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Hemispheric asymmetries and joke comprehension

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Abstract

Joke comprehension deficits in patients with right hemisphere (RH) damage raise the question of the role of the intact RH in understanding jokes. One suggestion is that semantic, or meaning, activations are different in the RH and LH, and RH meanings are particularly important for joke comprehension. To assess whether hypothesized differences in semantic activation in the two hemispheres were relevant to joke comprehension, we recorded event-related brain potentials (ERPs) as healthy adults read laterally presented "punch words" to one-line jokes and nonjoke controls. Jokes presented to the RVF/LH elicited larger amplitude N400 than the nonjoke endings; when presented to the LVF/RH, the joke and nonjoke endings elicited N400s of equal amplitude. This finding suggests that semantic activations in the two hemispheres do differ, with RH semantic activation facilitating joke comprehension.
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Keywords: Hemispheric asymmetries; Joke comprehension; Semantic activation

1. Hemispheric asymmetries and joke comprehension

The study of brain damaged patients suggests the two hemispheres differ markedly in their importance for language processing. For example, speech production, naming, and language comprehension deficits are typically produced by damage to the left, but not the right hemisphere (Blumstein, 1994; Damasio, 1992). Further, while lesions to the right hemisphere (RH) are far less likely to result in the profound linguistic deficits associated with left hemisphere (LH) damage, individuals with RH damage do exhibit a number of subtle semantic and pragmatic processing deficits, such as difficulty understanding the meaning of familiar idiomatic phrases (Van Lancker & Kempler, 1987), metaphors (Brownell, 1988), and indirect requests (Stemmer, 1994; Stemmer, Giroux, & Joanette, 1994). These findings suggest that the left hemisphere is crucial for fundamental aspects of language production and comprehension, while the right hemisphere is important for language tasks that require the listener to strategically recruit background knowledge, or to appreciate the relationship between an utterance and its context (Joanette, Goulet, & Hannequin, 1990).

One example of a high-level language phenomenon that underscores the functional asymmetry in the language processing capacity of the two hemispheres is joke comprehension because it presupposes the listener's ability to interpret language against background knowledge. For instance, in "I let my accountant do my taxes because it saves time: last spring it saved me ten years," the reader begins by constructing a mental model in which a busy professional pays an accountant to do his taxes. However, at "years" she is forced to go back and reinterpret "time" as time in prison, evoking a frame where a corrupt businessman pays an accountant to conceal his illegal business dealings. Coulson (2000) has called this sort of conceptual revision *frame-shifting*, and suggests that it reflects the operations of a semantic reanalysis process that reorganizes existing information into a new frame or schema retrieved from long-term memory. In the example above, frame-shifting involves mapping the information contained in the original busy-professional interpretation into the corrupt-businessman frame. Jokes such as this violate normal expectations, and in so doing, they highlight the way we rely on background knowledge to structure expectations and draw inferences that go beyond what's immediately present.

Frame-shifting in joke comprehension has been studied with event-related brain potentials (ERPs) by Coulson and Kutas (2001). These investigators manipulated the relationship between sentence final words and their preceding contexts by comparing ERPs for sentence fragments that ended either as jokes or with equally unexpected nonjoke endings. ERPs to jokes began to differ from controls after 250 ms post-onset. Among other things, the amplitude of the N400

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component was greater for joke than nonjoke endings, especially in sentences for which off-line measures suggested readers could commit to a particular interpretation of the scenario before the onset of the last word. Results suggest it was easier to integrate the unexpected nonjoke endings consistent with contextually evoked information than the joke endings that required frame-shifting.

