# Heliyon



Received: 31 January 2016 Revised: 26 May 2016 Accepted: 11 October 2016

Heliyon 2 (2016) e00180



## Grammatical markers switch roles and elicit different electrophysiological responses under shallow and deep semantic requirements

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#### Abstract

Static knowledge about the grammar of a natural language is represented in the cortico-subcortical system. However, the differences in dynamic verbal processing under different cognitive conditions are unclear. To clarify this, we conducted an electrophysiological experiment involving a semantic priming paradigm in which semantically congruent or incongruent word sequences (prime nouns–target verbs) were randomly presented. We examined the event-related brain potentials that occurred in response to congruent and incongruent target words that were preceded by primes with or without grammatical case markers. The two participant groups performed either the shallow (lexical judgment) or deep (direct semantic judgment) semantic tasks. We hypothesized that, irrespective of the case markers, the congruent targets would reduce centro-posterior N400 activities under the deep semantic condition, which induces selective attention to the semantic relatedness of content words. However, the same congruent targets with correct case markers would reduce lateralized negativity under the shallow semantic condition because

grammatical case markers are related to automatic structural integration under semantically unattended conditions. We observed that congruent targets (e.g., 'open') that were preceded by primes with congruent case markers (e.g., 'shutterobject case') reduced lateralized negativity under the shallow semantic condition. In contrast, congruent targets, irrespective of case markers, consistently yielded N400 reductions under the deep semantic condition. To summarize, human neural verbal processing differed in response to the same grammatical markers in the same verbal expressions under semantically attended or unattended conditions.

Keyword: Neuroscience

## 1. Introduction

Grammatical knowledge in natural language is often biologically distinguishable from other cognitive components, such as inference, reasoning, and intension [1], because of the domain specificity of the modularity of grammatical computation [2, 3]. Grammatical processing is related to the construction of verbal structures in the production and comprehension of complex verbal contents. In the English language, verbal processing that is based on grammatical knowledge requires a number of procedures, such as the checking of verb inflection (e.g., "He swims."), tense agreement of the verbs (e.g., 'Yesterday, he *swam*'), or case agreement of the pronouns before and after the verbs (e.g., "He likes him."). However, in contrast to content words, function words are sometimes ignored or omitted in ordinary language usage [4, 5]. The Japanese language is a head-final language with a subject/object/verb (SOV) word order. It overtly represents the relationship of nouns to verbs or other predicates with a case marker called a particle, which is attached immediately after a noun to indicate the syntactic role of the noun that is licensed as, for example, a subject ('-ga') or an object ('-o'). However, case markers are often deleted in colloquial speech. In Japanese, for example, the object case '-o' is deleted from the pronoun 'kare' ('him') in "kare (-o) mita?" ("Have you seen him?"). Although such omission phenomena are not ubiquitously observed across languages, theoretical investigations of static grammatical knowledge have suggested that verbal expressions in which function words do not appear overtly should be analyzed like those with overt function words with the support by phonologically covert elements [6]. In the above example, the pronoun 'kare' ("him") does not possess an overt object case marker '-o', but it is assumed to be the object in the presence of a covert case feature, such as [+ object case], which is supposed to be positioned immediately before the verb. The inevitable question about dynamic verbal processing is whether neural language processing is the same depending on function words. Some tension lies between linguistic knowledge and performance in a neural representation of natural language [7] because we do not always use a language as we know. For instance, we know that it is more informative and grammatically rigid to have a subject in a sentence, but in

colloquial or spoken Japanese, a subject word is often omitted in a casual manner, such as 'kinou/hon-o/yonda' ("yesterday"/"book-object"/"read"), which means "I read a book yesterday".

Based on the distinction between syntactic and semantic processing [8], function words may affect the processing of content words differently depending on whether the task requires simple lexical decisions of content words [shallow (SHL) semantic task] or when it requires explicit judgments on the semantic relationships between content words [deep (DP) semantic task]. When the processing of semantic contents is not required, as in a SHL semantic task, the syntactic properties of sentences are automatically assessed, which induces structural integration. Structural integration can be associated with procedural memory, which drives the automatic computation of a rule-based product or a verbal structure. This is likely supported by cortical areas, such as the inferior frontal gyrus and superior temporal area [9, 10].

In contrast, when the task requires semantic retrieval, as in a DP semantic task, function words may receive less attention. This may be more obvious in languages like Japanese that use explicit function words. Although automatic grammatical processing can take place under DP semantic conditions, the selective attention to sematic relatedness might result in the ignoring of function words and promoting of the semantic retrieval of lexical information, which would change the neurophysiological responses [11]. Attended semantic processing is thought to be related to declarative memory, which explicitly retrieves semantic information, and this is likely supported by a number of cortical areas [12, 13].

Task-dependent differences in verbal processing because of function words might be related to different event-related brain potential (ERP) effects. Function words in a SHL semantic condition may induce automatic syntactic processing, which is reflected by changes in lateralized negativity (LN). LN frequently has a leftlateralized, anterior-dominant distribution (left anterior negativity: LAN). LAN is elicited in syntactic violation paradigms, such as case [14, 15] and morphosyntactic agreement [16, 17, 18, 19] violations, which suggests that LAN is related to morpho-syntactic processing [8]. Alternatively, a DP semantic condition, which likely facilitates semantic processing that is based on lexical contents, yields changes in centro-posterior negative responses (N400) [20, 21, 22]. Changes in N400 have been observed in response to semantic anomalies: semantically deviant words elicited larger N400 responses than congruent words did [23]. Additionally, the N400 appears in response to semantically congruent (SC) but unexpected words [24]. Given that the N400 is not limited to violation paradigms, this component has been suggested to be related to semantic integration load [25, 26].

Based on this ERP distinction, the present study aimed to examine the influence of grammatical congruency (i.e., correct/incorrect use of function words) on simple

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sentence processing. We assumed that different ERP components would be affected depending on whether the task required DP semantic processing or not. For this purpose, we used a semantic priming paradigm [27] in which SC or semantically incongruent (SI) words (prime nouns-target verbs) were presented in order. In this paradigm, congruent targets, in contrast to incongruent ones, generally decrease N400 potentials [28]. The reduced N400 effects reflect the attenuation of the neural activity underlying the processing of the congruent targets because of the prospective activity of the neural populations that represent the targets [12, 29]. Concerning grammatical congruency, previous priming studies have not investigated how grammatical words spatio-temporally affect N400 and/ or LN activities for semantic relatedness. However, grammatical congruency likely promotes automatic structural processing and, hence, reduces the LN activity of structural integration, as has been suggested by syntactic violation studies [14, 15, 16, 17, 18, 19].

