Does degree of handedness in a group of right-handed individuals affect language comprehension?

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A B S T R A C T

The impact of handedness on language processing has been studied extensively and the results indicate that there is a relationship between the two variables; however, the nature of the relationship is not at all clear. In the current study we explored degree of handedness (DH) opposed to direction in a group of right-handed individuals. fMRI was used to explore the impact of DH on the sentence comprehension network. The results revealed that during sentence comprehension activation in regions linked to semantic memory (e.g., anterior temporal cortex) were modulated by DH. Also, unexpectedly the precuneus/posterior cingulate gyrus which has been linked to episodic memory was also affected by DH. These results extend those reported previously by showing that the neural architecture that supports sentence comprehension is modulated by DH. More specifically, together the results presented here support the hypothesis proposed by Townsend, Carrithers, and Bever (2001) that DH interacts with the language system and impacts the strategy used during sentence comprehension.

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1. Introduction

The co-occurrence of hemispheric language dominance to the left hemisphere and right hand dominance has led researchers to believe that the two are jointly inherited and, therefore, that they are intricately related. To support this view Josse and Tzourio-Mazoyer (2004) conducted a review and found that individuals who are on the left handed end of the continuum are more likely to have atypical hemispheric specialization for language. This atypical hemispheric specialization has been observed in a number of disorders including dyslexia and schizophrenia. For example, dyslexia, a reading disorder which is thought to be due primarily to a phonological processing deficit (Kovelman et al., 2010; Temple et al., 2003), has a higher rate of left-handedness (Eglinton & Annett, 1994; Geschwind & Behan, 1982) as well as increased right hemisphere activation during language tasks (Temple, 2002). Additionally, some studies have found that non-disordered left-handed individuals perform poorer on phonological processing tasks (Annett, 1992; Annett, 2002; Smythe & Annett, 2006). Similar language/handedness findings have been observed in schizophrenia in that there is a greater incidence of left-handedness and

atypical language lateralization (Dollfus et al., 2005) that may be related to the language deficits observed (see Michell & Crow, 2005 for a review). While the language deficits associated with these two disorders are quite different, together they illustrate a potential link between direction of handedness and language processing differences.

While the study of direction of handedness and language has a long history, recently there has been interest in the effect degree of handedness (DH) may have on language processing. Some of the earliest work in this area explored familial sinistrality. Bever, Carrithers, Cowart, and Townsend (1989)) suggested that while right-handed individuals with left-handed family members (FS[+]; more likely with weaker DH) and FS[−] individuals (with no left-handed family members; more likely with a strong DH) encode linguistic information similarly, they attend more to some linguistic units than others. More specifically, they propose that FS[+] individuals access words and meanings more readily than FS[−] individuals. Townsend et al. (2001) extended this idea to the sentence domain and found that FS[+] individuals rely more on a semantic strategy during sentence comprehension while FS[−] rely more on a syntactic strategy. Further support for this conclusion was found in a recent study by Koss, Van den Brink, and Hagoort (2012) that revealed individual variation in the late positive complex (LPC), an ERP response that follows the N400, during a semantic anomaly task. They found that half of their participants showed a negative

response in this time window while the other half showed an LPC. This variation was not explained by working memory differences. Interestingly, 14 of their participants reported having a left-handed parent, none of that 14 belonged to the group that revealed an LPC. The Koss et al. (2012) study supports the conclusions reported by Townsend and colleagues and suggests that the strategies used in sentence comprehension are different for FS+ and FS− participants and imply differences in strategy use by weak versus strong handed individuals.

The finding that individual differences impact the strategy used during sentence comprehension has been observed in a number of previous studies (Malaia, Wilbur, & Weber-Fox, 2009; Newman, Lee et al., 2009; Weber-Fox, Davis, & Cuadrado, 2003; Wekerly & Kutas, 1999). For example, an EEG study investigating the processing of object-relative clauses (Malaia et al., 2009) found that participants selectively relied either on syntactic (phrase structure) or semantic information for thematic role re-assignment, which in turn determined the timing of integrative processing for comprehension. The authors hypothesized that differential strategies used for complex sentence processing may arise due to the individual's linguistic proficiency and/or non-linguistic cognitive processes, such as working memory capacity (WMC) such that low proficiency individuals rely more heavily on semantic information while high proficiency syntactic information. Together with the Townsend et al. (2001) study evidence suggesting strategic differences were predicted.