Although Coulson and Kutas' ERP study of joke comprehension did not investigate hemispheric differences, a neuroimaging study in healthy adults indicates that joke comprehension elicits increased RH activity (Goel & Dolan, 2001). Further, researchers in neuropsychology have long noted that difficulty understanding jokes is associated with right hemisphere damage (RHD) (Bihrle, Brownell, & Gardner, 1986; Brownell, Michel, Powelson, & Gardner, 1983; Gardner, Ling, Flamm, & Silverman, 1975), especially damage to the right frontal lobe (Shammi & Stuss, 1999). Interestingly, there is reason to suspect that joke comprehension deficits associated with RHD relate to the conceptual demands of frame-shifting. Brownell and colleagues gave RHD patients jokes and asked them to pick the punch-line from an array of three choices: straightforward endings, non-sequitur endings, and the correct punch-line. While age-matched controls had no trouble choosing the punch-lines, RHD patients tended to choose the non-sequitur endings (Brownell et al., 1983). This finding suggests that RHD patients understand that jokes involve a surprise ending, but are impaired on the frame-shifting process required to re-establish coherence.

The pattern of deficits in RHD patients differs dramatically from those evidenced by LHD patients whose communicative difficulties are seemingly more severe. In order to compare the performance of LHD and RHD patients on joke comprehension, Bihrle and colleagues used both verbal and nonverbal materials (Bihrle et al., 1986). In addition to jokes of the sort used by Brownell and colleagues (Brownell et al., 1983), these investigators also used four-frame cartoons with the same narrative structure. Whether patients received verbal or nonverbal materials, they were asked to pick the punch-line (or punch frame) from an array of four choices: a straightforward ending, a neutral non-sequitur, a humorous non-sequitur, or the correct punch-line.

While both sorts of patients were impaired on this task, their errors were qualitatively different. In both verbal and non-verbal materials, RHD patients showed a consistent preference for non-sequitur endings over straightforward endings and correct punch-lines (Bihrle et al., 1986). In contrast, LHD patients (who participated only in the nonverbal task) more often chose the straightforward endings than either of the non-sequitur endings (Bihrle et al., 1986). These data suggest that the deficits RHD patients experience in the comprehension and production of humor are not attributable to the emotional problems associated with some kinds of RHD, as the RHD patients displayed preserved appreciation of the slapstick depicted in the humorous non-sequitur endings. Subsequent research has demonstrated that RHD patients also have difficulty interpreting *nonjoke* materials that require semantic reanalysis (Brownell, Michel, Powelson, & Gardner, 1986). These observations indicate that the difficulty that RHD patients experience in the comprehension of humorous materials is cognitive rather than emotional, and involves inferential reanalysis.

What, then, is the nature of right hemisphere involvement in joke comprehension among neurologically intact individuals? One suggestion from researchers working with healthy adults using the divided visual field (DVF) priming paradigm is that RHD joke comprehension deficits may be related to differences in the content of semantic activation in the left and right cerebral hemispheres. The DVF paradigm involves the presentation of written stimuli outside the center of gaze in either the left or the right visual field so that it preferentially stimulates the contra-lateral hemisphere (LVF/RH and RVF/LH) (Chiarello, 1988; Chiarello, Liu, & Faust, 2001).

While DVF priming studies consistently find that RVF/LH presentation leads to shorter reaction times on priming tasks, presentation to the RVF/LH does *not* always yield more robust priming effects, viz. better performance on words preceded by semantically related or associated material than when preceding material is unrelated. For example, though most single word priming studies using strongly associated words (such as CAT and DOG) report equivalent priming with right and left visual field presentation, non-associated category members such as GOAT and DOG yield greater priming effects with LVF/RH presentation (Chiarello, Burgess, Richards, & Pollock, 1990). Further, people benefit more from "summation" primes (three words weakly related to the target) when naming target words presented to the LVF/RH than the RVF/LH (Beeman et al., 1994).

Such differences in the sort of priming effects obtained with presentation to the left and right visual fields have led to the suggestion that joke comprehension deficits in RHD patients may be related to hemispheric differences in semantic activation in the healthy brain. One suggestion is that semantic activations in the LH are more specific than those in the RH, described as "fine" versus "coarse" coding (Beeman & Chiarello, 1998; Chiarello et al., 1990). The left hemisphere (LH) employs fine coding and strongly activates only information closely related to the input. The right hemisphere (RH) employs coarse coding and weakly activates a broad range of information related to the input. Beeman and colleagues have suggested that coarse coding in the RH makes it less effective than the LH for selecting contextually appropriate meanings for single words but more effective at detecting the overlap from multiple words and, perhaps between new input and established context (Beeman, 1993; Beeman et al., 1994). While information activated by the LH is usually adequate to connect discourse elements, information activated in the RH might be crucial for connecting distantly related elements such as those needed to get a joke.