Therefore, we prepared four experimental conditions. These conditions comprised an SI condition, which was used as a baseline for the comparisons, and three congruent conditions, depending on the presence or absence of case markers in prime words and, if present, the correct or incorrect choice of case markers: an SC condition without a case marker, an SC condition with a congruent case marker (SC/GC), and an SC condition with an incongruent case marker (SC/GI). These conditions were compared within and between SHL (lexical judgment about nonwords) and DP (explicit judgment about the semantic relatedness among words) semantic tasks. Taken together, the neurophysiological changes in verbal processing with or without case markers were investigated by examining the negative potentials in the SC conditions compared to those in the SI condition under different types of semantic attention.

We predicted that the SC/GC condition with congruent case markers would induce automatic structural integration in the SHL task and consequently reduce the LNs for target words compared to those in the SI condition. However, the SC/GI condition with incongruent case markers would increase the LNs in response to case violation compared to those in the SI condition. In the DP task, the congruent targets (SC, SC/GC, and SC/GI) were predicted to produce N400 reductions and not affect the LNs compared to the SI targets because case markers are usually ignored in attended semantic processing, which is driven by the direct semantic retrieval of lexical information. Taken together, an investigation of these ERP effects will elucidate whether grammatical case markers are processed similarly under SHL and DP semantic conditions.

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## 2. Materials and methods

## 2.1. Participants

Both participant groups consisted of 13 healthy Japanese participants. One participant group performed the SHL task, and the other group conducted the DP task. Both groups were matched for sex (SHL: 8 men, 5 women; DP: 10 men, 3 women; Fisher's exact test, p = 0.673), age [SHL: mean  $\pm$  standard deviation, 21.6  $\pm$  3.7 years; DP: 20.7  $\pm$  2.3 years;  $t_{(24)} = 0.757$ , p = 0.456], handedness [laterality quotient: SHL, 0.95  $\pm$  0.07; DP: 0.93  $\pm$  0.10;  $t_{(24)} = 1.120$ , p = 0.274] [30], short-term verbal working memory [reading span: SHL, 3.1  $\pm$  1.1; DP: 3.2  $\pm$  0.9;  $t_{(24)} = 0.198$ , p = 0.845] [31], and long-term verbal memory [estimated vocabulary transformed into z-scores: SHL,  $-0.151 \pm 1.179$ ; DP: 0.151  $\pm$  0.853;  $t_{(24)} = 0.075$ , p = 0.46; vocabulary test: http://www.kecl.ntt.co.jp/icl/mtg/goitokusei/goi-test. html]. The participants confirmed that they did not have any neurological or psychological illnesses. The participants provided written informed consents in accordance with the Declaration of Helsinki. The study was approved by the Human Subjects Ethics Committee of Tokyo Metropolitan University.

## 2.2. Experimental tasks

Two experimental tasks were prepared for the participant groups. Both tasks included four types of Japanese word sets (Fig. 1A). For the baseline comparison condition, we prepared an SI condition, in which incongruent prime nouns preceded the target verbs. The prime nouns did not possess grammatical case markers [SI: 'amado/samasu' ("shutter/cool")]. The SC conditions comprised three types of stimulus sets that differed according to the presence or type of case markers that were attached to the primes. The first SC condition included congruent prime nouns without case markers in order to examine the effects of semantic relatedness without case markers on ERP [SC: 'amado/akeru' ("shutter/ open")]. The second congruent condition involved SC primes with congruent object case markers [SC/GC: 'amado-o/akeru' ("shutter-object case/open")]. This condition was included to investigate how congruent case markers affected the processing of semantic relatedness. The third SC condition included SC primes with incongruent subject case markers [SC/GI: 'amado-ga/akeru' ("shutter-subject case/open")]. The SC/GI condition was introduced to explore how incongruent case markers canceled the ERP effects of the semantic associations.

In the SHL task, the participants decided whether the stimulus sequences involved non-words as soon as the target verbs appeared. They were not provided any information about the semantic relatedness of the nouns and verbs. In contrast, in the DP task, the participants viewed the same stimulus sets and directly determined the semantic relatedness of the content words. Both semantic tasks have been

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**Fig. 1.** The experimental procedure. (A) Four experimental conditions were prepared based on a semantic priming paradigm: (i) semantically incongruent (SI), (ii) semantically congruent (SC), (iii) semantically and grammatically congruent (SC/GC), and (iv) semantically congruent and grammatically incongruent (SC/GI) conditions. The grammatically congruent condition (SC/GC) included primes with a correct object case marker '-o', and the grammatically incongruent condition (GC/GI) comprised primes with the incongruent subject case marker '-ga'. All of the stimuli, except for the targets, appeared 500 ms (blank) after the preceding stimuli disappeared, and they were maintained for 300 ms (stimulus-onset-asynchrony: 800 ms). The targets remained on the cathode-ray-tube screen until the participants pressed a button on the response pad. (B) The two-dimensional scalp model of the locations of the 34 electrodes, which were in accordance with the International 10–20 System. The electrodes were used to conduct electroencephalography recordings, and they were clustered in sites (anterior, central, and posterior) in the lateral (left and right) and midline regions. The factor of site was included in the statistical tests.

shown to alter behavioral and ERP properties, and both are suited for investigating the task-related modulation of online verbal processing [32, 33, 34, 35].

#### 2.3. Experimental materials

A total of 448 word sequences were created for the present study. They consisted of 50 prime-target sets in each experimental condition (200 sets) and 248 filler sets. The prime nouns and target verbs were selected from a lexical database [36]. The prime-target combinations were repeated in the three SC conditions (SC, SC/GC, and SC/GI) to standardize the word processing. The prime-target pairs in the four experimental conditions are listed in Table 1. None of the prime nouns was a subjective agent. The target verbs were strongly transitive [e.g., the transitive verb 'a-keru' ("open") was used rather than the intransitive form 'a-ku' ("open")] and incongruent with the non-agents in the SC/GI condition. The primes and targets, which consisted of the three phonological units (mora), were rated as highly familiar based on a 7-point Likert scale (1 = "not familiar"; 7 = "familiar"; prime:  $5.96 \pm 0.32$ ; target:  $5.86 \pm 0.26$ ) [36]. As shown in Fig. 1A, the primes in the SC/ GC condition had a congruent object case marker [the suffix or sub-word element

