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Age-related differences in effective connectivity of brain regions involved in Japanese kanji processing with homophone judgment task

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ABSTRACT

Reading is a complex process involving neural networks in which connections may be influenced by task demands and other factors. We employed functional magnetic resonance imaging and dynamic causal modeling to examine age-related influences on left-hemispheric kanji reading networks. During a homophone judgment task, activation in the middle frontal gyrus, and dorsal and ventral inferior frontal gyri were identified, representing areas involved in orthographic, phonological, and semantic processing, respectively. The young adults showed a preference for a semantically-mediated pathway from orthographic inputs to the retrieval of phonological representations, whereas the elderly preferred a direct connection from orthographic inputs to phonological lexicons prior to the activation of semantic representations. These sequential pathways are in line with the lexical semantic and non-semantic routes in the dual-route cascaded model. The shift in reading pathways accompanied by slowed reaction time for the elderly might suggest age-related declines in the efficiency of network connectivity.

1. Introduction

Reading, an important aspect in everyday living, enables us to make sense of the surroundings. Fast and accurate recognition of written scripts in reading seems to be an automatic process for normal readers and involves a series of complex sensory and cognitive processes, many of which could be interrupted by several factors such as normal aging. While neuroimaging studies of cognitive aging have revealed age-related differences in brain activity relevant to a variety of cognitive functions such as working memory, episodic memory, semantic memory retrieval, perception and inhibitory control (e.g., Cabeza, 2002; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008), language-related issues, such as word-finding difficulties, have also been observed in healthy older adults. Behavioral studies have suggested that word-finding failures occur when the connections between lexical and phonological systems weaken due to aging or lack of recent or frequent use. This is often seen in the elderly where more word-finding difficulties are experienced than the young (Burke, MacKay, Worthley, & Wade, 1991; Burke & Shafto, 2004). The mapping between sounds and words/characters may be further complicated in a writing system such as that of Japanese kanji where the pronunciation of a kanji character is dependent on the semantic context in which the character appears. An arbitrary sound could also be allocated to a kanji character as is often seen in names, lyrics or advertisements (Matsuo et al., 2010). In this case, specific cognitive processes or neural strategies might be developed in order to extract phonological sounds from the logographic characters. Yet, little is known about how the neural mechanism of character reading, such as in Japanese kanji, might be influenced by healthy aging.

1.1. Word recognition processes and kanji

One of the most influential cognitive models of reading is the dual-route cascaded model (DRC; Coltheart, Curtis, Atkins, & Haller, 1993; Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001), which posits three possible processing pathways for reading. The first pathway is a lexical semantic route, in which reading requires the association between the visual word forms and their meanings. Successful reading is achieved when the orthographic form of a word activates the corresponding semantic lexicon, which is then

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linked to the phonological output. Second, successful phonological retrieval is possible via a lexical non-semantic route, in which the orthographic forms of characters are directly mapped to the corresponding phonological lexicons without recourse to the semantic system. However, when this lexical mapping becomes difficult or impossible for infrequent or pseudo words, the other route through a grapheme–phoneme correspondance (GPC) system comes into effect. The GPC route requires grapheme-to-phoneme conversion, by which the printed word is decomposed into several graphemes and transformed to phonemic components, and the pronunciation of the word is assembled by all phonemes. The meaning of the word becomes accessible after the pronunciation is available. While grapheme-to-phoneme conversion is applicable in alphabetic languages (such as English and Spanish), it seems impossible for Japanese kanji reading because there is no way to decompose a kanji character into small graphemes that correspond to phonemic components. As Japanese kanji characters are ideograms of which a symbol corresponds globally to meanings and pronunciations, the kanji recognition process may follow the lexical route whereas the GPC route is not applicable. On the other hand, it is worthwhile to note that for Japanese kana, a phonographic system that shares more similarities with alphabetic languages, both lexical semantic and GPC routes in the dual-route model may be adopted (Ischebeck et al., 2004).

The apparent complexity of kanji leads to the questions of how readers extract sounds and/or meanings from the printed word for kanji reading, and what roles the phonological and semantic factors play. In the current study, we aimed to examine the dynamics among orthographic, phonological, and semantic processing in the neural networks of kanji character reading. Five possible pathways were considered. First of all, we began with a parallel model (Model 1) where the orthographic information could activate both semantic and phonological processing with no preference for one or the other. Next, two sequential models were proposed according to the lexical routes in the DRC model (Coltheart et al., 1993, 2001). Here we considered that orthographic processing could either lead to semantic processing followed by phonological processing (Model 2) or lead to phonological processing followed by semantic processing (Model 3). Finally, two more models with the combination of the parallel and sequential pathways were considered. Both models consisted of parallel pathways from orthographic processing to both semantic and phonological processing, but they had an additional pathway either from semantic to phonological processing (Model 4) or from phonological to semantic processing (Model 5).

A number of regions have been identified to be involved in kanji reading. For its visual complexity of character forms, kanji reading was found to activate the inferior occipito-temporal regions, including the bilateral inferior occipital gyri (IOG) and the left fusiform gyrus (FG) (Sakurai et al., 2000; Thuy et al., 2004). It has also been proposed that the left posterior prefrontal cortex plays an important role in kanji reading, specifically with a functional segregation into three segments: the ventral inferior frontal gyrus (IFG), dorsal IFG, and the middle frontal gyrus (MFG), which are associated with selection of semantic, phonological, and morphological information, respectively (Matsuo et al., 2010). In the current study, we employed a kanji homophone judgment task, in which participants were required to judge whether two kanji characters had the same pronunciation. This task was thought to evoke print-to-sound mapping to retrieve the pronunciations, and thus would be a suitable task to examine the modeling pathways in the kanji recognition process. Based on the findings in the prior neuroimaging studies, we selected the following regions to examine effective connectivity of the proposed models: the left IOG (BAs 17/18), the left FG (BA 37), the left MFG (BA 9), and the left IFG. The left IFG was divided into ventral IFG (BA 47) and dorsal IFG (BA 44) as previous studies have suggested that the dorsal IFG is involved in phonological processing and the ventral IFG is associated with semantic processing during word recognition (Poldrack et al., 1999; Wu, Ho, & Chen, 2012). Along with the functional segregation in the left posterior prefrontal region proposed by Matsuo et al. (2010), the MFG, dorsal IFG, and ventral IFG were proposed to represent orthographic, phonological, and semantic processing regions in the kanji reading network.