To assess whether hypothesized differences in semantic activation in the two hemispheres are relevant to joke comprehension, we recorded ERPs as healthy adults read laterally presented "punch words" to one-line jokes. The

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N400 component, a negative-going deflection in the ERPs associated with the processing of meaningful stimuli, was of particular interest, as its amplitude can be interpreted as an index of processing difficulty (Kutas & Van Petten, 1994). The first ERP component to be clearly linked to a specific aspect of language processing, the N400 was initially elicited in experiments contrasting sentences that ended sensibly and predictably with others that ended with an incongruous word (Kutas & Hillyard, 1980). Subsequent research has shown that finer gradations of semantic context also modulate N400 amplitude. First, amplitude shows a strong inverse correlation with the predictability of the eliciting word within a given sentence context (cloze probability) (Kutas & Hillyard, 1984). Second, the size of the N400 declines across the course of congruous sentences, but not incongruous ones, an effect interpreted as reflecting the buildup of contextual constraints as a sentence proceeds (Van Petten & Kutas, 1990). In general, N400 amplitude is seen as an index of the difficulty of integrating a word into a given context: the larger the N400, the more difficult the task of lexical integration (Kutas, Federmeier, Coulson, King, & Munte, 2000). Further, previous ERP research on joke comprehension has shown that the critical word in a joke elicits a larger N400 than a similarly unexpected nonjoke ending for the same sentence: this has been called the N400 joke effect (Coulson & Kutas, 2001).

Sentence frames such as, “A replacement player hit a home run with my” were presented one word at a time in participants’ center of gaze, while the final word “girl” (joke ending) or “ball” (nonjoke ending) was presented para-foveally either to the left or the right of the fixation point. If hemispheric differences in semantic activation are relevant for joke comprehension, lateral presentation of joke versus nonjoke endings for these sentences should result in differential N400 joke effects as a function of visual field of presentation. That is, hemispheric differences in semantic activation might affect the difficulty of lexical integration in jokes more than nonjokes, and these differences would be indexed by the N400. If coarse coding in the RH results in the activation of information important for joke comprehension, N400 joke effects should be smaller when the critical word is presented to the LVF/RH than the RVF/LH. Alternatively, if N400 joke effects do not differ with LVF/RH versus RVF/LH presentation, then either hypothesized differences in semantic activation are not present, or else they are not relevant to joke comprehension.

2. Methods

2.1. Participants

Participants were 16 right-handed, monolingual English speakers. Handedness was assessed via the Edinburgh inventory (Oldfield, 1971). Nine participants were male, and all were healthy, college-aged adults with normal or corrected-to-normal vision. Informed consent was obtained, and all procedures conformed to ethical requirements of the University of California, San Diego.

2.2. Materials

Materials included 160 experimental sentences which could end either as a joke or with a nonjoke ending, and 80 filler sentences that ended as expected. Jokes were assembled from various anthologies of one-line jokes, chosen so that understanding the joke required reinterpretation of meaning established earlier in the sentence. In all cases, the point at which the reader could, in principle, realize the joke was the sentence-final word. Experimental sentences in joke and nonjoke conditions were thus identical until the sentence-final word, where joke endings required frame-shifting, while equally unexpected nonjoke endings were consistent with the contextually evoked frame. Each sentence was followed by a comprehension question, half of which were normatively answered by a ‘yes’, and half by a ‘no’. Table 1 contains a representative sample of stimuli and comprehension questions.