<sup>6</sup> http://dx.doi.org/10.1016/j.heliyon.2016.e00180

No.	Prime noun		Congruent target verb		Incongruent target verb	
	Japanese	English	Japanese	English	Japanese	English
1	雨戸	Shutter	開ける	Open	冷ます	Cool
2	意見	Opinion	述べる	State	建てる	Build
3	遺産	Inheritance	分ける	Divide	閉める	Shut
4	遺体	Corpse	埋める	Bury	鳴らす	Sound
5	植木	Garden plant	枯らす	Wither	受ける	Take
6	獲物	Game	逃がす	Lose	溶かす	Melt
7	落葉	Leaves	燃やす	Burn	交わす	Exchange
8	会社	Company	辞める	Leave	惜しむ	Spare
9	会話	Conversation	交わす	Exchange	染める	Dye
10	片目	One eye	閉じる	Close	済ます	Finish
11	楽器	Instrument	鳴らす	Sound	過ごす	Spend
12	危険	Danger	避ける	Avoid	降ろす	Unload
13	期限	Deadline	延ばす	Extend	埋める	Bury
14	基準	Standard	満たす	Satisfy	浮かす	Save
15	休暇	Holiday	過ごす	Spend	着せる	Dress
16	疑惑	Doubt	晴らす	Dispel	分ける	Divide
17	故人	Deceased	惜しむ	Spare	下げる	Lower
18	国旗	National flag	揚げる	Fly	入れる	Take
19	御飯	Dinner	食べる	Eat	燃やす	Burn
20	財布	Wallet	落とす	Lose	述べる	State
21	座席	Seat	空ける	Leave	果たす	Accomplish
22	砂糖	Sugar	溶かす	Melt	伸ばす	Straighten
23	資金	Money	貯める	Earn	逃がす	Lose
24	試験	Examination	受ける	Take	借りる	Rent
25	事件	Incident	起こす	Cause	替える	Change
26	事実	Truth	告げる	Tell	空ける	Leave
27	下着	Underwear	替える	Change	終える	Finish
28	上位	Higher rank	占める	Occupy	開ける	Open
29	食費	Food expenses	浮かす	Save	避ける	Avoid
30	白髪	Grey hair	染める	Dye	上げる	Make
31	新居	New house	建てる	Build	晴らす	Dispel
32	背筋	Back	伸ばす	Straighten	止める	Cease
33	煙草	Smoking	止める	Cease	満たす	Satisfy
34	貯金	Savings	増やす	Increase	揚げる	Fly
35	戸棚	Cupboard	閉める	Shut	散らす	Throw

**Table 1.** The 50 prime-target pairs used in the semantically congruent (SC, SC/GC, and SC/GI) and incongruent (SI) conditions.

(Continued)

#### Table 1. (Continued)

No.	Prime noun		Congruent ta	rget verb	Incongruent target verb	
	Japanese	English	Japanese	English	Japanese	English
36	荷物	Luggage	降ろす	Unload	占める	Occupy
37	任期	Term	終える	Finish	下ろす	Withdraw
38	任務	Duty	果たす	Accomplish	落とす	Lose
39	値段	Price	下げる	Lower	起こす	Cause
40	眠気	Sleepy	覚ます	Wipe	延ばす	Extend
41	火花	Spark	散らす	Throw	辞める	Leave
42	麦茶	Barley tea	冷やす	Chill	閉じる	Close
43	浴衣	Summer cotton Kimono	着せる	Dress	立てる	Manage
44	用事	Job	済ます	Finish	貯める	Earn
45	洋書	Foreign book	借りる	Rent	告げる	Tell
46	預金	Deposit	下ろす	Withdraw	冷やす	Chill
47	予定	Schedule	立てる	Manage	覚ます	Wipe
48	予約	Reservation	入れる	Take	枯らす	Wither
49	利益	Profit	上げる	Make	食べる	Eat
50	緑茶	Green tea	冷ます	Cool	増やす	Increase

SC: semantically congruent; SC/GC: semantically and grammatically congruent; SC/GI: semantically congruent and grammatically incongruent.

'-o'; for example, 'amado-o' ("shutter-object case")]. The primes in the SC/GI condition had an incongruent subject case marker [the suffix '-ga'; for example, 'amado-ga' ("shutter-subject case")]. In the SI condition, the same 50 targets were pseudo-randomly paired with the primes. The semantic relatedness of the congruent and incongruent prime-target sets was assessed on a 5-point Likert scale (5 = "strongly related"; 1 = "completely unrelated") by 12 participants who were not in the two experimental groups [congruent:  $4.88 \pm 0.18$ ; incongruent:  $1.53 \pm 0.23$ ;  $t_{(11)} = 35.354$ , p < 0.0001].

Two hundred pseudo-words (e.g., 'ryouru'; familiarity = 1.562) with low familiarity scores (1.57  $\pm$  0.015) were homogeneously inserted into the second position of the stimulus sequence in the four experimental conditions [familiarity: condition,  $F_{(3,147)} = 0.554$ , p = 0.646] (Fig. 1A). The pseudo-words, which were indispensable in the SHL task, were expected to inhibit or facilitate the attention given to semantic relatedness in the DP task. In the SHL task, the pseudo-words provided crucial information about the task-related response (i.e., 'YES' as a response for a non-word) before the appearance of the target words. Therefore, the participants were unlikely to explicitly commit to their judgment on the semantic relatedness of the words during the presentation of the final target verb. In contrast,

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in the DP task, the pseudo-words were expected to promote selective attention to the proceeding targets because the participants could not determine the semantic relatedness of the words until the presentation of the targets. To summarize, the pseudo-words helped to accentuate the differences in the semantic-processing loads between the SHL and DP tasks.

The 448 sequences were divided into four lists such that the same primes and targets did not appear repeatedly in the lists. The stimulus sequences in each list, as well as the four stimulus lists, were presented randomly.

## 2.4. Experimental procedure

The participants sat in an electrically shielded soundproof room and faced a 17-in cathode-ray-tube monitor that was 0.7 m in front of the participants. A test trial started when a fixation symbol (\*\*\*\*) was presented in black in the center of a light-gray screen. All of the words appeared 500 ms after the antecedents disappeared, and they were maintained for 300 ms, except for the target verbs (stimulus-onset asynchrony: 800 ms). The target verbs were shown until the participant responded by pressing the corresponding button on the response pad with either their left or right thumb (Fig. 1A). Correct and incorrect response types were assigned randomly to the left or right thumb, and these assignments were counterbalanced across the participants. The participants were instructed to respond as quickly and accurately as possible.

