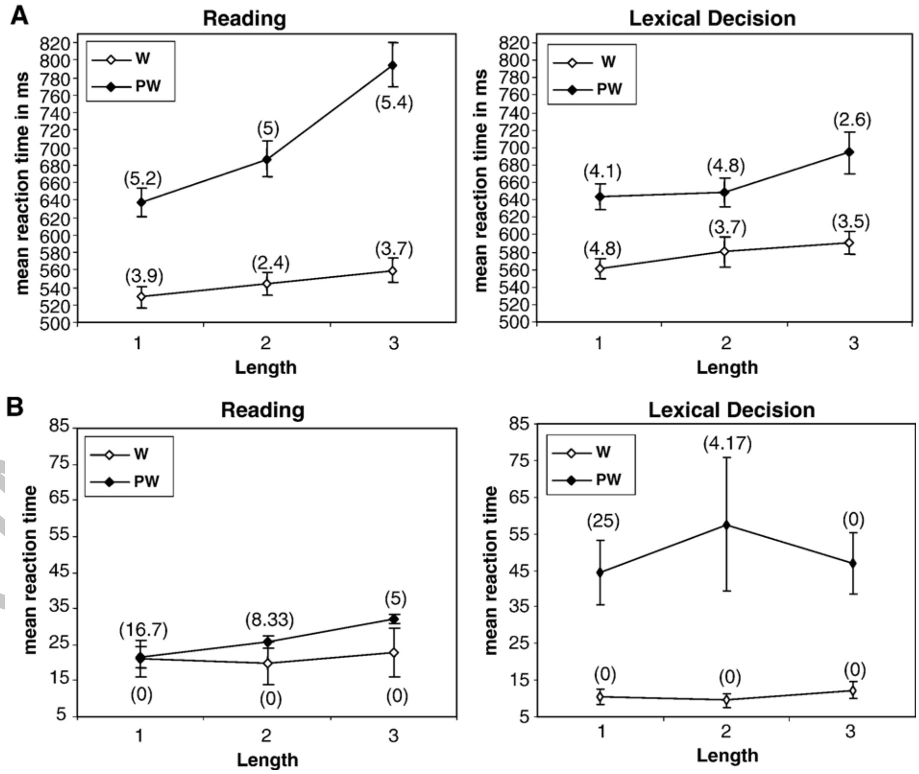

Fig. 1 – Mean naming latencies and reaction times obtained in reading and lexical decision for words and pseudo-words. (A) Experimental data; (B) simulations. Error number is indicated in parentheses; bars indicate standard error.

(F1(2,84) = 9.02, MSE = 1944.73, $P < 0.0003$; F2(2,120) = 7.93, MSE = 2227.32, $P < 0.0006$). The interaction was not significant when contrasting the 1–3 length levels (F1(1,42) = 1.65, MSE = 1594.02, $P = 0.20$; F2(1,120) = 0.85, MSE = 2227.32, $P = 0.36$). Mean RTs between 1- and 3-syllable items differed by 29.56 ms for the words and 51.45 ms for the pseudo-words. In lexical decision, the overall results thus show that, even if a slight length effect is observed for both words and pseudo-words, this effect is similar for the two types of items.

In summary, length has a similar and slight effect on RTs for both words and pseudo-words in lexical decision whereas the effect is far stronger for pseudo-words than for words in reading. This is supported by a very significant second order Length × Lexicality × Task interaction (F1 (2,84) = 13.62, MSE = 1112.22, $P < 0.00001$; F2(2,120) = 8.61, MSE = 1756.39, $P < 0.0004$). Finally, the Length (1–3) × Task interaction was found to be non-significant for words (F1 < 1 and F2 < 1), suggesting similar processing in the two tasks. In contrast, the interaction was highly significant for pseudo-words (F1(1,42) = 20.38, MSE = 3040.14, $P < 0.00006$; F2(1,120) = 33.71, MSE = 1756.39, $P < 0.00001$) as expected if different procedures were involved in the two tasks.

2.1.2. *Error analysis*

Fig. 1A shows that error rate is higher for pseudo-words than for words in the two tasks, but this difference only reaches significance in reading in the by-subjects analysis (F1(1,42) = 4.62, MSE = 25.11, $P < 0.04$). This trend is similar to that found with respect to RTs. Moreover, the error rate pattern is in no way the reverse of the RTs pattern in either task, thus showing the absence of trade-off between RTs and error rates.

2.1.3. *Simulations*

Simulations were conducted on the ACV98 network in both reading and lexical decision (cf. Fig. 1B). The indicator used in the present simulations to estimate word naming latencies was the same as in previous simulations reported by Ans et al. (1998). Time needed to clean up the noisiest phonological cluster was used as an indicator of naming latency. The simulation was run on a set of 71 words corresponding to the experimental words used in Experiment 1 minus the word “trajectoire” which was not part of the model’s lexical database (words on which the model was trained did not exceed 10 letters). As shown in Fig. 1B, the mean naming latencies were 20.99 (range 0.88–90.66) for 1-syllable words, 19.9 (range 1.26–95.02) for 2-syllable words and 22.62 (range 1.53–125.10) for 3-syllable words. The mean naming latencies did not differ significantly as a function of word length (all Fs < 1). All words were read accurately. Results of the simulations thus parallel the behavioral data in showing the absence of length effect on word naming latencies.