1.2. Aging and language

Much neuroimaging research has found that aging comes along with declines in a variety of cognitive functions, such as memory, executive function, and attention, and these declines are associated with changes in brain activity. However, less is known about age-related changes in the neural mechanism underlying language processing. The lack of aging literature in language could possibly be due to the understanding that verbal ability, considered as a domain of crystallized intelligence, has been found to be less affected by aging. Crystallized intelligence is the intellect gained from knowledge or experience, and past studies have shown that crystallized intelligence was higher for older adults (Horn & Cattell, 1967). For verbal abilities, studies have also shown that vocabulary increased with age (Verhaeghen, 2003), specifically showing increments to the middle age, reaching a plateau to the early-old age, and only showing modest decrements in the old–old individuals (i.e., 75 years old and above) (Giambra, Arenberg, Zonderman, Kawas, & Costa, 1995).

Despite the notion that language may be relatively preserved as we age, older adults tend to have more language-related complaints than young adults, such as word-finding difficulties (Burke et al., 1991; James & Burke, 2000) and difficulties in picture/object naming (Van Gorp, Satz, Kiersch, & Henry, 1986; Zec, Burkett, Markwell, & Larsen, 2007). Recently more neuroimaging studies have started to investigate age-related functional changes in the brain activity during language processing, and changes in regional activity have been observed in the frontal regions (e.g., Meinzer et al., 2009, 2012; Shafto, Stamatakis, Tam, & Tyler, 2009). Age-related declines in white matter integrity, especially in the frontal brain areas, have also been reported (Pfefferbaum, Adalsteinsson, & Sullivan, 2005; Salat et al., 2005). Moreover, the alterations in structural and functional connectivity within the language networks in healthy aging might be associated with deterioration of cognitive performance (Antonenko et al., 2013). Therefore, the combined influence of aging on regional brain activity as well as structural and functional network connectivity brought up a question of whether older adults might adopt a differential pathway for reading as compared to young adults. In particular, we hypothesized that the connections between language-related regions might be modulated by task conditions differentially with respect to age. To the best of our knowledge, no studies have investigated age-related effects on effective connectivity within language networks. Hence, it is important for the current study to fill this gap.

1.3. Study aims

Effective connectivity analysis with fMRI allows us to investigate how activated brain regions are connected under a task circumstance as well as how the regions and connections within this network might be modulated by external stimuli. Hence, to elucidate the neural pathways underlying kanji character processing, dynamic causal modeling (DCM) was selected in the current study to examine alternative models of reading. Through functional neuroimaging, we evaluated the processing pathways within the neural network of kanji reading in young and elderly Japanese speakers. Findings from the current study will provide further understanding of the neural network underlying Japanese kanji reading as well as shed light on age-related influence on the reading network.

2. Materials and methods

2.1. Participants

Twenty-three young adults (14 males; age range: 20–37, $M = 22.7$, $SD = 4.29$) and twenty-four elderly adults (12 males; age range: 62–75, $M = 67.9$, $SD = 3.30$) were initially recruited in the study. All participants were right-handed as measured using a Japanese handedness inventory (Hatta, 1996, 2007). None of them had any history or existing neurological diseases or psychiatric disorders. Written informed consent was obtained from all participants prior to participation, and the study protocol was approved by the Institutional Review Board of the National Center for Geriatrics and Gerontology.

All participants were administered the Mini-Mental State Examination (MMSE; Folstein, Folstein, & McHugh, 1975) to screen for possible cognitive impairments. None of them scored below 25 out of 30 for MMSE (Young: $M = 29.6$, $SD = 0.59$; Elderly: $M = 28.5$, $SD = 1.41$). A kanji reading test was also administered to measure the participants' competency in recognizing and reading kanji characters, which was crucial for the homophone judgment task. There were 100 kanji characters in total, and the accuracy score was defined as the number of kanji that participants could pronounce correctly.

A total of twelve participants (three from young and nine from elderly) were omitted from subsequent data analyses on the basis of one or more of the following conditions: 2.5 *SD* below the group mean for percent reading accuracy, less than 75% accuracy for the homophone judgment task, greater than 25% omission for the homophone judgment task, image artifacts, or head movement greater than 3 mm at any translation axis during the fMRI run. Hence, subsequent data analyses were conducted on 20 young participants (12 males; age range: 20–37, $M = 22.9$, $SD = 4.49$) and 15 elderly participants (8 males; age range: 62–69, $M = 66.1$, $SD = 2.12$).

2.2. Stimuli

The character stimuli were adopted from a previous study (Matsuo et al., 2010); only kanji characters that have one pronunciation (i.e., the ONE character pairs) were used. The characters were selected from the national kanji inventory known as *jouyou kanji* or "characters designated for everyday use". All selected characters were part of compulsory education in elementary school so as to ensure simplicity and familiarity of the chosen kanji characters to both the young and the elderly participants. Twenty-five pairs of homophonic and twenty-five pairs of non-homophonic characters were included. The homophonic pairs consisted of characters with the same pronunciation, while the non-homophonic pairs consisted of characters with different pronunciations. The characters were matched in frequency and the number of moras (i.e., phonological units) between character groups. For more details on character selection, readers are referred to the previous paper by Matsuo et al. (2010).