## 2.5. Data recording and analysis

Neurophysiological activity was continuously recorded electroencephalographically (Synamp1: Compumedics Neuroscan, Inc., Charlotte, NC). Thirty-four sintered Ag/AgCl electrodes were placed evenly across the participants' scalps according to the spatial norm for data recording (approximate distance between electrodes: 5 cm) and the International 10–20 System (Fig. 1B). Three additional electrodes were placed around the eyes for horizontal and vertical electro-oculographic recordings. All of the electrodes were referenced online to the left mastoid and rereferenced offline to the linked mastoids. The ground electrode was placed around the anterior prefrontal surface. The data were recorded with a sampling frequency of 250 Hz and band-pass frequency range of 0 to 70 Hz. The impedance was set to <5 k $\Omega$  throughout the experiment.

The continuously recorded electroencephalography data were filtered with bandpass frequencies ranging from 0.1 to 40 Hz (finite impulse response filter: 24 dB/ octave, zero-phase shift) and then segmented into 50 epochs from 200 ms before to 700 ms after the onset of the target verbs in each condition. Individual-averaged ERP waveforms were produced for each condition after baseline correction with the mean potential of the 200 ms before target onset and artifact rejection (peak-to-

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peak amplitude of  $\pm$  75 µV). The grand-averaged waveforms were smoothed with the moving average method (9 sampling points: 36 ms) for easier visualization. The grand-averaged waveforms for the left frontal (No. 3 in Fig. 1B) and midline parietal (No. 19 in in Fig. 1B) electrodes were plotted to visualize the results of the SHL task (Fig. 2A) and DP task (Fig. 2B). A semantic-related N400 effect that peaks approximately 400 ms post-stimulus in the midline centro-parietal region has been widely reported in priming studies since Kutas and Hillyard's work in 1980 [23]. The reductions in the negative potentials in response to semantic congruency (SC, SC/GC, or SC/GI minus SI) were reconstructed into two-dimensional scalp maps for every 100 ms between 300 and 700 ms, during which significant statistical effects were observed (Fig. 2A and B) with customized codes for GNU Octave, ver.4.0.2.

## 2.6. Statistical analysis

The changes in response accuracy and response time (RT) were tested with repeated-measures analysis of variance (ANOVA; n = 13 in each group). The twoway ANOVAs included the within-subjects factor of condition (four levels: SI, SC, SC/GC, and SC/GI) and between-subjects factor of group (two levels: SHL and DP). Multiple comparisons were conducted between the paired conditions in each task group or between the SHL and DP groups in each condition with permutation *t*-tests, as described below. The RT data were transformed logarithmically (log10) to normalize the distribution.

For the neurophysiological data for each 100-ms interval, we conducted ANOVAs utilizing the three within-subject factors of condition, hemisphere (left and right), and site (anterior, central, and posterior) for the lateral site and the two factors of condition and site for the midline site. The lateral anterior, central, and posterior sites all included four electrodes, and the midline central and posterior sites involved three electrodes each, while the midline anterior site only consisted of two electrodes because the ground electrode was placed at the anterior site (Fig. 1B). The amplitude averages, which were calculated separately for each lateral and midline site and each interval (25 data points for each 100-ms interval) in each of the four conditions, were utilized in the statistical tests.

We analyzed each task separately because strong morphological and amplitude waveform differences were expected between the SHL and DP tasks (Fig. 2A and B), and an analysis of the data for all of the tasks would likely mask statistically significant information on the ERP effects in each group [37]. That is, the overall variance in the amplitudes across the SHL and DP task groups would likely conceal amplitude effects that were specific for the SHL task group, which might have less amplitude variation. The group differences in amplitude strength might also yield apparent topographical differences between the two task groups, even

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**Fig. 2.** Behavioral test results. Comparisons of the response times of the four experimental conditions in the (A) shallow (SHL) and (B) deep (DP) semantic tasks. Compared to the semantically incongruent (SI) condition, the three related conditions [semantically congruent (SC), semantically and grammatically congruent (SC/GC), or semantically congruent/grammatically incongruent (SC/GI) minus semantically incongruent (SI) conditions] yielded faster response times for task-related decisions in both the SHL and DP tasks.

though the data for both task groups in the present study might multiplicatively yield ERPs with similar scalp distributions, as was suggested in a previous study [38].

Hence, in order to directly compare the function-related topographic differences of the ERP effects (congruent minus incongruent) of the two task groups, the data were normalized with vector length [38, 39, 40]. The ANOVAs including the condition and topographic factors were conducted with the data that were normalized by vector length according to the following formula:  $\left[\sqrt{\Sigma} \left(x_{i,i}^2\right); x = a\right]$ amplitude; i = an electrode; i = a condition or group]. That is, the vector length was calculated by the square root ( $\sqrt{}$ ) of the sum of squares of the raw amplitudes (x) from the recording electrodes. Subsequently, the amplitudes observed at the scalp electrodes were divided or scaled by their vector lengths. The vector normalization was conducted separately within each group in order to test differences of scalp distributions between the SHL and DP groups. However, when we needed to test different scalp distributions of the ERP effects among the congruent conditions within each task group, the vector normalization was applied to each scalp region of interest within each condition. Significant interaction effects of condition/group and the topographic factors (hemisphere and/or site) that remained after scaling were considered indices of different neuro-functional backgrounds of the two task groups: That is, different neural sources may be related to different conditions. Even if the same cortical areas contributed to the

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results obtained with the different conditions, their stimulus-related activity changes would differ between the conditions, and these changes would indicate functional segregation [40].

Follow-up ANOVAs that were based on the recalculated error terms of each level in order to correspond with the sphericity problem were conducted to elucidate the significant effects of a condition. The Greenhouse-Geyser correction was applied, if necessary. In order to further examine the differences between the SI and congruent (SC, SC/GC, and SC/GI) conditions for each topographic level, triple multiple comparisons were performed with two-tailed paired *t*-tests. Because we needed to conduct up to 216 post-hoc paired *t*-tests, if necessary [2 task groups  $\times 4$ time windows  $\times$  9 scalp sites  $\times$  3 comparisons (SI vs. SC, SC/GC, or SC/GI)], we performed permutation tests to avoid type-I errors [41], as previously described [42, 43]. This resampling method is based on the idea that statistical test distributions are created just by multiple permutation analyses to avoid type-I error. The core notion is that a tested probability distribution is itself derived by a multiple comparison test that discards the false positives that result from multiple testing. The data for the paired conditions  $(13 \times 2 \text{ sets})$  were repeatedly resampled from the acquired data  $(216 \times 26 \text{ participants})$  so that the same resampling patterns were not included. The resampled data were compared with paired *t*-tests in order to obtain dummy t-values. Because the number of permutations was too vast to compute overall t-values, and, alternatively, the 216 resampled data values were too small for a probability resolution, the permutation procedures were repeated only 10,000 times for a probability resolution of p = 0.0001. The actual t-values were tested with a uniform permutation distribution of 10,000 dummy *t*-values, and they were considered significant at a corrected  $\alpha$ -level of p < 0.05 when the original values were outside the 95% confidence interval (CI). We reported both the original t-values and the 95% CIs of the dummy t-values. The permutation procedure (10,000 resamples from 4 conditions  $\times$  26 participants) was also applied to the paired and unpaired *t*-tests of the RTs in the behavioral analyses. Statistical significance was set at an  $\alpha$ -level of 0.05 or less for all of the analyses. The neurophysiological results that were obtained with the overall and follow-up ANOVAs are summarized in Table 2 and Table 3, respectively. The statistical tests were conducted with IBM SPSS Statistics (IBM Japan, Tokyo, Japan) and customized codes for GNU Octave, ver.4.0.2.