Pseudo-word naming latencies could not be estimated using the same indicator as for real words since pseudo-word latencies mainly reflect the number of attentional captures required for analytic processing to be completed. Thus and following Plaut (1998), the number of attentional captures required to generate a correct pronunciation was taken as the most appropriate estimation of pseudo-word naming latencies.[1] One-syllable pseudo-word reading was completed after 3.05 attentional captures on average, whereas 3.68 and 4.58 attentional captures were required for 2 and 3-syllable pseudo-words respectively. The simulation results were characterized by a main length effect (F (2,54) = 6.44, MSE = 1.73, $P < 0.004$) with a higher number of attentional captures for 3-syllable pseudo-words as compared to 1-syllable ($F(1,54) = 12.76$, MSE = 1.73, $P < 0.0008$) or 2-syllable ($F(1,54) = 4.38$, MSE = 1.73, $P < 0.05$) pseudo-words (cf. Fig. 1B[2]). The difference between 1- and 2-syllable pseudo-words did not reach significance ($F(1,54) = 2.18$, MSE = 1.73, $P = 0.15$).

With respect to lexical decision, the indicator of reaction times was the same as the indicator of word naming latency except that time to clean up was estimated at the output orthographic level. As for phonological responses, the output orthographic echo has to be entirely stabilized (that is, all the clusters have to be clean) before a comparison can be made between the orthographic input and the orthographic output. It was assumed that response latency was determined by the orthographic cluster which had the longest clean-up time. To check the absence of any length effect in lexical decision, we submitted 139 items used in Experiment 1 to the ACV98 network (1 word and 4 pseudo-words were discarded because they exceeded 10 letters). The network yielded 5.04% erroneous decisions. As shown in Fig. 1B, RTs were far longer for pseudo-words than for words ($F(1,102) = 27.54$, MSE = 0.1482, $P < 0.000001$). The analysis revealed the absence of any length effect for either words or pseudo-words (all Fs < 1) and the absence of Lexicality by Length interaction ($F < 1$). Overall and as expected, simulations showed the absence of length effect for words in both reading and lexical decision whereas they highlighted a strong length effect for pseudo-words in the reading task only.

2.2. *Experiment 2 (neuroimaging data)*

Results of the contrasts between conditions are presented in Table 1. Each condition (type of item) was contrasted to the control condition (fixation cross), then long items were contrasted to short ones and vice versa. In order to assess a significant length effect during pseudo-word reading as compared to length effect during word reading, the following contrast was calculated: [(3-syllable pseudo-words vs. 1-syllable pseudo-words) vs. (3-syllable words vs. 1-syllable words)] masked inclusively by [3-syllable pseudo-words vs. 1-syllable pseudo-words]. The inclusive masking was performed in order to avoid activations which could in fact reflect “deactivations” provided by the contrast (3-syllable pseudo-words vs. 1-syllable pseudo-words).

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[1] Additional naming latencies related to phonological clean-up time at each step of analytic processing would be insignificant as compared to the time needed for each new attentional capture.

[2] In Fig. 1B, the number of attentional captures has been arbitrarily multiplied by 7 to allow comparison with the word latency indicator.

Table 1 – Anatomical regions activated during reading and lexical decision for words and pseudo-words versus fixation cross and for the relevant contrasts

Contrasts ($P < 0.05$ corr)	Lexical decision activated regions	Talairach coordinates (x, y, z)	p	Z	T	Reading activated regions	Talairach coordinates (x, y, z)	P corr	T	Z
W1 vs. fixation	Left supramarginal gyrus (BA 40)	–51, –28, 52	0.000	(>8)	10.43	Left inferior temporal gyrus (BA 37)	–40, –66, –5	0.000	8.56	(>8)
	Left infero-occipital gyrus (BA 18)	–32, –81, 4	0.000	(>8)	9.07	Left medial occipital gyrus (BA 19)	44, –70, –5	0.000	7.42	(7.30)
	Left inferior frontal gyrus (BA 45, 47)	–44, 32, 17	0.000	(6.04)	6.13	Left supramarginal gyrus (BA 40)	–28, –56, 53	0.000	5.64	(5.59)
	Right middle frontal gyrus (BA 10)	44, 44, 21	0.000	(5.77)	5.86	Right cerebellum	44, –56, –22	0.000	5.63	(5.58)
	Left supplementary motor area (BA 6)	–4, 18, 50	0.000	(5.75)	5.84	Left cerebellum	–16, –59, –18	0.003	5.21	(5.17)
	Left middle temporal gyrus (BA 21)	–51, –35, –2	0.002	(5.27)	5.34	Right supramarginal gyrus (BA 40)	24, –60, 44	0.004	5.11	(5.07)
	Right angular gyrus (BA 39)	40, –58, 12	0.009	(4.91)	4.94					
PW1 vs. fixation	Left precentral gyrus (BA 4)	–44, –17, 56	0.000	(>8)	9.98	Right medial occipital gyrus (BA 19)	40, –81, 4	0.000	5.87	(5.81)
	Left inferior frontal gyrus (BA 44)	–51, 5, 32	0.000	(7.11)	7.27	Left inferior temporal gyrus (BA 37)	–40, –66, –5	0.000	5.78	(5.72)
	Right cerebellum	20, –48, –19	0.000	(6.80)	6.94	Left premotor cortex (BA 6)	–48, –2, 37	0.013	4.84	(4.81)
	Left fusiform gyrus (BA 37, 19)	–32, –81, 4	0.000	(6.78)	6.92					
	Supplementary motor area (BA 6)	0, 6, 50	0.000	(5.67)	5.75					
	Right infero-medial occipital gyrus (BA 18, 19)	40, –74, –1	0.000	(5.61)	5.69					
	Right supramarginal gyrus (BA 40)	44, –33, 48	0.000	(5.53)	5.60					
	Left putamen	–16, 4, 4	0.001	(5.42)	5.49					
	Anterior cingulated gyrus (BA 32)	0, 21, 36	0.012	(4.84)	4.89					
W2 vs. fixation	Left primary sensory–motor cortex (BA 4, 3, 2, 1)	–51, –25, 52	0.000	(7.50)	7.70	Left middle and inferior occipital gyrus (BA 19, 18)	–36, –67, –9	0.000	8.72	(>8)
	Right cerebellum	28, –51, –18	0.000	(7.43)	7.62	Left premotor cortex (BA 6)	–44, –1, 51	0.000	7.24	(7.13)
	Left cerebellum	–32, –48, –19	0.000	(6.37)	6.49	Right medial occipital gyrus (BA 19)	36, –81, 13	0.000	7.05	(6.95)
	Left middle occipital gyrus (BA 19)	–28, –81, 9	0.000	(6.26)	6.37	Left superior parietal lobule (BA 7)	–24, –59, 58	0.000	6.52	(6.44)
						Right premotor cortex (BA 6)	55, 2, 32	0.000	5.73	(5.67)
PW2 vs. fixation	Left primary sensory–motor cortex (BA 4, 3, 2, 1)	–51, –28, 52	0.000	(>8)	9.89	Left inferior temporal gyrus (BA 37)	–40, –63, –9	0.000	8.16	(>8)
	Left infero-medial occipital gyrus (BA 18, 19)	–32, –81, 4	0.000	(>8)	8.82	Left superior parietal lobule (BA 7)	–28, –56, 53	0.000	8.15	(>8)
	Right cerebellum	20, –47, –14	0.000	(7.72)	7.93	Right cerebellum	32, –59, –18	0.000	8.05	(>8)