2.3. Task paradigm and procedure

The fMRI task paradigm employed a blocked design with three conditions alternating in 24 s blocks for 5 cycles within the scanner (see Fig. 1). The task consisted of 3 conditions: homophone judgment, line orientation judgment and rest. An additional rest block was included at the beginning of the run to ensure a steady state for the hemodynamic response function, so the run lasted for 6 min and 24 s in total. During the homophone judgment condition, kanji character pairs were displayed and the participants were asked to judge whether the presented character pairs had the same pronunciation. During the line orientation judgment condition, two sets of lines were presented and the participants were required to respond whether the lines had the same orientation. Each character pair and each line pair was vertically arranged against a black background for 2000 ms with an interstimulus interval (ISI) lasting for 400 ms. Participants responded to the task with a button press using their right-hand. A fixation cross was displayed during the ISI and the rest blocks. It should be noted that the present study focused on homophone judgment, and the line orientation judgment condition served as a visuospatial control.

The task was presented using the E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA, USA). Participants went through a practice session of the task prior to entering the scanner suite. In the scanning session, participants were guided to minimize head movement in the scanner and stimuli were presented on a back projection via a mirror fixed onto the head coil.

2.4. Image acquisition

All imaging was performed in a 3 Tesla MR scanner (Tim Trio, Siemens, Erlangen, Germany) with a 12-channel quadrature head coil. The following sequences and image acquisition parameters were employed for all participants. The echo planar imaging (EPI) sequence was used to obtain functional images: repetition time (TR) = 3000 ms, echo time (TE) = 30 ms, flip angle (FA) = 90°, field of view (FOV) = 192 mm, 64 × 64 matrix, voxel size 3 mm × 3 mm, slice thickness 3 mm with 0.75 mm gap, and 39 axial slices with a total of 128 volumes. A T2-weighted image was acquired with TR = 5920 ms, TE = 95 ms, FA = 150°, FOV = 192 mm, 256 × 256 matrix, voxel size = 0.8 mm × 0.8 mm, slice thickness 3 mm with 0.75 mm gap, and 39 axial slices. A high resolution T1-weighted 3D MPRAGE whole-brain scan was also acquired using TR = 2500 ms, TE = 2.63 ms, FA = 7°, FOV = 256 mm, and voxel size 1 × 1 × 1 mm^3.

2.5. Behavioral data analysis

Accuracy rate and reaction time for the homophone judgment task were analyzed for each participant. They were allowed to respond during the stimulus display and the ISI. Inaccurate responses occurred when participants incorrectly identified homophones in a non-homophonic pair and vice versa. Omission occurred when participants failed to respond during the allocated time (stimulus display + ISI). Accuracy rate was defined as the proportion of accurate responses over total possible responses excluding omissions. Mean reaction time was calculated by the average of all reaction time of accurate trials only. Independent-samples *t*-tests were conducted to examine if the young and the elderly groups had different performance in terms of accuracy rate and reaction time.

2.6. Image analysis

Functional image preprocessing and analyses were performed using Statistical Parametric Mapping software (SPM8; Wellcome Department of Cognitive Neurology, London, UK) in Matlab (Mathworks Inc., Sherborn, MA, USA). All structural and functional images were reoriented to the origin at the anterior commissure. Thereafter, preprocessing of images followed a conventional procedure which included slice timing correction to the middle slice acquired in time (Sladky et al., 2011), realignment to the first volume, co-registration of structural images to functional images,

Fig. 1. The fMRI task paradigm. F: fixation (i.e., rest condition); L: line orientation judgment; H: homophone judgment. Each block lasted for 24 s.

normalization to the Montreal Neurological Institute (MNI) space, and smoothing using a Gaussian kernel of 8 mm full-width at half-maximum (FWHM).

General linear model (GLM) was used to access condition-specific effects through the convolution with a canonical hemodynamic response function for each participant. The homophone judgment condition was contrasted with the rest condition to examine kanji processing. At the second-level analysis, a random-effect one-sample *t*-test was applied on all participants in each group to obtain the group activation maps. In addition, an independent-samples *t*-test was conducted to compare activation differences between the young and the elderly groups.

Voxel-based morphometry (VBM) analysis (Ashburner & Friston, 2000) using the VBM8 toolbox in SPM8 was employed to extract the volumes of gray matter (GM), white matter (WM) and cerebrospinal fluid (CSF). Values of the total intracranial volume were computed and the ratio of gray matter volume to the total intracranial volume was used as a covariate in the subsequent data analysis to rule out brain size differences between the young and the elderly due to atrophy in normal aging (Devanand et al., 2007).

2.7. Effective connectivity

Five a priori regions-of-interest (ROIs) were specified in the left hemisphere for the homophone judgment contrast: IOG (BAs 17/18), FG (BA 37), MFG (BA 9), ventral IFG (BA 47) and dorsal IFG (BA 44). An anatomical mask was created for each ROI using the WFU PickAtlas tool (Maldjian, Laurienti, Kraft, & Burdette, 2003; available at fmri.wfubmc.edu/software/PickAtlas) in SPM8 and then applied to the activation map of each group (thresholded at $p < 0.001$ uncorrected with clusters $\geqslant 20$ voxels) to obtain the group maximum within each ROI (see Fig. 2A for an illustration of the ROI locations and Table 1 for group maxima of the ROIs). At the individual level in each group, the activation maps were thresholded at $p < 0.005$ (uncorrected) and the ROI masks were applied. Volumes of interest (VOIs) were defined as 8 mm radius spheres centered at the peak coordinates within the ROI masks, and the eigenvariates of the activated voxels within the VOIs were extracted as regional responses. The distance between the centers of the individual VOIs and the group maxima was controlled within 10 mm. However, for cases where the distance exceeded 10 mm, the next strongest coordinate was specified as the centers of VOIs