In addition to studies that show an interaction between language processing and familial handedness, recently there have been studies focused on the impact degree of handedness has on cognition generally and language processes more specifically. A recent review found that inconsistent handedness, or a lower DH, is associated with increased interhemispheric interaction. This increased interhemispheric interaction is thought to increase access to processes localized to the right cerebral hemisphere (Prichard, Propper, & Christman, 2013). For example, in a study by Sontam and Christman (2012) a semantic priming task in which the targets were ambiguous words and the related prime/target pair referenced either the dominant meaning (e.g., bank/money) or subordinate meaning (e.g., bank/river) was investigated. There the weak DH participants showed priming for both while the strong DH participants only showed a priming effect for the related dominant condition, suggesting that the weak DH participants have greater access to right hemisphere processes. This finding corresponds to Bever and colleagues' (1989) hypothesis discussed above. Additionally, in a study exploring semantic fluency Sontam, Christman, and Jasper (2009) found that weak DH individuals exhibited greater switching between categories than did the strong DH participants. This suggests that the semantic networks may be organized differently as a function of DH. Additionally, as it relates to the current study, these previous findings demonstrate semantic processing differences as a function of DH. These semantic differences may be expected to impact sentence comprehension.

One of the goals of the current study was to explore whether DH is a potential source of individual differences that has been observed in language studies, particularly those of sentence comprehension. An fMRI study that examines the relation between degree of handedness and activation related to sentence processing is presented. Previous studies of sentence comprehension have primarily limited the participant population to right-handed individuals without taking into account their degree of right-handedness. Therefore the current study, unlike much of the research on DH, investigated only individuals who report being right-handed so that comparisons can be made with the sentence comprehension literature. It was predicted that the results would mirror those found by Townsend et al. (2001) for familial handedness: weak DH individuals were expected to show a greater reliance on semantic strategies than strong DH participants. What that means here is that weaker DH participants will be more engaged in extracting sentence level meaning and may be expected to show increased activation in regions associated with this process than strong DH participants. Additionally, the current study explored two sentence constructions, conjoined active (e.g., *The pilot scared the escort and broke the mirror on the closet.*) and object-relative constructions (e.g., *The pilot that the escort scared broke the mirror on the closet.*). These two sentence constructions differ in syntactic complexity which has a significant impact on both syntactic level processing as well as sentence level semantic processing. DH may be expected to differentially affect these two sentence types. Because object-relative sentences involve movement, serial order must be attended to in order to adequately comprehend the sentence which may draw attention away from semantics for weaker DH participants. In other words, the canonical structure of conjoined active sentences may allow for greater freedom in terms of the use of different strategies than the non-canonical object-relative sentences.

2. Methods

2.1. Participants

Forty participants took part in this study. They were all Indiana University students without any history of neurological disorders (22 female, age = 21.7 ± 3.1). All participants gave signed informed consent which was approved by the Indiana University Institutional Review Board.

While participants were unselected for degree of handedness, only those who reported being right-handed took part in the study. Degree of handedness was measured with the Edinburgh handedness inventory (Oldfield, 1971). Although participants all reported being right-handed and all wrote with their right hand, their degree of handedness scores showed some variance, with scores ranging from 33.3 to 100 (Mean = 77.1 ± 20.1). Three of the participants had handedness scores of 33.3 and 7 had scores of 100; the remaining scores ranged from 50 to 91.7. No left-handed participants were included. However, the three participants with a score of 33.3 (in the ambidextrous range) were included.