(continued on next page)

Table 1 *(continued)*

Contrasts (P < 0.05 corr)	Lexical decision activated regions	Talairach coordinates (*x*, *y*, *z*)	*p*	Z	T	Reading activated regions	Talairach coordinates (*x*, *y*, *z*)	P corr	T	Z
PW2 vs. fixation	Supplementary motor area (BA 6)	0, 6, 50	0.000	(6.13)	6.23	Left premotor cortex (BA 6)	−44, 3, 51	0.000	7.02	(6.92)
	Right middle frontal gyrus (BA 46)	44, 44, 21	0.000	(6.04)	6.14	Right superior parietal lobule (BA 7)	32, −52, 53	0.000	5.94	(5.88)
	Left inferior frontal gyrus (BA 47)	−44, 19, −5	0.000	(5.65)	5.73	Left angular gyrus (BA 39)	−28, −65, 26	0.011	4.80	(4.85)
	Right middle temporal gyrus (BA 21)	59, −23, −3	0.003	(5.16)	5.22					
	Right anterior cingulated gyrus (BA 32)	16, 25, 31	0.003	(5.14)	5.20					
	Right primary sensory–motor cortex (BA 4, 3, 2, 1)	55, −17, 47	0.027	(4.65)	4.70					
W3 vs. fixation	Left fusiform gyrus (BA 37, 19)	−40, −67, −9	0.000	(>8)	10.01	Left inferior temporal gyrus (BA 37)	−40, −67, −9	0.000	8.26	(>8)
	Left primary somatosensitive area (BA 3, 2, 1)	−51, −28, 52	0.000	(>8)	8.24	Right cerebellum	32, −59, −18	0.000	7.00	(6.90)
	Left superior parietal lobule (BA 7)	−36, −51, 58	0.000	(6.51)	6.63	Left supramarginal gyrus (BA 40)	−44, −40, 53	0.000	6.42	(6.34)
	Right supramarginal gyrus (BA 40)	48, −29, 47	0.000	(5.82)	5.91	Left premotor cortex (BA 6)	−51, −2, 42	0.000	6.40	(6.32)
	Right superior temporal gyrus (BA 22)	44, 40, 21	0.000	(5.61)	5.69	Right cerebellum	12, −36, −28	0.000	6.00	(5.93)
	Left putamen	−16, 4, 9	0.001	(5.41)	5.49	Right superior parietal lobule (BA 7)	32, −52, 53	0.001	5.40	(5.35)
	Right anterior cingulated gyrus (BA 32)	8, 21, 36	0.007	(4.96)	5.01	Left supplementary motor area (BA 6)	−4, 7, 60	0.002	5.25	(5.21)
						Left inferior frontal gyrus (BA 44)	55, 5, 32	0.005	5.09	(5.05)
PW3 vs. fixation	Left supramarginal gyrus (BA 40)	−51, −28, 52	0.000	(>8)	9.98	Left superior parietal lobule (BA 7)	−28, −56, 53	0.000	9.91	(>8)
	Left middle occipital gyrus (BA 19)	−28, −81, 9	0.000	(>8)	8.90	Left inferior temporal gyrus (BA 37)	−36, −67, −9	0.000	9.79	(>8)
	Right superior parietal lobule (BA 7)	32, −48, 58	0.000	(6.13)	6.24	Right middle frontal gyrus (BA 9)	−51, 2, 41	0.000	9.48	(>8)
						Right superior parietal lobule (BA 7)	28, −56, 53	0.000	6.91	(6.82)
						Right premotor cortex (BA 6)	48, 2, 46	0.000	5.59	(5.54)
PW3 vs. PW1						Left lingual gyrus (BA 18)	−12, −81, 4	0.000	(6.84)	6.94
						Left middle frontal gyrus (BA 9)	−51, 6, 37	0.000	(6.04)	6.10
						Left inferior frontal gyrus (BA 44, Broca)	−51, 4, 33	0.000		
						Right posterior cingulate gyrus (BA 31)	16, −73, 13	0.000	(5.82)	5.88