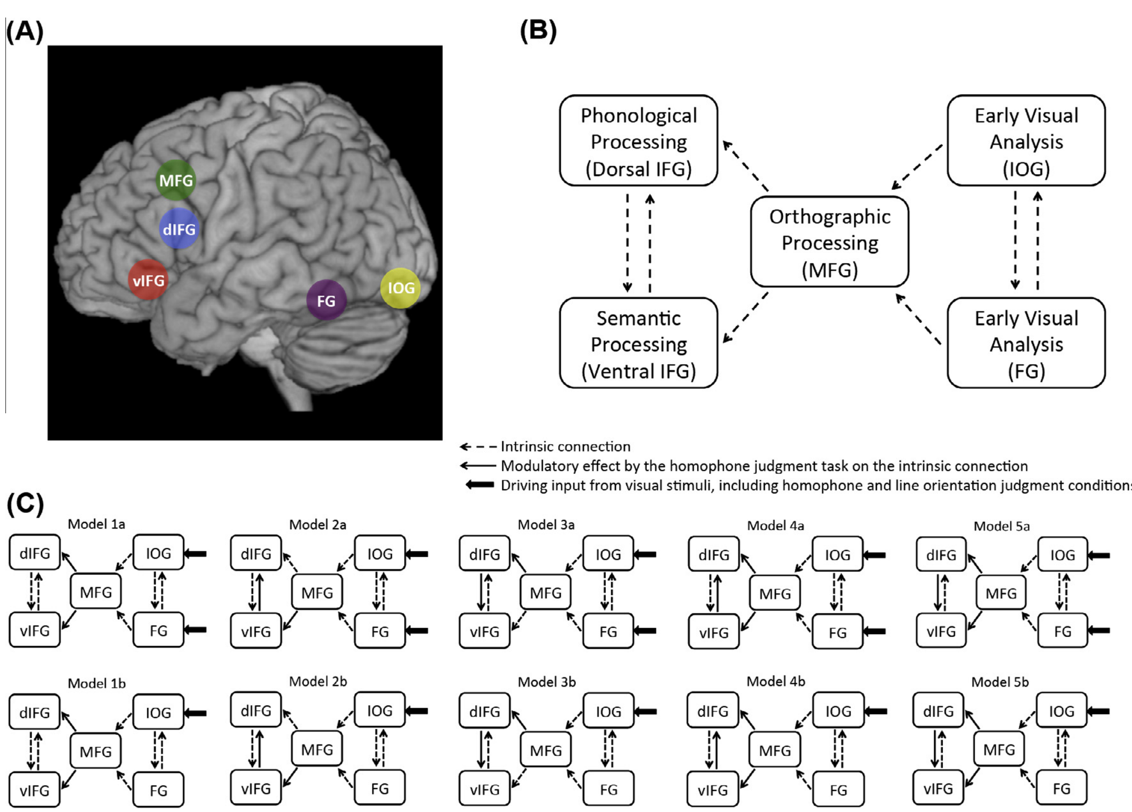

Fig. 2. Regions-of-interest and models. (A) An illustration of the approximate locations of the left-hemispheric ROIs. (B) The intrinsic connections within the proposed models. (C) Ten proposed models for comparison, which differed in the modulatory effects by the homophone judgment condition and the driving inputs from the visual stimuli conditions. IOG: inferior occipital gyrus; FG: fusiform gyrus; MFG: middle frontal gyrus; vIFG: ventral inferior frontal gyrus; dIFG: dorsal inferior frontal gyrus.

Table 1
MNI coordinates of the group maxima in the ROIs.

Region	BA	Young				Elderly			
		x	*y*	*z*	*T*	*x*	*y*	*z*	*T*
Fusiform gyrus	37	−48	−57	−16	11.56	−33	−48	−20	10.5
Inferior occipital gyrus	17/18	−36	−84	−8	8.54	−36	−84	−8	18.75
Middle frontal gyrus	9	−42	9	29	10.99	−45	3	41	10
Ventral inferior frontal gyrus	47	−42	18	−1	5.97	−48	18	−5	8.68
Dorsal inferior frontal gyrus	44	−54	9	18	8.07	−57	3	18	9.55

Notes: Coordinates of the largest *T* values within the ROIs were selected from the one-sample *t*-tests on all participants in each group (young $n = 20$, elderly $n = 15$; $p < 0.001$ uncorrected with minimum clusters $\geqslant$ 20 voxels). BA: Brodmann Area.

until the distance was within 10 mm from the group maxima. This criterion was adopted to ensure that the individual VOIs did not fall out of the ROI and were not distantly located at different regions within the ROI. Two young participants were excluded from the subsequent effective connectivity analysis as they did not show significant activation within at least one ROI. Moreover, the distance between two VOIs was calculated to ensure that the neighboring VOIs did not contain overlapping data.

Effective connectivity analysis was performed with the DCM10 tool provided in SPM8 (Friston, Harrison, & Penny, 2003; Penny, Stephan, Mechelli, & Friston, 2004) using the following parameters: slice timing for each region set as the timing of the reference slice at the slice timing correction in preprocessing (Kiebel, Klöppel, Weiskopf, & Friston, 2007), echo time = 0.03 s, bilinear modulatory effects, one state per region, and no stochastic effects. DCM is a nonlinear systems identification procedure based on a generic Bayesian framework to make inferences about the underlying connectivity between neural regions and how this connectivity might be influenced by experimental manipulations (Stephan et al., 2010). It quantifies neurobiological activity as posterior estimates, which could be taken to refer to the effective strength of neural connectivity among neuronal states and their context-dependent modulation (Stephan et al., 2010). In DCM, three parameters were estimated: intrinsic connections between regions, the modulatory effects of experimental manipulations on intrinsic connections, and the direct influence of the experimental task on regional neuronal activity.