#### 3. Results

#### 3.1. Behavioral results

The participants performed very well in both the SHL and DP tasks. No significant differences were observed in the accuracy among the conditions and task groups

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[SHL: 96.3  $\pm$  1.2%; DP: 93.1  $\pm$  2.1%; condition:  $F_{(3,72)} =$  1.749, p = 0.165; condition × group:  $F_{(3,72)} =$  1.068, p = 0.368].

For RT, both groups showed similar patterns in the SC conditions. The participants generally detected the target verbs more quickly in the three SC conditions (SC: 775 ± 85 ms; SC/GC: 721 ± 78 ms; SC/GI: 771 ± 79 ms) than in the SI condition (969 ± 100 ms) [condition:  $F_{(3,72)} = 30.243$ , p < 0.0001; multiple comparisons (95% CI of dummy paired *t*-values in a permutation test: -2.216 to 2.188): SC vs. SI,  $t_{(25)} = 4.727$ , p = 0.0006, corrected; SC/GC vs. SI:  $t_{(25)} = 5.482$ , p = 0.0002, corrected; SC/GI vs. SI:  $t_{(25)} = 6.565$ , p < 0.0001, corrected].

The post-hoc analyses of the significant interaction effects in each task group [condition × group:  $F_{(3,72)} = 6.476$ , p = 0.008] also indicated that the participants in the SHL group responded more rapidly to the targets in the SC conditions (SC: 492 ± 148 ms; SC/GC: 476 ± 137 ms; SC/GI: 477 ± 142 ms) than in the SI condition (SI: 546 ± 152 ms) [condition:  $F_{(3,36)} = 11.607$ , p = 0.0003; multiple comparisons (95% CI of dummy paired *t*-values: -2.216 to 2.188): SC vs. SI,  $t_{(12)} = 3.247$ , p = 0.007, corrected; SC/GC vs. SI:  $t_{(12)} = 4.232$ , p = 0.001, corrected; SC/GI vs. SI:  $t_{(12)} = 5.638$ , p = 0.0002, corrected] (Fig. 2A).

The participants in the DP task group also responded faster in the SC conditions (SC:  $1058 \pm 438$  ms; SC/GC:  $967 \pm 426$  ms; SC/GI:  $1065 \pm 364$  ms) than in the SI

		SHL $(n = 1)$	3)			DP $(n = 13)$			
Effects	df	<i>F</i> -values				F-values			
		300–400 ms	400–500 ms	500–600 ms	600–700 ms	300–400 ms	400–500 ms	500–600 ms	600–700 ms
Lateral									
С	3,36	2.813	3.919*	3.111*	4.539**	3.321	5.309*	6.775**	6.148**
$C \times H$	3,36	0.135	0.608	0.593	0.524	1.041	1.530	3.641*	2.367
$C \times S$	6,72	1.730	0.798	1.279	0.575	1.545	2.159	2.732*	4.494*
$C \times H \times S$	6,72	1.847	2.154	1.165	1.093	1.007	0.465	1.208	0.909
Midline									
С	3,36	5.179**	3.385*	1.982	2.804	4.133*	8.222***	10.436***	9.249***
$C \times S$	6,72	1.193	0.790	1.328	1.102	3.605**	4.688***	5.258***	6.915***

**Table 2.** Results of the overall analysis of variance (ANOVA) of the neurophysiological effects in the shallow (SHL) and deep (DP) semantic tasks.

df: degrees of freedom; C: condition; H: hemisphere; S: site.

The ANOVAs of the lateral and midline regions included the mean amplitudes across the channels of the anterior, central, and posterior sites, as represented in Fig. 1B.

\* p < 0.05.

<sup>\*\*</sup> p < 0.01.

 $^{***} p < 0.001.$ 

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		DP $(n = 13)$						
Effects	df	F-values						
		300–400 ms	400–500 ms	500–600 ms	600–700 ms			
Lateral								
Central	3,36			7.069***	5.848**			
Posterior	3,36			8.049***	9.773****			
Midline								
Central	3,36	6.069**	11.419***	14.471***	13.368***			
Posterior	3,36	3.644*	5.806**	9.147***	9.744***			

**Table 3.** Neurophysiological results of the follow-up ANOVAs examining the main effect of condition in the deep (DP) semantic task group.

df: degrees of freedom.

The lateral and midline ANOVAs included the mean amplitudes across the channels, as represented in Fig. 1B.

\* p < 0.05.

<sup>\*\*</sup> p < 0.01.

\*\*\*\* p < 0.001.

condition (SI: 1392 ± 371 ms) [condition:  $F_{(3,36)} = 20.135$ , p = 0.0002; multiple comparisons (95% CI of dummy paired *t*-values: -2.216 to 2.188): SC vs. SI,  $t_{(12)} = 4.229$ , p = 0.001, corrected; SC/GC vs. SI:  $t_{(12)} = 5.028$ , p = 0.0002, corrected; SC/GI vs. SI:  $t_{(12)} = 5.310$ , p = 0.0002, corrected] (Fig. 2B).

Moreover, the participants in the DP task responded to the SC targets with congruent case markers (SC/GC) more quickly compared to those without case markers (SC) [multiple comparisons (95% CI of dummy paired *t*-values: -2.216 to 2.188):  $t_{(12)} = 3.837$ , p = 0.003, corrected] (Fig. 2B). However, the participants in the SHL group did not show such behavioral patterns [multiple comparisons (95% CI of dummy paired *t*-values: -2.216 to 2.188): SC/GC vs. SC,  $t_{(12)} = 1.857$ , p = 0.091, corrected]. These findings suggest that the congruent grammatical markers had different effects in the two semantic tasks.