Table 1 *(continued)*

Contrasts ($P < 0.05$ corr)	Lexical decision activated regions	Talairach coordinates (*x*, *y*, *z*)	*p*	Z	T	Reading activated regions	Talairach coordinates (*x*, *y*, *z*)	*P* corr	T	Z
PW3 vs. PW1						Left superior parietal lobule (BA 7)	−24, −59, 54	0.000	(5.69)	5.75
						Right medial occipital gyrus (BA 19)	32, −63, −9	0.005	(5.02)	5.06
						Right superior parietal lobule (BA 7)	32, −56, 53	0.017	(4.76)	4.79
W3 vs. W2	Left inferior frontal gyrus (BA 47)	−24, 23, 3	0.002	(5.26)	5.33					
	Left middle occipital gyrus (BA 19)	−20, −70, −5	0.006	(5.00)	5.06					
	Right fusiform gyrus (BA 37, 19)	32, −62, −5	0.007	(4.96)	5.01					
W1 vs. W2	Left superior parietal lobule (BA 7)	−32, −64, 49	0.000	(6.17)	6.27					
	Left inferior frontal gyrus (BA 45)	−48, 28, 17	0.000	(5.68)	5.76					
	Left frontal inferior gyrus (BA 44)	−36, 5, 27	0.001	(5.47)	5.54					
	Left middle temporal gyrus (BA 21)	−51, −35, −2	0.003	(5.16)	5.22					
	Left inferior frontal gyrus (BA 47)	−44, 43, −2	0.008	(4.92)	4.97					
	Right dorso-medial frontal cortex (BA 8)	4, 29, 45	0.016	(4.77)	4.82					
Contrasts ($P < 0.005$ uncorr)						Activated regions	Talairach coordinates	P uncorr	Z	T
PW3 vs. PW1/W3 vs. W1 inclusively masked with PW3 vs. PW1*						Left superior parietal lobule (BA 7)	−24, −56, 53	0.000	4.10	4.12
						Right lingual gyrus (BA 19)	28, −47, 2	0.000	3.95	3.97
						Left precuneus (BA 7)	−8, −60, 40	0.000	3.83	3.84
						Left cerebellum	−32, −71, −22	0.000	3.69	3.71
						Left middle temporal gyrus (BA 21)	−40, −47, 2	0.000	3.64	3.65

2.2.1. *Reading and lexical decision*

The anatomical regions activated during reading and lexical decision for each items' type versus fixation cross are summarized in Table 1.

2.2.2. *Words and pseudo-words*

Independently of the task and stimulus length, words and pseudo-words activated a large network of common brain areas (cf. Table 1). In both words versus baseline contrast and pseudo-words versus baseline contrast, the most highly activated regions were the left fusiform gyrus (BA 37, 19) and bilaterally the extrastriate cortex (BA 18, 19) and the supramarginal gyrus (BA 40). The superior parietal lobule (BA 7) was also activated bilaterally by both types of items. The direct comparison of words versus pseudo-words and pseudo-words versus words revealed that no brain region was more strongly activated by either words or pseudo-words.

2.2.3. *Length effects*

Only the contrast 3-syllable pseudo-words (PW3) *versus* 1-syllable pseudo-words (PW1) during reading induced significant brain activations. Long pseudo-words elicited greater neural activity than short pseudo-words (cf. Table 1, PW3–PW1 contrast) within the bilateral extrastriate visual cortex (BA 18, 19) and superior parietal lobule (BA 7), the left middle and inferior frontal gyri (BA 9, BA 44) and the right posterior cingulate gyrus (BA 31). None of the other contrasts (PW1 vs. PW3, W3 vs. W1, W1 vs. W3) yielded statistically significant results. In particular, silent reading of the longest words (W3) yielded no additional activation as compared to silent reading of the shortest words (W1). Fig. 2 presents the functional maps obtained by contrasting 3-syllable pseudo-words versus 1-syllable pseudo-words during reading.

None of the contrasts performed between long and short items induced significant activation during the lexical

Fig. 2 – This figure represents the functional maps obtained by contrasting three-syllable vs. 1-syllable pseudo-words (PW3–PW1) and three-syllable vs. 1-syllable words (W3–W1) during reading. The activations obtained from the group analysis were projected onto 2D axial template at different levels to the bicommissural plane. The activation induced by word contrasts appears in green, while that induced by pseudo-word contrasts is in red. None "green" activation was present on these maps during reading, suggesting the absence of word length effect. "Red" activation was obtained during pseudo-word reading only, in the following regions: Broca's area, the superior parietal lobule, the left middle frontal gyrus, the visual extrastriate areas and the right posterior cingulate gyrus. These regions were more intensively activated during reading three-syllabic pseudo-words than monosyllabic pseudo-words. All images are represented in neurological convention (left hemisphere is on the left). All activations were obtained for a value of the *P* < 0.05 corrected for multiple comparisons.

decision task, suggesting that cerebral activity was not affected by item length in this task.

Length effect during pseudo-word reading was significantly greater than length effect during word reading as shown by the contrast [PW3 vs. PW1]–[W3 vs. W1]. This effect was characterized by significant activations within the right lingual gyrus (BA19), left superior parietal lobule and precuneus (BA7), left middle temporal gyrus (BA21) and left cerebellum (cf. Fig. 3).

3. Discussion

Length effects on naming latency were investigated in the present study because they place important constraints on theories of reading (Ans et al., 1998; Plaut, 1998; Weekes, 1997). The analysis of reading performance revealed that naming latencies were far more affected by length for pseudo-words than for words. Only a slight length effect characterized reaction times in lexical decision, and this effect was not modulated by the items' lexicality. Furthermore, similar length effects were obtained for words in reading and lexical decision whereas they were far stronger in reading than in lexical decision for pseudo-words. The overall behavioral findings suggest that word processing was similar in both reading and lexical decision and that processing was not particularly affected by word length as expected if words were globally processed. In contrast, pseudo-words were differently processed in reading and lexical decision. The strong length effect observed in pseudo-word reading suggests that processing relied on a serial mechanism. In contrast, pseudo-word length only minimally influenced reaction times in lexical decision as expected if decision was based on global processing.