To examine the kanji reading process within the language network, five modulated pathways from orthographic to phonological and semantic processing were proposed. Task modulation effect was specified using the homophone judgment condition. In Model 1, the homophone judgment condition modulated the connections from MFG to ventral IFG and dorsal IFG in parallel. Model 2 represented a sequential processing where the homophone judgment condition modulated the connections from MFG to ventral IFG and from ventral IFG to dorsal IFG, whereas for Model 3 task modulation took place on the connections from MFG to dorsal IFG and from dorsal IFG to ventral IFG. Similar to Model 1, Models 4 and 5 included task modulations on the connections from MFG to ventral IFG and dorsal IFG in parallel, but they had an additional modulation on the connection from ventral IFG to dorsal IFG (Model 4) or in the other direction (Model 5). All models shared the same intrinsic connections, including bidirectional connections between IOG and FG, from IOG and FG to MFG, from MFG to ventral IFG and dorsal IFG, and bidirectional connections between ventral IFG and dorsal IFG (Fig. 2B). For driving inputs, while both IOG and FG have been shown to be associated with external kanji word stimuli (Sakurai et al., 2000), electrophysiological studies suggest that the processing latency of the occipitotemporal cortex is earlier than that of the fusiform gyrus (Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). Hence, for each model, we also examined whether general visual inputs (including both homophone judgment and line orientation judgment conditions) influenced on either both IOG and FG (Models 1a, 2a, 3a, 4a and 5a) or IOG only (Models 1b, 2b, 3b, 4b and 5b). This resulted in 10 models for comparison (Fig. 2C).

Model comparison was performed using random effects Bayesian Model Selection (BMS; Stephan, Penny, Daunizeau, Moran, & Friston, 2009), which accounts for inter-subject heterogeneity explicitly. The BMS method estimates the parameters of a Dirichlet distribution, which entails the probabilities of all models considered in the model space. The Dirichlet distribution can be used to compute the expected likelihood of which one particular model generates the data of a random subject or the exceedance probability (xp) that one model is more likely than any other models compared. We extracted the exceedance probabilities for models ranking at the group level. The model with higher exceedance probability provides more confidence that this model is more superior compared to the other models given the group data. In the current study, two steps of model selection were performed in each group. The first step was conducted to determine whether visual inputs modulated on both IOG and FG or on IOG only. Model space partitioning was used to compare two partitions of the models, i.e., Models 1a to 5a versus Models 1b to 5b. After the winning partition was selected, a random effects BMS was performed to select the optimal model with the highest exceedance probability. For the winning model, one-sample *t*-tests were conducted to test the significance of the parameters of each intrinsic connection, modulatory effect, and driving input within each group.

3. Results

3.1. Behavioral performance

The *t*-test on accuracy scores of the kanji reading test showed no significant age differences between the young ($M = 99.7$, $SD = 0.57$) and the elderly participants ($M = 99.6$, $SD = .63$), $t(33) = 0.49$, $p = .63$, at $\alpha = .05$ level. The results for the accuracy rate of the homophone judgment task also observed no significant differences between the young ($M = 95.2$, $SD = 4.78$) and the elderly groups ($M = 95.5$, $SD = 5.99$), $t(33) = -0.17$, $p = .86$, at $\alpha = .05$ level. On the other hand, significant age differences were found for reaction time in the homophone judgment task between the young ($M = 1167$, $SD = 158$) and the elderly participants ($M = 1359$, $SD = 154$), $t(33) = -3.58$, $p = .001$, at $\alpha = .05$ level. As a result, reaction time and ratios of gray matter to the total intracranial volume were used as covariates in all subsequent group comparison analyses to rule out any potential influence of reaction time and atrophy on brain activity (see Table 2 for the summary of behavioral performance).

3.2. fMRI analysis

The young and the elderly participants showed a similar pattern of activation for the homophone judgment task in the left inferior frontal gyrus, the left middle frontal gyrus, the left parietal regions,

Table 2
Summary of demographics and behavioral performance.

	Young (12 males, 8 females)		Elderly (8 males, 7 females)	
	Range	*M* (*SD*)	Range	*M* (*SD*)
Age	20–37	22.9 (4.49)	62–69	66.1 (2.12)
MMSE	28–30	29.5 (0.61)	27–30	28.9 (1.03)
Reading test accuracy	98–100	99.7 (0.57)	98–100	99.6 (0.63)
Task accuracy (%)	86–100	95.2 (4.78)	78.6–100	95.5 (5.99)
Task reaction time (ms)	935–1463	1167 (158)	1162–1710	1359 (154)

Notes: Results were obtained after the removal of 3 participants from the young group and 9 from the elderly group. Total sample size = 35. No significant age group differences were found for reading and homophone judgment accuracy scores, whereas significant age differences were found for homophone judgment reaction time at $\alpha = .05$ level.