The DP task generally resulted in longer RTs than the SHL task did [DP vs. SHL (95% CI of dummy unpaired *t*-values: -2.216 to 2.188): SI,  $t_{(24)} = 9.16$ , p < 0.0001, corrected; SC:  $t_{(24)} = 5.906$ , p < 0.0001, corrected; SC/GC:  $t_{(24)} = 5.484$ , p = 0.0002, corrected; SC/GI:  $t_{(24)} = 6.645$ , p < 0.0001, corrected]. These results support the prediction that the DP task requires more cognitively loaded verbal processing.

#### 3.2. Neurophysiological results

Several discrepancies were observed in the ERP effects from approximately 300 ms after the presentation of the target verbs between the SHL (Fig. 3A) and DP

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(Fig. 3B) task groups. Table 2 and Table 3 summarize the results of the overall ANOVAs of both tasks and the follow-up ANOVA of the DP task, respectively.

In the SHL task, grammatical congruency affected the ERP patterns both spatially and temporally (Fig. 3A). To summarize so far, the SC condition without case markers transiently reduced the N400 around 300 ms post-stimulus. However, the SC/GC condition with the congruent case markers reduced the LN in later time windows.

The overall ANOVAs of the condition and topographic factors showed significant main effects of condition in the lateral site [condition: 400–500 ms,  $F_{(3,36)} = 3.919$ , p = 0.017; 500–600 ms:  $F_{(3,36)} = 3.111$ , p = 0.042; 600–700 ms:  $F_{(3,36)} = 4.539$ , p = 0.009] and midline site [condition: 300–400 ms,  $F_{(3,36)} = 5.179$ , p = 0.004; 400–500 ms:  $F_{(3,36)} = 3.385$ , p = 0.031] (Table 2).

The post-hoc multiple comparisons (SC, SC/GC, and SC/GI vs. SI) that were conducted with the permutation procedure (Fig. 3C) showed that the congruent case markers (SC/GC) reduced the LNs for the target verbs at the lateral site [SC/GC vs. SI (95% CI of dummy paired *t*-values: -2.064 to 1.987): 400–500 ms,  $t_{(12)} = 4.432$ , p < 0.0001, corrected; 600–700 ms:  $t_{(12)} = 2.955$ , p = 0.005, corrected] and midline site [SC/GC vs. SI (95% CI of dummy paired *t*-values: -2.064 to 1.987): 300–400 ms,  $t_{(12)} = 3.172$ , p = 0.002, corrected; 400–500 ms:  $t_{(12)} = 4.111$ , p = 0.0002, corrected]. In contrast, the N400 reductions for the congruent target verbs without case markers (SC) appeared transiently at the midline site only [SC vs. SI (95% CI of dummy paired *t*-values: -2.064 to 1.987): 300–400 ms,  $t_{(12)} = 3.926$ , p = 0.0002, corrected]. The incongruent case markers (SC/GI) did not produce significant ERP effects in any of the intervals.

To test the spatial distributions of the negativity reductions for semantic congruency (SC and SC/GC minus SI), vector-normalized ANOVAs were conducted on the condition (SC and SC/GC) and topographic (hemisphere and/ or site) factors. A significant interaction of condition and site was found at the lateral site [300–400 ms: condition × site,  $F_{(2,24)} = 5.876$ , p = 0.021], which suggests that the SC and SC/GC conditions yielded different N400 and LN reductions, respectively (Fig. 3A).

The DP task yielded similar centro-posterior N400 reductions in the SC, SC/GC, and SC/GI conditions irrespective of the presence or congruency of the case markers. Additionally, a congruent case marker temporally promoted the onset of the N400 reduction in the SC/GC condition because the effect appeared about 100 ms earlier than those in the other conditions (Fig. 3B).

As the maximal (max) statistical values across the four time windows indicated in the overall ANOVAs, the main and interaction effects according to the condition factors were significant in the lateral [condition (max): 500–600 ms,

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**Fig. 3.** Neurophysiological test results. The scalp distributions of the event-related potential effects of semantic congruency at the target position are shown every 100 ms after 300 ms post-stimulus in the (A) shallow (SHL) and (B) deep (DP) semantic task groups [semantically congruent (SC), semantically and grammatically congruent (SC/GC), or semantically congruent/grammatically incongruent (SC/GI) minus semantically incongruent (SI) conditions]. The darker red areas indicate greater reduction of negative amplitudes for semantic congruency. The colored asterisks above the maps indicate significant main effects of the condition in the analysis of variance (ANOVA) of the lateral (red) and midline (green) sites. The potential maps that are shown against the light-green background indicate significant effects (p < 0.05, corrected) of the multiple comparisons between the SI condition and each of the three

 $F_{(3,36)} = 6.775, p = 0.0009$ ; condition × hemisphere (max): 500–600 ms,  $F_{(3,36)} = 3.641, p = 0.023$ ; condition × site (max): 600–700 ms,  $F_{(6,72)} = 4.494, p = 0.009$ ] and midline site [condition (max): 500–600 ms,  $F_{(3,36)} = 10.436, p < 0.0001$ ; condition × site (max): 600–700 ms,  $F_{(6,72)} = 6.915, p = 0.0008$ ] (Table 2). The follow-up ANOVAs of each site showed significant condition effects at the lateral central (LC) and lateral posterior (LP) sites [condition (max): LC (500–600 ms),  $F_{(3,36)} = 7.069, p = 0.0007$ ; LP (600–700 ms):  $F_{(3,36)} = 9.773, p < 0.0001$ ] and midline central (MC) and midline posterior (MP) sites [condition (max): MC (500–600 ms),  $F_{(3,36)} = 14.471, p < 0.0001$ ; MP (600–700 ms):  $F_{(3,36)} = 9.744, p < 0.0001$ ] (Table 3).

The planned pairwise comparisons (three times: SC, SC/GC, and SC/GI vs. SI) of the central and posterior sites revealed earlier N400 reductions in the SC/GC condition at the MC and MP sites (300–400 ms) [SC/GC vs. SI (95% CI of dummy paired *t*-values: -2.064 to 1.987): MC,  $t_{(12)} = 3.479$ , p = 0.0008, corrected; MP:  $t_{(12)} = 2.933$ , p = 0.005, corrected] (Fig. 3B). In later time windows, similar N400 reductions were observed in all of the congruent conditions at the MC, MP, and LP sites. The maximum effects were observed from 500 to 600 ms [SC vs. SI (95% CI of dummy paired *t*-values: -2.064 to 1.987): LP,  $t_{(12)} = 3.493$ , p = 0.0008, corrected; MC:  $t_{(12)} = 3.665$ , p = 0.0004, corrected; MP:  $t_{(12)} = 4.823$ , p < 0.0001, corrected; SC/GC vs. SI: LP,  $t_{(12)} = 4.332$ , p < 0.0001, corrected; MC:  $t_{(12)} = 5.613$ , p < 0.0001, corrected; MP:  $t_{(12)} = 3.925$ , p = 0.0002, corrected; SC/ GI vs. SI: LP,  $t_{(12)} = 3.514$ , p = 0.0008, corrected; MC:  $t_{(12)} = 3.510$ , p = 0.0008, corrected; MP:  $t_{(12)} = 3.697$ , p = 0.0002, corrected].