In line with previous studies (Weekes, 1997), the present results are not a priori compatible with models which assume that words and pseudo-words are similarly processed, whatever their length, in both reading and lexical decision (Harm and Seidenberg, 1999; Plaut et al., 1996; Seidenberg and McClelland, 1989; see Plaut, 1998 for an attempt to account for letter length effects within the PDP framework). They are however in keeping with the dual-route model and the ACV98 multitrace model which both assert that a serial mechanism is involved in pseudo-word reading in contrast to familiar words which are globally processed. The simulations conducted on the ACV98 network paralleled the behavioral data in showing a strong length effect on naming latencies for the pseudo-words only. As expected, simulations revealed the absence of any length effect in both reading and lexical decision for words and in lexical decision for pseudo-words. Accordingly, the slight and unreliable length effect experimentally obtained on both words and pseudo-words in reading and lexical decision might reflect some more general difficulty to visually process items extending up to 11 letters.

Investigation of the brain regions involved in word and pseudo-word processing relative to fixation cross revealed that a large network of common brain areas was activated for both types of items. The activated regions corresponded to those typically reported as being activated in reading and/or lexical decision (Cohen et al., 2002; Pammer et al., 2004; see Price, 1997 or Fiez and Petersen, 1998 for a review). Results are also consistent with previous studies showing that similar regions are activated during the processing of all types of orthographic strings (Chen et al., 2002; Mechelli et al., 2003; Petersen et al., 1990; Tagamets et al., 2000). The direct contrasts between words and pseudo-words, independent of item length, failed to reveal significant differences in the cortical regions involved in the processing of words and pseudo-words in reading and lexical decision. This finding differs from a number of previous reports of activation differences between words and pseudo-words in reading (Jobard et al., 2003; Hagoort et al., 1999; Herbster et al., 1997) and lexical decision (Fiebach et al., 2002). However, studies comparing words and pseudo-words have yielded inconsistent results that might in part be due to methodological differences (Mechelli et al., 2003; Price et al., 1996). Furthermore, the sublexical characteristics of items—such as letter length, number of syllables or syllable frequency—known to

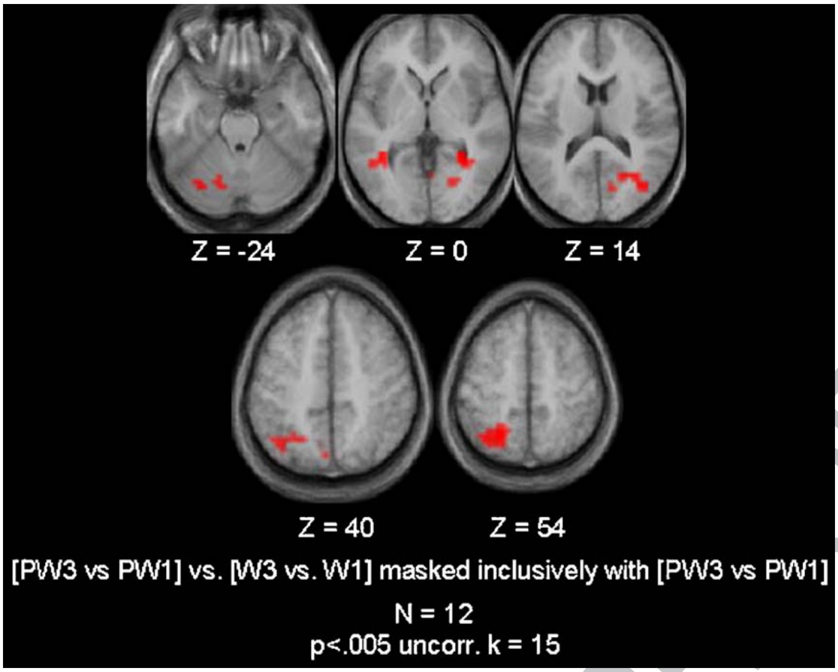

Fig. 3 – This figure shows maps with significant activation ($P < 0.005$ uncorrected, $k = 15$) from the group analysis obtained by contrasting [(three-syllable versus one-syllable pseudo-words, PW3 vs. PW1) vs. (three-syllable versus one-syllable words, W3 vs. W1)] masked inclusively by the contrast [three-syllable versus one-syllable pseudo-words, PW3 vs. PW1] during reading. As presented in red, the activated regions were, to the left, the superior parietal lobule, precuneus, middle temporal gyrus and cerebellum and, to the right, the lingual gyrus. The activation was projected onto 2D template (axial slices) at different levels with respect to the bicommissural plane. All functional maps are shown in neurological convention (left hemisphere to the left).

have an impact on processing (Hutzler et al., 2005; Indefrey et al., 1997; Levelt and Wheeldon, 1994) were not always systematically controlled.

More interestingly, the present findings revealed that brain activation was affected by pseudo-word length in reading whereas no difference in brain activity was observed when contrasting long and short words in either reading or lexical decision. Critically, in reading, the current analysis revealed that brain activation elicited by length effects for pseudo-words was significantly higher than the activation corresponding to length processing for real words. These results closely parallel those found in the behavioral analysis and in the simulations. At the cerebral level, length effects for pseudo-words in reading were mostly characterized by increased cerebral activity in the brain regions involved in visuo-spatial and visual attentional processing.

In silent reading, long pseudo-words elicited greater cerebral activity than short pseudo-words within the visual extrastriate cortex. Bilateral activation of the extrastriate cortex (BA 18, 19) is typically related to visual processing of orthographic strings (Fiez and Petersen, 1998; Hagoort et al., 1999; Pammer et al., 2004; Tagamets et al., 2000). Indefrey and collaborators (1997) explicitly investigated the effect of string-length on the activation pattern observed in this region. Activations in the medial extrastriate cortex were found for both pseudo-words and false-font strings when contrasted with single characters. In contrast, activations disappeared when pseudo-words were compared to false-fonts matched in length. The authors concluded that the length difference alone was sufficient to account for extrastriate activation, suggesting that this region was primarily sensitive to the physical characteristics of the input stimuli. However, in the present study, increased activation of the extrastriate regions was obtained by contrasting long with short pseudo-words but not by contrasting long with short real words in reading. Furthermore, item length had no impact on extrastriate activation in lexical decision. Such results do not support the hypothesis that differences in physical length are responsible for medial extrastriate activations.