2.2. Experimental stimuli

The study examined a sentence comprehension task using two sentence types – object-relative and conjoined active constructions. Sentence materials were taken from Keller, Carpenter, and Just (2001) which were derived originally from Just, Carpenter, Keller, Eddy, and Thulborn (1996). Stimuli were equated across conditions for word frequency, word length, sentence length and noun animacy. Sentence comprehension was assessed via comprehension probes that were constructed by asking if one of the nouns performed the act denoted by one of the two verbs. Half of the probes questioned the first verb and the other half the second verb. Thirty-three percent of the probes were false. There was no sentence repetition.

Each experiment was composed of 4 runs. There were 40 stimuli of interest, 20 for each sentence type, no sentence was repeated. There were 40 filler stimuli. The fillers were either sentences presented one word at a time (Lee & Newman, 2010), sentences that contained semantically related nouns (Newman, Ikuta, & Burns, 2010) or sentences with the same features as the experimental stimuli (Newman, Ratliff, Muratore, & Burns, 2009). The fillers were treated as conditions of no interest. The handedness scores were compared across these three groups and no significant differences were observed (p's > 0.12).

2.3. Experimental procedure

The study was composed of a training and an imaging session. During the training session, participants were introduced to the sentence comprehension task, completing 16 practice trials, in order to familiarize them with the experimental procedure.

The fMRI protocol was a slow, single trial event-related design in which each trial was treated as an event block (Kruggel & von Cramon, 1999; Zarahn, 2000; Zarahn, Aguirre, & D'Esposito, 1997). A trial could be divided into two phases; a sentence reading phase and a responding to a comprehension probe phase. Participants were instructed to read each sentence thoroughly and respond as quickly and accurately as possible to probes that were presented 6 s later. Participants were told to place a greater weight on accuracy than speed of responding.

The duration of each trial was 16 s. A trial began with a sentence being presented in the middle of the screen for 5 s. After 5 s, an X was presented on the screen for 6 s to allow the hemodynamic response to approach baseline. By inserting the 6 s delay the online sentence reading phase and off-line comprehension phase could be distinguished. Finally, a comprehension probe was presented for 5 s with a cue (i.e. F|T). The cue indicated the appropriate response (a right index finger for true and the left index finger for false). After each trial, a 12 s ITI was presented to allow the hemodynamic response to return to baseline.

Each run contained 3, 28 s fixation periods located at the beginning, middle and end of each run. The baseline hemodynamic response was measured by averaging the signal during the 28 s fixation periods (fixation to a star sign, *). Stimuli were presented on the screen located behind the scanner and viewed by participants via a mirror attached on the head coil. Fiber optic button boxes in each hand were used to record behavioral responses. Incorrect responses were removed from the response time analysis and the fMRI data analysis.

2.4. fMRI acquisition and analysis

Functional MRI was conducted on a 3T Siemens TRIO scanner with an 8-channel radio frequency head coil located in the Imaging Research Facility at Indiana University. Functional images were obtained in eighteen oblique axial slices with 5 mm thickness and a 1 mm gap (TR = 1000 ms, TE = 25 ms, flip angle = 60 degrees, matrix size = 64×64, FOV = 240×240 mm^2) by a gradient echo planar imaging (EPI) sequence. Before statistical analysis, for all functional images, conventional preprocessing procedures such as slice timing correction, head motion correction by realignment and spatial normalization were conducted using SPM8 software (Wellcome Department of Imaging Neuroscience; http://www.fil.ion.ucl.ac.uk/spm). In the spatial normalization step, all functional images were warped to the Montreal Neurological Institute (MNI) EPI template and resampled to $2 \times 2 \times 2$ mm^3 voxels. A canonical hemodynamic response function (HRF) with trial onsets and durations for each phase (including the delay period) was used to generate a statistical parametric map for each individual participant. Contrasts examining each sentence type (conjoined active and object-relative) and each phase (sentence and probe) were examined.

An analysis to explore the correlation between whole brain activation and handedness scores was performed using multiple regression analysis using SPM8. The significance level was determined using a t-test. In addition, a standard one sample t-test was performed to explore activation patterns without regard to handedness. A threshold of $p < 0.001$, uncorrected was used with an extent threshold of 62 voxels. Monte Carlo simulations via AlphaSim (a part of the Afni software package) was used to determine the extent threshold that corrected for multiple comparisons.