The degree to which sentence-final words were predictable from context was assessed in a separate off-line “cloze”, or sentence completion task. In this task 80 people from the same population as the participant pool for the main experiment were given sentence frames minus their final words and asked to fill in the blank with the first word that came to mind. The percentage of people who choose a given word is known as the *cloze probability* of the word

Table 1
Sample stimuli and comprehension questions

Stimulus	I still miss my ex-wife, but I am improving my aim/ego
Joke question	I am shooting at my ex-wife (yes)
Nonjoke question	I am starting to feel better about myself (yes)
Stimulus	It is not hard to meet expenses: they are everywhere/affordable
Joke question	It is easy to pay the bills (no)
Nonjoke question	You should be able to pay all your bills (yes)
Stimulus	The last time a guy in a mask took all my money, I was in surgery/shock
Joke question	I had been mugged (no)
Nonjoke question	I had been mugged (yes)
Stimulus	My mechanic could not fix my brakes, so he fixed my horn/clutch
Joke question	He figures if I cannot stop, I will have to honk at people (yes)
Nonjoke question	My clutch was also broken (yes)
Stimulus	A man who has lost ninety percent of his brain is called a widower/zombie
Joke question	His wife was not very smart (no)
Nonjoke question	A zombie still has an intact brain (no)
Stimulus	The only ones who want me for my body are mosquitoes/losers
Joke question	People find me very sexy (no)
Nonjoke question	Everybody finds me very attractive (no)

in that particular sentence context. Cloze probability of the "expected" completions in the filler sentences was 80.8% (S.E. = 11.3%). Because jokes are, by definition, surprising, the cloze probability of joke endings was considerably lower: 0.9% (S.E. = 1.3%). In contrast to the joke endings, which were hypothesized to prompt frame-shifting, nonjoke endings were consistent with the contextually evoked frame, and thus formed congruous endings to experimental sentences. Because N400 amplitude is known to be sensitive to cloze probability, the cloze probability of the nonjoke endings used in the experiment (2.2%, S.E. = 1.5%) was not significantly greater than that of the joke endings.

Sentence-final words were also matched for word length, word frequency, and word association, three factors known to influence the amplitude of the N400 (Coulson & Federmeier, in press; Kutas & Van Petten, 1994). The average number of characters in the critical words in jokes was 6.8 (S.E. = 1.6), nonjokes was 6.8 (S.E. = 1.6), and expecteds 6.8 (S.E. = 1.0). Frequency per million as assessed by the Kucera and Francis database (Kucera & Francis, 1967) was 47.2 for jokes (S.E. = 53.2), 46.8 for nonjokes (S.E. = 52), and 47.1 for expecteds (S.E. = 53.2). The presence of lexical associates was checked by looking up joke and nonjoke endings in the on-line version of the Edinburgh Associative Thesaurus (Coltheart, 1981) to see whether sentence-final words were produced in response to any of the words in the sentence context (i.e. whether the sentence-final word was "primed" by words in the sentence). Approximately 11% of the joke endings were preceded by a semantic associate, as were 8% of the nonjoke endings. The associative index for these stimuli, that is the percentage of people who produced the sentence final word in response to a word from the sentence context was 12% for the jokes (S.E. = 14%), and 10% for the nonjokes (S.E. = 11%). Collapsed across all stimuli, the associative index for the jokes was 1.3% (S.E. = 2.3%), and was 1.6% for the nonjokes (S.E. = 3%). Effects of associative priming were thus assumed to be negligible, and in any case would be expected to be the same for both sorts of experimental stimuli.

The 160 pairs of experimental sentences were presented in two different lists; joke endings in one list were replaced by nonjoke endings in the other list, and vice versa so that no participant saw both versions of the experimental stimuli. The 80 filler sentences were the same in both lists. Each type of stimulus (jokes, nonjokes, and expecteds) occurred equally often in each visual field. Further, each of these two stimulus lists was duplicated in order to counterbalance visual field of presentation. Each participant viewed one of the four lists. In this within-participants design, then, Sentence Type (joke/nonjoke/expected), and Visual Field were fully counterbalanced.