It is noteworthy however that the right lingual gyrus (BA19) alone was significantly more activated during pseudo-word length processing as compared to word-length processing. Tagamets et al. (2000) found that the volume of activity in the right medial occipital gyrus increased as the stimuli progressed from most familiar to least familiar items. Stronger activation of this region for long pseudo-words as compared to short pseudo-words might therefore result from additional demands associated to the visual processing of unfamiliar multi-syllabic pseudo-words during reading.

Increased activation of the extrastriate cortex might also result from the fact that perception-related occipital activations were enhanced by visual attention (Clark et al., 1997; Corbetta et al., 1990; Kanwisher and Wojciulik, 2000; Karstner et al., 1998). Activation of the superior parietal lobule bilaterally (BA 7), of the left middle frontal gyrus (BA 9) and of the right posterior cingulate gyrus (BA 31) does suggest that attentional processes are more strongly involved during analytic processing of long than short pseudo-words. The role of the parietal lobe, particularly BA 7 area, for initiating and maintaining visual attention and for shifting the focus of attention from one element of interest to another is well documented (for a review Lynch et al., 1977; Vidyasagar, 1999, 2004). The superior parietal area is further involved in visuo-spatial analysis and attention (for a review Posner and Petersen, 1990; Kanwisher and Wojciulik, 2000) and is sensitive to the amount of attention allocated to a particular task (Fiez et al., 1995). Tagamets et al. (2000) argued that activation of the superior parietal cortex (BA 7) might reflect spatial processing that is necessary for ordering the symbols in unfamiliar strings and/or greater effort in processing novel unfamiliar stimuli. Specific activation of the left superior parietal cortex for long pseudo-word reading might therefore be related to the properties of the task which requires spatial processing allowing serial shifts of attention from one syllable to another and ordering the syllables into a single string.

It might be argued that the recruitment of areas involved in visual spatial attention rather reflects differences in eye movements that might also account for the activity increase in the cerebellum and extrastriate visual areas (Mesulam, 1981, 1990, 1998; Konen et al., 2004). However, data suggesting the absence of overt eye movements are twofold. First, item presentation was limited to 200 ms in the fMRI experiment, thus preventing overt saccadic movements. Second, the absence of activation of the frontal eye field (FEF) area—involved in the motor programming of saccadic movements (Goldberg, 2000)—also suggests that overt eye movements did not occur when reading long pseudo-words. The absence of FEF activation during long pseudo-word reading further suggests that only reflexive, automatic spatial attention was engaged (Handy et al., 2001). It is further worth noting that our interpretation in attentional terms does remain even if eye movements were overtly observed. Indeed, if they reflected bottom–up processes, eye movements should occur in both reading and lexical decision for both words and pseudo-words, so reflecting the adaptation of the oculomotor system to item length. Against this interpretation, activity increase in the brain regions potentially related to overt eye movements was only observed when processing long pseudo-words in reading. This implies that eye movements if they had occurred should be rather viewed as reflecting top–down processes linked to the allocation of spatial attention during reading (see Prado et al., in revision for converging data).

The present study further revealed that the left inferior frontal gyrus (BA 44) was more strongly activated during long than short pseudo-word processing. This region is typically associated with phonological processing (Démonet et al., 1992; Price, 1998; Price et al., 2003; Pugh et al., 1996; Rumsey et al., 1997); it is in particular involved in the phonological recoding of orthographic input strings at a sublexical level (Fiez and Petersen, 1998; Hagoort et al., 1999; Pammer et al., 2004). Increased activation in the left inferior frontal gyrus might suggest that phonological analysis was more strongly involved in the processing of long than short pseudo-words. Such an increased activity might in particular reflect stronger involvement of verbal working memory (Paulesu et al., 1993; Cabeza and Nyberg, 2000, for a review) when a novel articulatory rehearsal program is effortfully assembled and initiated (Naveh-Benjamin and Jonides, 1984; Chein and Fiez, 2001). However, activity for long pseudo-words vs. short pseudo-words elicited no more activity in area 44, as compared to long words vs. short words. This latter finding suggests a trend for Broca's area to increase its activity with items' length, be they words or pseudo-words. Such an activity increase might thus in part reflect the additional load put on sub-vocal articulation during the processing of long letter strings.

4. Conclusion

The present study reports converging evidence from both behavioral, neuroimaging and simulation data in support of the specific involvement of a serial mechanism in pseudo-word reading. The behavioral data highlight the existence of strong length effects on naming latencies for pseudo-words only. The neuroimaging results parallel these behavioral findings in showing that some brain regions are specifically involved in the processing of long pseudo-words as compared to short pseudo-words in silent reading but not in lexical decision. Silent reading of long pseudo-words specifically engages a network of brain regions involved in visual and visual attention processing. The present findings thus place constraints on theories of word reading in suggesting the involvement of a serial mechanism based on visual attentional processing in long pseudo-word reading.

5. Experimental procedures

5.1. *Experiment 1*

5.1.1. *Participants*

Forty-four undergraduate students (40 females, 4 males) from the University of Chambéry (France) participated in the experiment. They were given course credits for their participation and were randomly selected for doing either the reading task (for half of them) or the lexical decision task (for the other half). The participants were 20 years and 2 months old on average. They were native speakers of French and reported neither visual nor reading disorders. All of them gave informed written consent prior to participation in the study.