In the vector-normalized ANOVA on the negativity reductions (SC, SC/GC, and SC/GI minus SI), the three congruent conditions did not show significantly different spatial patterns at the lateral sites [600–700 ms: condition × hemisphere,  $F_{(2,24)} = 0.632$ , p = 0.54; condition × site:  $F_{(4,48)} = 0.61$ , p = 0.993; condition × hemisphere × site:  $F_{(4,48)} = 2.646$ , p = 0.077] or midline site [condition × site:  $F_{(4,48)} = 1.188$ , p = 0.328]. These results suggest that the ERP effects of the three congruent conditions had similar neuro-functional backgrounds.

Finally, we examined whether the presentation of the congruent case markers differentially affected the ERP effects in the SHL and DP tasks. We removed the

congruent conditions. The red arrows indicate the centro-posterior N400 reduction, and the green arrow indicates the lateralized negativity (LN) reduction. The grand-averaged waveforms of the left frontal (No. 3) and midline parietal (No. 19) electrodes are plotted for both groups [SI (baseline for comparison): black; SC: green; SC/GC: red; SC/GI: blue]. The negative potential value is plotted upward, and the potential amplitude is scaled in  $\mu$ V. (C) Permutation distribution of the dummy *t*-values (n = 10,000) for the post-hoc test of multiple comparisons between the incongruent (SI) and congruent (SC, SC/GC, and SC/GI) conditions. The *t*-values outside the 95% confidence interval (–2.064 to 1.987) were considered significant at a corrected  $\alpha$ -level of p < 0.05.

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amplitude strengths with the vector normalization procedure within each group and then directly compared the spatial patterns of the ERP effects (congruent minus incongruent) with ANOVAs of the group and topographic (hemisphere and/or site) factors in each task [37]. The significant interaction effects [300–400 ms: lateral, group × hemisphere × site,  $F_{(2,24)} = 3.504$ , p = 0.046; midline: group × site,  $F_{(2,24)} = 3.589$ , p = 0.043] suggest that, when the congruent case markers appeared in the primes (SC/GCs in Fig. 3A and B), the SHL and DP tasks produced distinct neurophysiological components. That is, the congruent case markers yielded LN reductions in the SHL task and centro-posterior N400 reductions in the DP task.

However, when case markers were not present in the SC primes (SCs in Fig. 3A and B), both the SHL (mean values for 300–400 ms) and DP (mean values for 400–700 ms) tasks showed centro-posterior N400 reductions, as revealed by the nonsignificant group-related interactions [lateral: group × hemisphere,  $F_{(1,12)} = 0.027$ , p = 0.872; group × site:  $F_{(2,24)} = 0.106$ , p = 0.900; group × hemisphere × site:  $F_{(2,24)} = 1.677$ , p = 0.208; midline: group × site,  $F_{(2,24)} = 3.370$ , p = 0.059]. These results suggest that the overlapping neurophysiological activities occurred in response to the congruent targets without case markers in the SHL and DP tasks.

#### 4. Discussion

In the current study, we set out to conduct neurophysiological experiments to examine the hypothesis that the accessibility to grammatical words in verbal processing induces different neurophysiological responses under the SHL and DP semantically attended conditions. Thus, we manipulated the presence and types of grammatical case markers and compared four conditions: the SI condition, SC condition without case markers, and SC conditions with congruent (SC/GC) or incongruent (SC/GI) case markers.

The behavioral results showed that the processing of the congruent targets was generally more rapid than the processing of the incongruent targets. In addition, the congruent case markers facilitated target processing solely in the DP task. These results suggest that case markers have different effects in the SHL and DP tasks.

The neurophysiological results demonstrated that only the SC/GC condition with congruent case markers in the SHL task yielded LN reductions, which exhibited a scalp distribution that differed from typical centro-posterior N400 reductions. In the DP task, the three congruent conditions yielded similar N400 reductions. Thus, the novel finding in this study is that the processing of the same words through the same case markers yielded different LN and N400 reductions under the SHL and DP semantic conditions, respectively.

A parsimonious interpretation of the findings is that case markers function differently under the SHL and DP semantic conditions after spreading the

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activation [12, 44] of the lexical representations. In the SHL task, the correct case markers might have induced automatic structural integration, while the correct case markers likely facilitated semantic retrieval in the DP task.

The spreading activation of the lexical representations decays immediately after sensory input without strategic relief, but it is potentiated by higher cognitive functions [44, 45]. The transient N400 reduction (300–400 ms) in the SC condition in the SHL task probably reflected automatic lexical activation [46]. Because the SHL task did not require explicit semantic relatedness between the words, the neurophysiological effects of the SC condition probably remained at the transient neural activation level and therefore, were not reinforced.

In contrast, the LN reduction effects of the congruent case markers (SC/GC in the SHL task) might have been functionally segregated from transient lexical activation. Although the LN reduction in the SC/GC condition did not indicate significant left dominancy, visual inspection of Fig. 3A shows left fronto-central LN reductions in the SC/GC condition. These LN reductions might be a reverse pattern that is comparable to LAN enhancements in morpho-syntactic processing [8], such as case violation [14, 15] and morpho-syntactic agreement violation [16, 17, 18, 19]. Case markers that were correctly used in the SHL task likely reduced the structural integration difficulty [47] that was less dependent on transient lexical activation and yielded the LN reduction.

The above argument is also supported by the canceling of the presumed ERP effects in the SC/GI condition in which the incongruent case markers prevented the LN reductions in response to the structural integration between the primes and targets, even though they were lexically congruent with each other.

In the DP task, verbal processing through congruent case markers (SC/GC) generally showed similar N400 reductions as those in the SC and SC/GI conditions, which was consistent with previous findings of priming [14]. The centro-parietal N400 has been widely observed in response to semantic integration load [25, 26], such as semantic violation [23] and semantic unexpectancy [24]. Hence, the present N400 reductions in all of the congruent conditions were likely related to semantic processing that was based on the lexical information of words.

The scalp distributions of the N400 reductions in the DP task did not differ from the distribution of the transient N400 reductions in the SC condition in the SHL task. Hence, the N400 reductions in the DP task might have been related to enhancements of the transient lexical activation as well as semantic integration [48]. These processes likely inhibited the automatic structure-dominant integration that is assisted by grammatical case markers, and they might have been associated with the direct determination of semantic relationships.