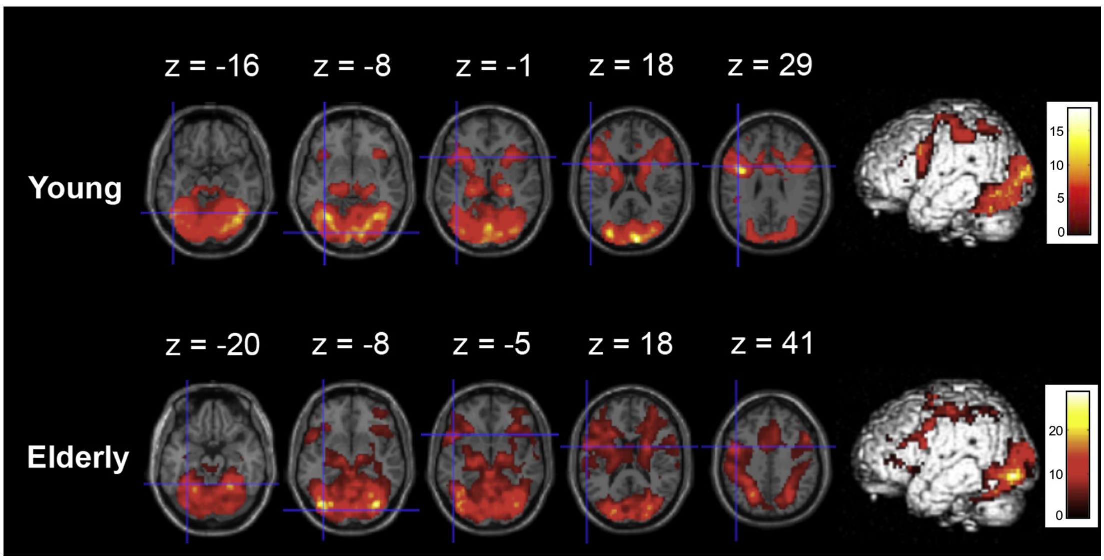

Fig. 3. Brain activation maps for the homophone judgment > fixation contrast for the young and the elderly groups. The slice views showed the activation at the group maxima for the ROIs ($p < 0.001$ uncorrected with minimum clusters $\geqslant$ 20 voxels). For visualization purpose, the rendered images on the rightmost column were thresholded at $p < 0.05$ (FWE corrected) to distinguish the activation clusters.

and the bilateral ventral occipito-temporal regions (Fig. 3). The independent-samples *t*-test showed no significant activation difference between the two groups at the threshold of $p < 0.001$ with an extent of 20 voxels, with reaction time and gray matter volume ratio controlled as covariates.

3.3. Bayesian model selection

For the young group, the initial model space partitioning revealed a very strong preference for the group of models with driving inputs on the IOG only (Models 1b, 2b, 3b, 4b and 5b; xp = 0.99) compared to the other group of models with driving inputs on both IOG and FG (Models 1a, 2a, 3a, 4a and 5a: xp = 0.01). The next model selection analysis was conducted on the models in the winning group. The highest exceedance probability was found in Model 2b (xp = 0.46), in which the homophone judgment condition modulated the connections from MFG to ventral IFG and from ventral IFG to dorsal IFG. The exceedance probabilities for the other models were 0.10 (1b), 0.35 (3b), 0.04 (4b), and 0.05 (5b). The elderly group also showed a strong preference for the partition of models with driving inputs on the IOG only compared to the other (xp = 0.95 versus 0.05). The model selection analysis within the “IOG only” group resulted in the highest exceedance probability for Model 3b (xp = 0.54), while the exceedance probabilities for the other models were 0.19 (1b), 0.13 (2b), 0.04 (4b), and 0.10 (5b). In Model 3b, the homophone judgment condition modulated the connections from MFG to dorsal IFG and from dorsal IFG to ventral IFG.

3.4. Parameter estimates in the selected model

The mean parameter estimates of the intrinsic connections, modulatory effects, and driving inputs within the selected model for each age group are summarized in Fig. 4. One-sample *t*-tests were performed to examine if the parameter estimates were significant, with Bonferroni correction for multiple comparisons at the alpha level of 0.05. For both groups, most of the intrinsic connections were significant in each age group, except for the intrinsic connections from FG to MFG (young: $M = -0.10$, $SD = 0.29$, $t(17) = -1.48$, $p = .16$; elderly: $M = -0.35$, $SD = 0.43$, $t(14) = -3.16$, $p = .007$) and from ventral IFG to dorsal IFG (young: $M = -0.075$, $SD = 0.30$, $t(17) = -1.07$, $p = .30$; elderly: $M = -0.073$, $SD = 0.19$, $t(14) = -1.47$, $p = .17$), at the corrected threshold of $p < .006$. The modulatory effects and the driving input were also significant for each age group. As different models were selected for the young and the elderly participants, direct comparisons of the parameter estimates between two groups were not meaningful.

4. Discussion

In the current study, an fMRI homophone judgment task with kanji character pairs was applied to examine age-related effects