5.1.2. *Material*

The complete set of items consisted of 348 items (174 French words and 174 pseudo-words) including 144 experimental stimuli, 168 fillers and 36 practice items. Seventy-two words and 72 pseudo-words were selected as experimental stimuli (they are listed in Appendix A). One third of the target words and pseudo-words were 1-syllable long, one-third had two syllables and the remaining third had three syllables. The words were selected on the basis of the BRULEX lexical database for French (Content et al., 1990). They were of medium frequency (mean log frequency = 284.5; standard deviation = 34.02; range = from 186 to 390). The three sets of 1-syllable, 2-syllable and 3-syllable words were closely equated in frequency (*m* = 284.5, SD = 34.02; *m* = 281.7, SD = 23.3 and *m* = 295.3, SD = 39.5 respectively). Moreover, the same number of words (10 out of 24) with a final mute «e» was included in each syllable length set. In French indeed, words ending with a mute «e» are ambiguous as to their number of syllables. Although it is clear that words like "tapis" /tapi/ or "cinéma" /sinema/ have 2 and 3 syllables, respectively, a word like "porte" /port^/ (which can be pronounced either [poRt] or [poRtoe]) can be considered as either a 1- or 2-syllable word. Given that words ending with a mute "e" are quite frequent in French and could not be discarded, their number was closely equated in each set of syllable length. Finally, all the experimental words began with a stop consonant (/k/, /d/, /g/, /p/, /t/ or /b/) so that differences in naming latencies cannot follow from differences across conditions in the ability of the items to trigger the vocal key. The 72 experimental pseudo-words were created from the word stimuli. Polysyllabic pseudo-words were build up by recombining the syllables of the target words with the constraint that syllable position remained unchanged (e.g., the pseudo-word «crovier» was generated using the first syllable of the word «**cro**chet» and the second syllable of the word «gra**vier**»). The letters at syllable boundaries were checked to conform to the French phonotactic rules. Mono-syllable pseudo-words were generated by recombining the syllabic components (corresponding to the onset, nucleus and coda) from mono-syllable words. The letters and syllables taken from words were occasionally modified in order for the pseudo-word to be orthographically and phonologically legal. In these cases, consonants were systematically substituted by consonants and vowels by vowels; so, that syllabic structure remained identical in words and pseudo-words. The experimental words and pseudo-words of each syllable length were equated in number of letters – mean number of letters for 1-syllable words and pseudo-words respectively: 4.6 (SD = 0.7; range: 4 to 6) and 4.8 (SD = 0.9; range: 4 to 7); for 2-syllable words and pseudo-words: 7 (SD = 0.8; range: 5 to 9) and 7 (SD = 0.9; range: 5 to 9); for 3-syllable words and pseudo-words: 9.3 (SD = 0.8; range: 8 to 11) and 9.4 (SD = 0.9; range: 8 to 11). Similarly as words, all experimental pseudo-words began with a stop consonant and 10 out of 24 ended with a mute «e» in each set of syllable length. The 168 fillers included 84 words and 84 pseudo-words of 1, 2 or 3 syllables. Half of them ended with a mute «e». The filler words were selected in such a way that the total set of words (targets and fillers) was representative of French written words. They had a mean log frequency of 350, and most of them began with either a vowel or a non-stop consonant. The filler pseudo-words were created from the filler words as the experimental pseudo-words. As the items increased in length, their number of orthographic neighbors decreased but orthographic neighborhood size remained very low in all length sets. Orthographic neighborhood was defined as the number of same length words differing from a target (word or pseudo-word) by a single letter (Coltheart et al., 1977); neighbors exceeding 100 occurrences per 100 million in the Brulex database alone were taken in the analysis. On average, the number of neighbors was 1.08, 0.50 and 0.33 for 1-syllable, 2-syllable and 3-syllable words respectively; it was 1.33, 0.17 and 0 for 1-syllable, 2-syllable and 3-syllable pseudo-words, respectively. In all cases, neighborhood size remained very low.

In the reading task, words and pseudo-words were presented in 4 blocked lists. The order of the word and pseudo-word lists was counterbalanced so that the session began with a word list for half of the participants and with a pseudo-word list for the other half. Each sub-list began with 9 practice items (3 words or pseudo-words of each syllable length) followed by 78 items (36 experimental items and 42 fillers) of 1, 2 and 3 syllables that were randomly presented. Each sub-list was equated in frequency, number of items of each syllable length and number of items ending with a mute "e".

For the lexical decision task, the same 348 items were divided in two equivalent sub-lists. Each sub-list began with 18 practice items (3 words and 3 pseudo-words of each syllable length) followed by 156 randomly presented items including 72 experimental items (36 words and 36 pseudo-words of 1, 2 and 3 syllables) and 84 fillers (42 words and 42 pseudo-words of 1, 2 and 3 syllables).

5.1.3. *Design and procedure*

Stimulus presentation and reaction time recording were controlled by the E-prime software which was run on a Dell PC computer with a 17″ color monitor. The participants were seated 50 cm from the computer monitor. The stimuli were displayed in lowercase letters (bold Courier new 22) in the center of the computer screen. They were presented in black on a white screen. Their angular size varied from 2.4° to 6.1° for mono-syllabic items, from 4.1° to 7.9° for the bi-syllable items and from 6.8° to 9.5° for the 3-syllable items.

In the reading task, each trial began with a fixation point displayed at the center of the computer screen for 500 ms followed by a white screen for 150 ms. The stimuli (word or pseudo-word) were presented one at a time and remained on the screen until the participant began to speak into a microphone connected to a voice key. They disappeared after a 2000 ms deadline when no response was given. After the participant's response, a new white screen was displayed for 1000 ms before the next trial. During this interval, the experimenter recorded naming accuracy by pressing a keyboard button. The real-time clock in the computer timed the response latencies in milliseconds from the appearance of the stimulus to the onset of the subject's response. The participants were instructed to read each item aloud as accurately and as quickly as possible.