2.3. Procedure

Participants sat in an electrically shielded, sound-attenuated chamber at a distance of 37 in. from the computer monitor. They were told that they would be reading sentences one word at a time in the center of the screen, and were instructed to focus their eyes centrally at all times. When the critical word appeared (displaced to the left or the right), they were to read it silently without moving their eyes, and then to say it aloud when the blue question mark appeared, or to say "No" if they had been unable to read it. The experimenter, a native English speaker, recorded on a paper form whether or not the correct word was produced. After each sentence, a comprehension sentence was presented (in its entirety) and participants were instructed to judge whether or not it was consistent with the first sentence, and to respond by making a 'yes' or 'no' button press. Response hand was counterbalanced across participants.

Stimuli were presented in a custom black Helvetica font against a white background to maximize contrast. The first sentence of each pair was preceded by a fixation cross to orient the participant to the center of the screen. Each word of the first sentence was then presented in the center of the screen for a fixed duration of 200 ms with an inter-stimulus-interval (ISI) that varied as a function of word-length (i.e., 200 ms + 32 ms/character). The final, target word of each sentence was followed by a blank screen for 2500 ms before the presentation of the naming prompt (a question mark). The comprehension sentence was then presented for 4 s, and followed by a blank screen for 2 s until the next trial began.

Simultaneous with the onset of the lateralized probe, a fixation cross appeared in participants' center of gaze. Left visual field stimuli were presented so that their right-most character was 2° of visual angle to the left of the fixation point. Right visual field probes were presented so that their left-most character was 2° of visual angle to the right of the fixation point. The session began with a brief practice block of four trials, and participants were asked to repeat the practice block until the experimenter was satisfied that they were able to comply with task demands (refrain from horizontal eye movements during the presentation of the critical word, wait until prompted by the blue question mark to name the critical word, and answer the comprehension question with a button-press). Experimenters monitored participants' eye movements on-line via the EOG. When participants moved their eyes during the presentation of the critical word, data collection was paused and the experimenter re-explained the instructions. (Trials in which eye movements were evident in the EOG signal were not included in averaged ERP data.)

2.4. EEG recording

Participants' electroencephalogram (EEG) was recorded from 29 tin electrodes mounted in an Electro-Cap, referenced to the left mastoid. Electrode sites included the following 10–20 sites: FP1, FPZ, FP2, F7, F3, FZ, F4, F8, FT7, FC3, FCZ, FC4, FT8, T3, CZ, T4, TP7, CP3, CPZ, CP4, TP8, T5, P3, PZ, P4, T6, O1, OZ, and O2 (Jasper, 1958; Nuwer et al., 1998). Horizontal eye-movements were moni-

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tored via a bipolar montage of electrodes placed at the outer canthi. Blinks were monitored via an electrode placed on the infraorbital ridge of the right eye and referenced to the left mastoid. The EEG was also recorded at the right mastoid, and all data were re-referenced off-line to the average of the right and left mastoids. Electrode impedances were kept below 5 kΩ. EEG was processed through SA Instrumentation Co. amplifiers set at a band pass of 0.01–40 Hz. EEG was continuously digitized at 250 Hz and stored on a hard disk.

The EEG data recorded from each participant were visually inspected, and trials were rejected when contaminated by artifacts such as excessive vertical or horizontal electro-oculographic potentials, excessive muscle activity, and amplifier blocking or drift. Artifact contamination in the digitized data was determined off-line by using computer algorithms that calculated peak-to-peak voltage amplitudes, voltage deviations from baselines and polarity inversions between the lower eye and prefrontal recordings.

2.5. Data analysis

Naming accuracy scores expressed as percent correct were subjected to repeated measures ANOVA with factors Sentence (expected/nonjoke/joke) and Visual Field (LVF/RVF).

Sentence-final words were particularly important for understanding the experimental sentences in our stimulus set, as indicated by the fact that when participants were unable to name the sentence final word, their performance on comprehension questions approximated that predicted by chance (jokes: 54.1%, nonjokes: 52.3%). Consequently, we assessed performance on the comprehension questions by dividing the number of sentences for which a given participant both named the sentence-final word and provided the correct answer for the subsequent comprehension probe by the number of correctly named words. That is, if a participant was unable to name the sentence-final word, his response to the comprehension probe for that sentence was discarded.