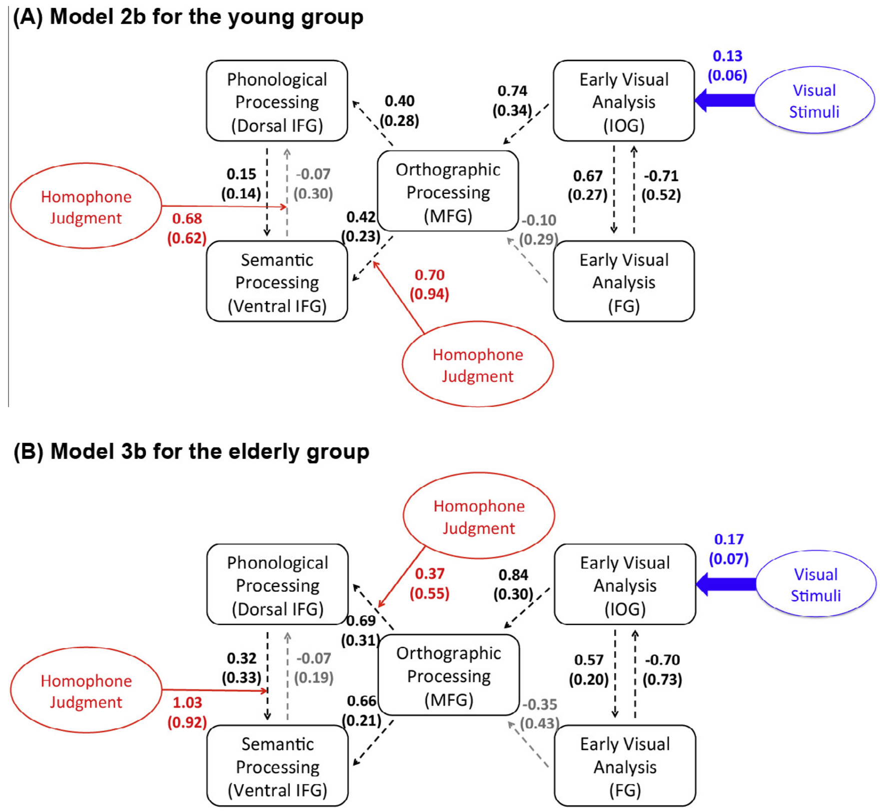

Fig. 4. DCM parameter estimates of the selected (A) Model 2b for the young group and (B) Model 3b for the elderly group. The numbers along-side connections or modulations summarize the *M*(*SD*) of parameter estimates (in Hertz). The significance of parameter estimates was examined using one-sample *t*-tests, with Bonferroni correction for multiple comparisons at the alpha level of 0.05. The dashed lines in black indicate significant intrinsic connections ($p < .006$), whereas the dashed lines in gray are insignificant intrinsic connections. The red arrows represent significant modulatory effects from the homophone judgment condition ($p < .025$), while the blue arrows indicate significant driving input from visual stimuli ($p < .05$).

on character reading processes. We aimed to identify the pathway models of kanji reading for young and elderly Japanese speakers, and investigate whether the reading network might be influenced by healthy aging. Voxel-wise analysis did not show differences in regional brain activation between the young and the elderly adults. The Bayesian model selection revealed higher probabilities for sequential pathways for both groups. However, the young adults showed a preference to adopt a semantically-mediated pathway from the orthographic input to the phonological output (Model 2b), whereas the elderly activated phonological processing directly after orthographic input, followed by semantic processing (Model 3b). Although no age-related differences were found in regional brain activation, effective connectivity analysis demonstrated differential reading pathways for young and elderly adults. These findings highlight the importance of examining effective connectivity for studying aging effects on the neural networks underlying language processing.

4.1. Age effects on regional activation

Our results showed that the elderly participants had a similar pattern of activation as the young participants, indicating that no age-related changes were found in the Japanese homophone judgment task. To the best of our knowledge, this is the first study that investigates aging effects on the neural mechanism underlying kanji processing in Japanese speakers. The lack of age-related changes seems to be inconsistent with previous findings from alphabetic language speakers. For instance, Shafto et al. (2009) demonstrated that older adults showed reduced activity in the left insula during tip-of-the-tongue states when they had word-finding failures in a picture naming task; Meinzer et al. (2009) found increased activity in the right frontal regions in older adults, which was associated with poorer performance in a semantic fluency task. By contrast, no age-related changes in the neural activity were observed in the homophone judgment task in the current study, suggesting that the neural mechanism supporting language processing may be relatively preserved in older Japanese speakers. However, the discrepancies in findings could be attributed to several reasons given that the studies differ in many aspects, such as task paradigms, scanning protocols, and participant populations. Although our findings have a potential implication that aging might have differential effects on the neural representations of language processing across different language systems, direct comparisons between findings across studies are limited. Hence, more research is required before a solid conclusion could be drawn.

An alternative explanation is that the homophone judgment task did not tax the participants' cognitive resources enough to show age-related changes, especially since the kanji characters chosen were of the elementary level and both groups achieved very high accuracy rates (above 95%) in the task. The resources view proposed by Craik and Byrd (1982) states that processing capacity is supported by a limited supply of attentional resources that decrease with age. Thus, older adults would need to take on more neural units through engaging other brain areas, such as the contralateral homologous regions and other less specialized brain areas, to cope with the cognitive demands. According to the resources view, age-related deficits tend to be most pronounced with high cognitive loads, since the elderly have less attentional resources as compared to the young to deal with an increase in cognitive loads (Craik & Byrd, 1982). It is plausible that the homophone judgment task in the current study was not demanding enough to induce significantly different loads of attentional resources to be reflected in brain activation.

4.2. The kanji reading pathways

We first examined whether the driving input from general visual stimulation modulated the activity in both IOG and FG, or IOG only in the left hemisphere. For both the young and the elderly groups, the family-level comparison revealed very clear preference for the models with driving input on IOG only, indicating that IOG is the primary area for visual processing in the proposed reading network. Moreover, there was a positive intrinsic connection from IOG to FG, suggesting that the activity in IOG has a positive influence on the activity in FG. Our findings are in line with the electrophysiological evidence for face recognition, which have reported two event-related potential components located at the bilateral inferior occipital and temporal cortices. One N170 component was identified from the bilateral posterior lateral occipitotemporal source for structural encoding of faces and the other N250 component from the bilateral fusiform gyri for face recognition (Schweinberger et al., 2002). This shows that the processing latency of the occipitotemporal cortex is earlier than that of the fusiform gyrus, suggesting that the information processing may flow from IOG to FG in a reading network. While the parameter estimates for all other intrinsic connections were positive, only the connection from FG to IOG was negative. The negative parameter estimate indicates that there is a negative effect or ''inhibition'' from one region to the next; in other words, the increase of activation in one region is correlated with the decrease of activation in the other region. In this case, it appeared that while IOG sent excitatory influence to FG, the activation of FG inhibited the activation of IOG in return. This finding could be interpreted as the following: after visual information is transferred from IOG to FG for recognition processes, the activity in IOG would be suppressed and relevant information would be delivered to the next brain region (e.g., MFG in our models) for further processing.