Using the acquisition imaging parameters resulted in a corrected extent threshold of 8 voxels in acquisition space which translates into 62 voxels in the transformed MNI space.

3. Results

3.1. Behavioral results

A regression analysis was performed to examine the correlation between DH and accuracy and reaction time to the active and object-relative sentences as well as the syntactic complexity effect (object-relative minus conjoined active). No relationship was observed between behavioral performance and degree of handedness (error rate: $r = -0.15$; RT: $r = -0.05$; p-values were greater than 0.3) indicating that DH has no impact on behavioral performance.

The reaction time and error data for the object-relative and conjoined active sentences were also compared. As observed in previous studies, both measures revealed a significant effect of syntactic complexity [error: object-relative $M = 15.5 \pm 11.1\%$, conjoined active $7.7 \pm 8.4\%$, $t = 5.6$, $p < 0.001$; reaction time: object-relative $M = 2425.6 \pm 462.4$ ms, conjoined active $M = 2084.1 \pm 413.4$ ms; $t = 8.5$, $p < 0.001$].

3.2. fMRI results

3.2.1. Conjoined active constructions

The conjoined active sentences, when compared to fixation, elicited activation in the typical language network (see Fig. 1) that included the left inferior frontal gyrus, and bilateral temporal cortex. The activation level in a number of regions was found to be negatively correlated with DH including the left middle temporal cortex, anterior cingulate cortex and cerebellum as well regions in the right hemisphere (see Fig. 2; Table 1).

For the comprehension probe, activation was observed in the inferior frontal gyrus and inferior parietal cortex. No regions showed a significant correlation with DH.

3.2.2. Object-relative constructions

The object-relative sentences, when compared to fixation, elicited activation in the traditional language network (see Fig. 1). For object-relative sentences, no regions showed a significant correlation for the sentence phase.

The comprehension probe elicited widespread activation that included the traditional language regions including the inferior frontal gyrus, temporal cortex and inferior parietal cortex, in addition to the cerebellum, basal ganglia and anterior cingulate cortex. The correlation analysis revealed a single region's activation was correlated with DH; a positive correlation between DH and the posterior cingulate/precuneus cortex was observed (see Fig. 2; Table 1).