In the lexical decision task, the experimental procedure was the same but the participants were instructed to indicate as accurately and as quickly as possible whether the printed item was a real word or a pseudo-word. They responded by pressing keyboard buttons (response YES, right hand, key ","; response NO left hand, key "w").

5.2. *Experiment 2*

5.2.1. *Participants*

Twenty healthy volunteers (14 males, 6 females) participated in the fMRI experiment; they were 22 years and 6 months old on average, had a university education and were fully right-handed according to the Edinburgh handedness inventory (Olfield, 1971). All were drug-free, had no neurological or psychiatric history and had normal anatomical MRIs. All participants gave their written informed consent. Brain activity was recorded during reading for 12 participants and during lexical decision for the other 8 participants.

5.2.2. *Stimuli and paradigm*

A pseudo-randomized ER-fMRI paradigm with six types of stimuli (words composed of 1, 2 and 3 syllables and pseudo-words composed of 1, 2 and 3 syllables) was used. The same 144 words and pseudo-words used in Experiment 1 were presented during two fMRI sessions. In addition to the experimental stimuli, 34 null events (ten of them at the end of the session) composed of a blank screen and a fixation cross on the center of the screen were also included. Each stimulus was presented for 200 ms followed by a white screen. A stimulus (word, pseudo-word or null event) was displayed every 2 s. The order of presentation of the stimuli was optimize (Friston et al., 1999). During one fMRI session, the twelve participants assigned to the reading task were instructed to read each item silently, without articulating and vocalizing. The eight participants assigned to the lexical decision task had to judge whether each presented stimulus was a real word or a pseudo-word. They gave manual motor responses by means of two response keys pressed with the index (for words) and with the middle finger (for pseudo-words). The stimuli were generated by means of Psyscope V.1.1 (Carnegie Mellon Department of Psychology) running on a Macintosh computer (Power Macintosh 9600). They were transmitted into the magnet by means of a video projector (Eiki LC 6000). The projection screen was located behind the magnet, and the mirror was centered above the patient's eyes. The design was such that the angular size of stimuli was the same as in Experiment 1.

5.2.3. *MRI acquisition*

Functional MR imaging was performed on a 1.5 T MR imager (Philips NT) with echo-planar (EPI) acquisition. Twenty-three adjacent, axial slices (thickness 5 mm each) were imaged. The imaging volume was oriented in parallel to the bicommissural plane. Positioning of the image planes was performed on scout images acquired in the sagittal plane. An EPI MR pulse sequence was used. The major MR acquisition parameters of the EPI sequence were: TR = 2000 ms, TE = 45 ms, flip angle = 90°, field-of-view = $256 \times 256\ \text{mm}^2$, imaging matrix = 6 × 64, reconstruction matrix = 12 × 128. Subsequent to the functional scan, a high resolution 3D anatomical MR scan was obtained from the volume previously examined.

5.2.4. *Data processing*

Data analysis was performed based on the general linear model (Friston et al., 1995) for event-related designs, implemented in SPM'99 software (Welcome Department of Cognitive Neurology, London, UK) running on a Unix workstation under the MATLAB environment (Mathworks, Sherbon, USA).

5.2.4.1. Spatial pre-processing. MR images were processed using the following steps. First, during the *slice timing* step, the functional volumes were corrected for sampling bias effects caused by the different time acquisition of each slice composing the functional volume, relative to the hemodynamic response. In the second step, the realignment or motion correction was applied by using rotations and translations in order to realign each functional volume to the first acquired one. In a third step, the anatomical volume was spatially normalized into the Talairach and Tournoux (1988) reference space using as template a representative brain from the Montreal Neurological Institute series. The anatomical normalization parameters were subsequently applied to functional volumes. Finally, in conformity with the assumption that data are normally distributed, the functional images were spatially smoothed by using a Gaussian filter (8 mm width).

5.2.4.2. Statistics. For each type of individual events, regressors of interest were created by convolving a delta function at each event onset with a canonical haemodynamic response function. A fixed effect group analysis was performed. Among significant isolated voxels (voxelwise threshold of $P < 0.001$), only the clusters that were composed of at least 5 adjacent voxels and were statistically significant above a certain threshold ($P < 0.05$ corrected; except for the [PW3 vs. PW1]–[W3 vs. W1] contrast for which an uncorrected $P < 0.005$ was used, according to the method described by Friston et al., 1995, for the validation of a priori hypotheses in terms of activated regions) were retained.

6. Uncited references

Mechelli et al., 2000
Plaut, 1997
Poldrack et al., 1999

Appendix A. List of the experimental items

1-syllable words: Biais brut clerc clos craie drap golf gris grue prêt talc teint test truie crabe crêpe croûte grade grippe guêpe pioche quille taupe tresse.

2-syllable words: beignet brasier clameur convoi crapaud crochet dauphin gradin gravier tambour tennis torrent transfert tuyau brigade clôture critère grillage guirlande guitare parade pillage présage.

3-syllable words: toiture bâtiment bigorneau brusquerie complément continent garantie guéridon président prévention processus protection provision tourbillon tribunal crocodile dépendance gratitude porcelaine précipice préfecture projectile propagande tolérance trajectoire.

1-syllable pseudo-words: bial brost clêt clie dauc gat grais guerc praie psau queint quos talf thoue craupe crite crouche crupe grêde grube piêppe teille trope tesse.

2-syllable pseudo-words: bravoi clonnis crovier doutain grafert guisier pagon plasson prédin toipaux toureux tournau trachon tuchet chaillage clagage contare crituge gralande grisare guirrade pitège teillare transture.

3-syllable pseudo-words: barantion belluquet croplession gajecteur grelanton guésition palméteau poufequin prébillon prépament prosacté provendon togrement trapension gracipile brustidance comburance dériтude porquenale préjectoire prétilaine procégance tourjectine trilédence.

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