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In addition, the observation of a significant N400 reduction from 300 to 400 ms in the SC/GC condition indicated that the neurophysiological effects appeared more rapidly in the DP task. Therefore, a congruent case marker facilitated the neurophysiological activation of a given lexical representation and semantic integration under attentional control. Such an attention-based temporal change is analogous to the facilitation of visual searches under prepared attention [49]. The behavioral finding that the RTs of the targets in the SC/GC condition were faster than those in the SC condition, both of which possessed the same prime-target stimulus sets but not the same case markers, might also support this argument.

To summarize the overall findings, case markers facilitated automatic structural integration in the SHL task and, in turn, accelerated semantic processing in the DP task.

The present results have potential implications on models of neural language processing. The time window of approximately 400 ms post-stimulus in language processing is considered the critical time domain for syntactic and semantic processing, and it is reflected by LAN and N400, respectively [20, 21, 22]. However, it is unclear why online verbal processing forks into two branches in this latency and how the two processes interact [50]. The results of the present study suggest that this temporal window is related to the decay of automatic lexical neural activation. More precisely, this temporal domain may correspond to the stage in which online verbal processing diverges after spreading the activation decay based on different cognitive demands, as represented in Fig. 4.

Under the DP semantic condition (Fig. 4A), the automatic spreading of the activation of the lexical representations is enhanced across the related features, such as "Tool", "Open", and "House", and maintained by selective attention to the semantic relatedness. When target words (e.g., "Open") with a related feature are presented, the N400 reductions are consistently produced because of the prospective neural activities of related neural populations [12, 29]. Such activation-based N400 effects may be supported by the distribution of concept-specific and concept-general cortical areas [12, 13].

Conversely, under the SHL semantic condition (Fig. 4B), the verbal processing is not supported by case markers, the spreading activation briefly decays, as was observed in the SC condition. However, verbal processing through congruent case markers may not depend mainly on the spreading activations of the related features but rather derive structural integration from the case information. Primes with congruent case markers likely evoke not only lexical but also structural information, which is exemplified by the lexical conceptual structure of the transitive verb used in the present study (e.g., [X ACT [Y BECOME <STATE>] in Fig. 4B) [51]. For example, the prime "Shutter" activates related features, including "Open," which is consistent with the "STATE" slot in the causative

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**Fig. 4.** Dual processing model of local verbal processing. Verbal processing after the spread of the activation of the lexical representations separates into the two main streams around 300 ms after the verbal inputs. (A) Semantic processing: under deep semantic conditions requiring direct decisions on semantics, the spreading activation of the lexical representations is enhanced and maintained by selective attention to semantic relatedness, which consequently yields a centro-posterior N400 reduction, which was observed in the semantically and grammatically congruent condition (SC/GC) in the deep semantic task. (B) Syntactic processing: under shallow semantic conditions without explicit decisions on semantics, verbal processing through congruent case markers not only depends on lexical activation but also evokes structural information (e.g., [X ACT [Y BECOME <STATE>]), which promotes the structural integration of primes and targets. Facilitated automatic structural integration yields a lateralized negativity (LN) reduction, as has been observed in the SC/GC condition in the shallow semantic task.

structural frame. Hence, when the target word "Open" is preceded by a case marker that constrains the structural frame, the target word that fits the structure is easily integrated into the structural frame. Such structural integration through grammatical words may be automatically promoted under the SHL semantic conditions, which consequently yield LN reductions. Although little is known about the neural correlates of the switching between syntactic and semantic processing under different cognitive requirements, the results of an intra- and intro-cranial neurophysiological study has suggested that the thalamus is associated with the verbal switching mechanism [52]. Subcortical structures [53], including the thalamus, are candidate regions that are associated with the switching mechanism for the facilitation or inhibition of structure-dominant verbal processing. Basal ganglia-thalamo-cortical circuits remove and strengthen neural inhibition for not only motor but also cognitive processes [54, 55], and these circuits may contribute to cognitive switching under different cognitive requirements [56]. The present study did not provide precise spatial information about the neural correlates of the verbal switching mechanism. Thus, future neuroimaging studies should be conducted to elucidate whether subcortical structures are critically responsible for the switching of alternative neural verbal processes in association with cortical language areas, such as the inferior frontal areas [57, 58], thereby adapting to changes in cognitive demands.

### 5. Conclusions

In the present study, we conducted a neurophysiological experiment with a semantic priming paradigm, in which SC or SI prime-target sequences were randomly presented. The aim of the study was to examine the uniformity of grammatical processing, i.e., whether the grammatical words in verbal processing yielded different neurophysiological responses under the SHL and DP semantic conditions. Congruent case markers yielded LN reductions in response to congruent targets in the SHL semantic task, while, irrespective of case markers, congruent targets similarly yielded N400 reductions in the DP semantic task. In summary, the human brain processes the same grammatical items in the same verbal expressions differently in accordance with SHL and DP semantic requirements.

#### Declarations

#### Author contribution statement

Takahiro Soshi: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Heizo Nakajima, Hiroko Hagiwara: Conceived and designed the experiments; Analyzed and interpreted the data; Wrote the paper.

<sup>22</sup> http://dx.doi.org/10.1016/j.heliyon.2016.e00180

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## **Funding statement**

This work was supported by a Grant-in-Aid for Young Scientists (B), The Ministry of Education, Culture, Sports, Science and Technology, Japan (No. 17720116), and a Grant-in-Aid for Challenging Exploratory Research from the Japan Society for the Promotion of Science (No. 15K12884).

## **Competing interest statement**

The authors declare no conflict of interest.

## **Additional information**

No additional information is available for this paper.

## Acknowledgments

This study was based on the dissertation of the first author. The authors would like to thank all of the participants and anonymous reviewers. We also appreciate Kazuyuki Nakagome, Shinya Kuriki, Kenji Itoh, Kuniyasu Imanaka, Masami Ishihara, Ken-ichi Takami, Hiroshi Hasegawa, Takeru Honma, Sadayoshi Ogawa, Shiro Ojima, Natsuko Tatsuta, Ayumi Koso, Izumi Kishida, Ryuichiro Hashimoto, and Fumitaka Homae for their help. We are also thankful to a professional editor at Editage, a division of Cactus Communications, for performing the edit of the manuscript. Finally, we would like to express our gratitude for the valuable contributions of the late Prof. Hiroko Hagiwara to the linguistic and cognitive neuroscience domains of natural language.

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<sup>24</sup> http://dx.doi.org/10.1016/j.heliyon.2016.e00180

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