4. Discussion

The aim of this study was to explore the impact of degree of handedness on language processing. The results revealed significant correlations between DH and fMRI activation associated with sentence comprehension. These regions included those that have been linked to semantic memory (temporal cortex) as well as those linked to episodic memory (the precuneus/PCC). However, a differential response was observed for the two levels of syntactic complexity with DH having a much weaker impact on the more difficult object-relative sentences than the canonical conjoined active sentences. Below is a discussion of how these results fit within the current literature.
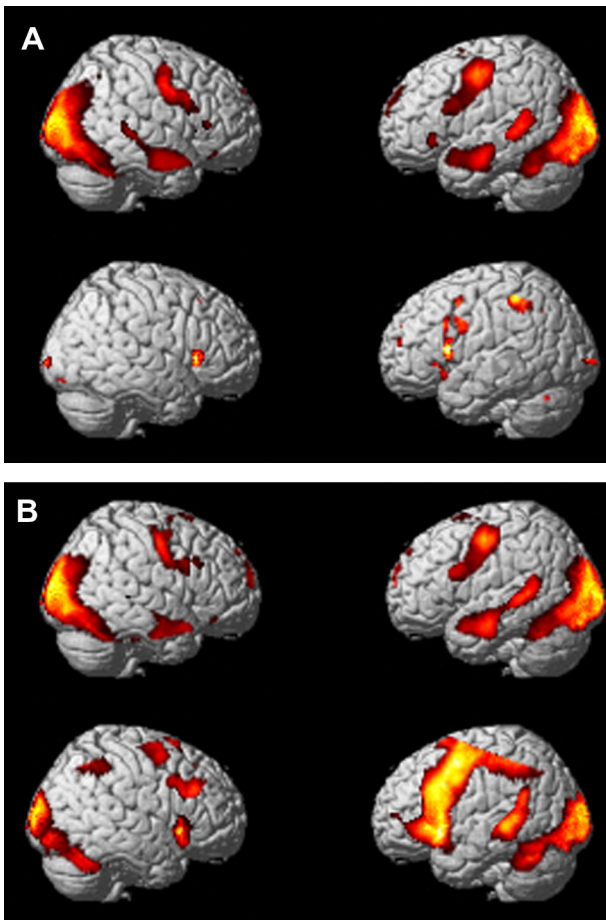
Fig. 1. Depicted are the activation maps for the two sentence types and each processing phase compared to fixation (corrected for multiple comparisons, FWE $p < 0.05$, extent threshold = 20 voxels). (A) are the maps for the conjoined active constructions (top sentence phase bottom probe phase (a different threshold was used for the probe phase: uncorrected $p < 0.001$). (B) Are the maps for the object-relative constructions.
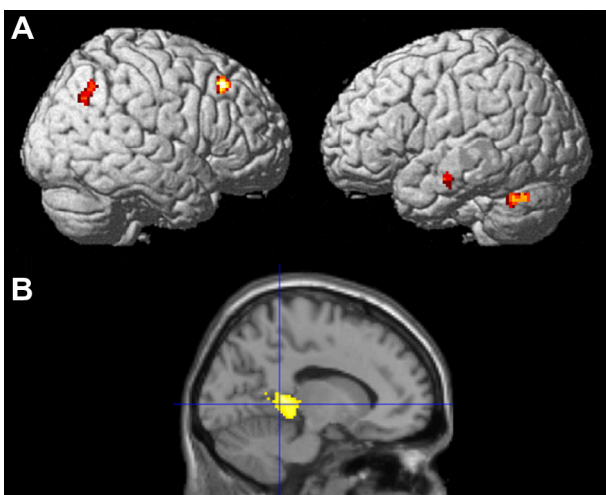
Fig. 2. (A, top) Regions that revealed a significant negative correlation with DH during the sentence phase for conjoined active sentences. (B) Regions that revealed a significant positive correlation with DH during the probe phase for object-relative sentences.

4.1. Semantic memory

Previous studies strongly suggest not only semantic memory differences between DH groups but also that the use of semantics in service to sentence comprehension may be different (see Sontam et al., 2009; Townsend et al., 2001). The results presented here support this idea. A region with strong links to semantic memory, the left temporal cortex (Ralph, Cipolotti, Manes, & Patterson, 2010; Simmons & Martin, 2009), was found to show activation that was modulated by DH. More anterior portions of the superior and middle temporal cortex were found to be negatively correlated with DH for the conjoined active sentence phase. This result demonstrates that stronger DH individuals accessed semantic memory less than did weaker DH individuals when reading conjoined active sentences. This fits Townsend et al. (2001) hypothesis suggesting that FS⁺/weaker DH individuals use semantics more readily.

In the current study effects of DH were found during the processing of canonical active sentences, not complex object-relative sentences. One potential explanation for this difference is derived from the hypothesis proposed by Bever et al. (1989) – DH influences the linguistic information that is the focus of attention. For simple structures there may be more freedom in choosing which information to attend to because the word order is as expected. However, for more complex constructions, in this case one that requires syntactic movement, the syntax, or serial word order, must be the focus of attention. As a result this may weaken the effect of DH during sentence processing.

4.2. Episodic memory

Although the primary goal of the current study was to investigate the impact of DH on the language processing system, here a region that has been associated with episodic memory was found to be correlated with DH. This finding was somewhat unpredicted given that there are no strong connections between episodic memory processing and sentence comprehension. However, episodic memory processes have been found to be affected by DH (Christman & Butler, 2011; Lyle & Jacobs, 2010). For example, weaker DH individuals have been shown to have better source memory (Christman, Propper, & Dion, 2004; Lyle & Jacobs, 2010) as well as more "Remember" judgments versus familiarity, 'Know' judgments during a recollection task (Propper, Christman, & Phaneuf, 2005). One explanation for the differences in episodic memory is related to the increased collaboration between the left and right hemisphere. In support of the findings of superior episodic memory performance by weaker DH participants, studies have shown that the size of the corpus callosum is larger in weaker versus stronger DH participants (Clarke & Zaidel, 1994; Cowell, Kertesz, & Denenberg, 1993; Luders et al., 2010).