While comparable parameter estimates for the driving input and intrinsic connections were shown for the young and the elderly adults, age-related differences were observed in the task modulatory effects. At the second-stage model selection, higher exceedance probability was found for a sequential model relative to a parallel model (Model 1) or a combined model (Models 4 and 5) in both young and elderly adults. In particular, the young adults showed preference for the sequential pathway in which task modulated the connections from MFG to ventral IFG and then from ventral IFG to dorsal IFG in the left hemisphere. This sequential pathway might reflect the lexical semantic route in the dual-route cascaded (DRC) model, in which the orthographic inputs are linked to the semantic lexicons prior to the activation of phonological outputs (Coltheart et al., 2001). On the other hand, the elderly preferred the other sequential pathway in which task modulated the connections from MFG to dorsal IFG and then from dorsal IFG to ventral IFG in the left hemisphere. This pathway might represent a sequential processing from orthographic to phonological, followed by semantic systems, and it is partly similar to the lexical non-semantic route in the DRC model, in which the activation of phonological lexicon output may or may not link to semantic lexicon but directly links to the phoneme system for speech generation (Coltheart et al., 2001). The finding of different winning models for the young and elderly adults indicated that differential reading pathways were adopted by different age groups even in the same task circumstances.

Studies have shown that the selection of processing pathway for reading may be an automatic process that depends on word properties (Levy et al., 2009; Zevin & Balota, 2000) or task requirement (Bitan et al., 2005). The efficiency of alternating between different reading pathways according to the word stimuli, i.e., using the lexical route for reading real words and the GPC route for pseudowords, was found to be correlated with reading performance (Levy et al., 2009). Our results showed a shift from the lexical semantic pathway in the young adults to the lexical non-semantic pathway in the elderly under the same task, which demonstrated that the selection of reading pathway may also be influenced by aging. It should be noted that for the young adults Model 3b (orthographic–phonological–semantic, xp = 0.35) showed comparably high model exceedance probability as Model 2b (orthographic–semantic–phonological, xp = 0.46), while for the elderly Model 3b was more prominent compared to the other models. In light of the aforementioned evidence of pathway selection, individuals might select a reading pathway among the alternatives depending on the task conditions or their own reading style. Therefore, we postulate that both routes might be readily available for young adults as shown in high exceedance probabilities for Model 2b and Model 3b. The young adults were able to alternate between the two pathways depending on the properties of the encountered kanji characters. As age increased, however, the older adults shifted towards the lexical non-semantic pathway, in which the orthographic information directly activated phonological processing and the semantic information only became available later.

The shift in the selection of reading pathways might reflect neurocognitive changes between the two age groups. Under the homophone judgment condition, rather than recourse to the semantic representations prior to retrieving the phonological lexicons, the elderly tend to link the orthographic inputs directly to phonological processing. However, as implicated in significantly slower reaction time for the elderly as compared to the young adults, the direct mapping from orthographic inputs to their phonological representations did not appear to be a more efficient pathway for homophone judgment. The direct pathway with yet longer reaction time might suggest declined efficiency of the connections within the reading network for the older adults. The current findings for the reading network may have important implications for the neural mechanisms underlying common language problems in older adults. For instance, word-finding failures may not only result from changes in regional activation (Meinzer et al., 2009; Shafto et al., 2009) but also from reduced connectivity efficiency within the word production network. This view is in line with the transmission-deficit model, which postulates that production failures could occur when aging weakens the connections between nodes in the language production model (Burke & Shafto, 2004).

Furthermore, the preference for the semantically-mediated pathway in the young adults may imply the importance of semantic information in mediating the retrieval of phonological representations in reading Japanese kanji. Many of the Japanese kanji characters have more than one pronunciation, and the correct pronunciation is determine by the context. Therefore, recourse to semantic processing after the recognition of orthographic forms might help the retrieval of possible pronunciations. The elderly, however, failed to make use of this semantically-mediated pathway. Nevertheless, it should be taken into account that the results might simply reflect individual differences in strategy selection for reading among the sampled participants. To distinguish between individual preference or age-related changes in reading strategies requires longitudinal studies and larger samples to be examined.

4.3. Limitations

While the current study provides novel insights to the understanding of Japanese kanji processing, several limitations should be considered. The first limitation is the small and unequal sample size: 12 males and 8 females in the young group, whereas 8 males and 7 females in the elderly group. Future studies with larger and equal samples are warranted to verify the consistency of the reading pathway networks in different age cohorts. Second, the current study compared several candidate models focusing on the dynamics among orthographic, phonological, and semantic processing under task modulation. However, it is important to note that there may be other pathway models of kanji processing (e.g., Sakurai et al., 2000; Sasanuma, 1975). Moreover, the area of study is limited within the scope of specified left-hemispheric ROIs. The results of the current study would not be able to provide information about age-related effects on bilateral effective connectivity and thus the interplay between intra- and inter-hemispheric language networks. Future studies are needed to test other possible models of kanji processing and include homologous brain regions in the right hemisphere in addition to the specified ROIs.

5. Conclusion

We employed DCM with fMRI to examine the neural networks underlying kanji reading in young and elderly participants. Although no age-related differences were observed in functional activation and behavioral accuracy rate, we demonstrated that aging had effects on the effective connectivity of the language network, suggesting changes in reading strategies for the elderly. Aging effects on the neural mechanism underlying language processing have not caught much attention in the aging literature most likely because previous studies suggest that verbal ability as one domain of crystallized intelligence may be increased or preserved with aging due to accumulated knowledge and experience (Giambra et al., 1995; Verhaeghen, 2003). However, the current study demonstrated that aging had effects on the connectivity level within the left-lateralized language network. These findings highlight the importance of examining connectivity in the neural network for understanding aging effects on language processing. In addition, more research is necessary to resolve age-effects on inter-hemispheric connectivity within the whole-brain language network.

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