Here a region, the precuneus, that has been linked to episodic memory revealed activation that was modulated by DH (Aggleton & Pearce, 2001; Binder & Desai, 2011; Binder, Desai, Graves, & Conant, 2009; Epstein, Parker, & Feiler, 2007; Vincent et al., 2006). The precuneus showed a positive correlation with DH during the probe phase when processing object-relative sentences. This region is a part of the default-mode network (Raichle et al., 2001) and has often been found to show decreased activation relative to baseline. Therefore the positive correlation found in this study corresponds to less activation (more negative activation and less perturbation of the activity of the region) for the weaker DH group and greater activation (more positive activation and more perturbation of activity) for the stronger DH group. In other words, the stronger DH group relied more heavily on the functioning of this region than did the weaker DH group. This suggests that the weaker DH participants who have greater access to the contextual, semantic information may then require less use of episodic

Table 1
Activation correlated with degree of handedness for each sentence type.

	Region	Brodmann area	k	R^2	z-Score	MNI coordinates		
						x	y	z
Conjoined active sentence phase (negative correlation)								
Left	Cingulate gyrus	23/31	490	0.38	4.25	−4	−24	24
Right	Cingulate gyrus	23			4.03	6	−24	26
Left	Temporal	20	138	0.34	3.92	−44	−14	−20
Right	Middle frontal	8	97	0.32	3.74	44	28	48
Right	Precuneus	39/7	73	0.29	3.62	38	−64	36
Left	Cerebellum (Posterior Lobe)		83	0.28	3.53	−46	−54	−32
Object-relative probe phase (positive correlation)								
Left	Posterior cingulate	29	1024	0.38	4.16	−16	−44	2

memory when answering the probe. There is some suggestion that this may be the case; when the threshold is lowered similar regions within temporal cortex that revealed a negative correlation with DH when processing conjoined active sentences also showed a negative, albeit weaker, correlation when processing object-relative sentences, suggesting that weaker DH individuals are still attending to semantic information more than strong DH individuals when processing this more complex structure. It should also be noted that the correlation between DH and the activation of the precuneus was observed during the probe phase, not the sentence phase. This is when the participant was required to recall information processed and stored during the sentence phase. Together the results presented support the hypothesis that weak DH individuals attend to semantic information more than strong DH individuals and that this attentional bias has implications for not only sentence-level processing but how information stored during sentence processing is retrieved.

5. Conclusions

The results presented here replicate and extend those reported previously by showing that the neural architecture that supports sentence comprehension is modulated by DH. It should be noted that there were no behavioral differences as a function of DH. This indicates that both strong and weak DH participants are equally adept at comprehension, but that the strategy used may be different. These results extend previous research investigating degree of handedness as well as individual differences in language comprehension. Here we focused exclusively on right-handed individuals and found DH differences in this group that excluded left-handed individuals. Additionally, these results demonstrate that simply using direction of handedness does not control as much variance as once thought and that this individual difference may impact the observance to temporal cortex activation during sentence tasks. It also suggests that degree of handedness may actually be a more important variable to consider than direction of handedness.

Finally, the source of the effect of DH is not at all clear. One possibility is a complex interplay between experience and genetics. As suggested by Townsend et al. (2001) in discussing familial sinistrality, genetics may contribute to hemispheric dominance for language and therefore impact the extent to which encoding is a left versus right hemisphere process. Because the two hemisphere are thought to process information in different ways (see Beeman & Chiarello, 1998), this will impact how language in processed. Additionally, over the course of development and via education these genetic predispositions can be either reinforced or discouraged. Further research is necessary to determine the precise mechanism responsible for the effect of degree of handedness on language processing. It could prove to be important to characterize as it may contribute to the language impairments observed in disorders such as dyslexia.

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