ERPs were computed for recording epochs extending from a 100 ms pre-stimulus onset baseline to 920 ms post-stimulus onset. Averages of artifact-free ERP trials were calculated for each type of target word in each visual field after subtraction of the 100 ms pre-stimulus baseline. Only words that were correctly named in the delayed naming task were allowed to contribute to the ERP averages. Unnamed words were removed from ERP data in order to minimize the impact of hemispheric differences in the ability to decode written text (Jordan, Thomas, & Patching, 2003) and maximize that of semantic processing differences. ERPs were quantified by measuring the mean amplitude of the waveforms 300–500 ms, and 500–900 ms post-onset relative to the 100 ms pre-stimulus baseline and analyzed with repeated measures ANOVA. In all analyses, P values are reported after epsilon correction (Huhyn–Feldt) for repeated measures with more than 1 degree of freedom in the numerator. Interactions between the experimental variable and electrode site were followed up by analyses of data collected from midline, dorsal, and lateral sites. Midline sites refer to: FPZ, FZ, FCZ, CZ, CPZ, PZ, and OZ; dorsal sites refer to: FP1, FP2, F3, F4, FC3, FC4, CP3, CP4, P3, P4, O1, and O2; lateral sites refer to F7, F8, FT7, FT8, T3, T4, TP7, TP8, T5, and T6.

3. Results

3.1. Naming

Accuracy rates on the delayed naming tasks can be seen in Table 2. Analysis revealed a main effect of sentence due to greater accuracy for expected completions (96.7%) than for either of the two experimental conditions: nonjoke endings 81.9%, joke endings 78.6% ($F(2, 30) = 32.6$, $P < 0.0001$, $e = 0.80$). Analysis also revealed a reliable right visual field advantage as 95.3% of stimuli presented to the RVF were named correctly, in contrast to a mere 76.2% of stimuli presented to the LVF ($F(1, 15) = 38.22$, $P < 0.0001$). However, main effects were qualified by an interaction between Sentence and Visual Field ($F(2, 30) = 21.41$, $P < 0.0001$, $e = 0.94$). The interaction results from the relatively small right visual field advantage in the expected condition (see Table 2).

Separate analysis of accuracy rates on joke and nonjoke endings revealed a non-significant trend towards greater accuracy on nonjoke stimuli ($F(1, 15) = 4.38$, $P = 0.05$), a reliable right visual field advantage ($F(1, 15) = 41.21$, $P < 0.0001$), but no indication that the visual field effect varied as a function of sentence type ($F(1, 15) = 0.03$). Naming tasks in the divided visual field (DVF) priming paradigm typically result in an advantage for stimuli presented to the RVF (Chiarello, 1988), consistent with the fact that speech production is lateralized to the left hemisphere in most right handed adults (Knecht et al., 2000).

3.2. Comprehension

Accuracy rates on the comprehension questions can be found in Table 3. Overall, performance (93% correct) on

Table 2
Accuracy on the delayed naming task

	LVF (%) (S.E.)	RVF (%) (S.E.)
Expected	94 (1.8)	99 (0.4)
Nonjoke	69 (4.7)	95 (2.1)
Joke	65 (5.6)	91 (1.9)

Table 3
Accuracy on the comprehension probes

	LVF (%) (S.E.)	RVF (%) (S.E.)
Expected	95 (3.5)	94 (4.8)
Nonjoke	95 (4.5)	93 (5.9)
Joke	92 (9)	91 (6.8)

these questions was excellent. Analysis revealed a main effect of sentence, as participants averaged 95% on expected sentences, 94% on nonjokes, and 91% on jokes ($F(2, 30) = 3.79$, $e = 0.92$, $P < 0.05$). However, neither the visual field effect ($F(1, 15) = 1.08$), nor the visual field by sentence type interaction ($F(2, 30) = 0.10$) approached significance.

3.3. Visual potentials

Besides the RVF advantage that participants displayed on the delayed naming task, the DVF presentation also affected the amplitude and latency of the N1 component. The N1 is a well-studied ERP component implicated in high-level visual processing (Hillyard & Anllo-Vento, 1998). To assess the amplitude of the N1, we measured the mean amplitude of ERPs elicited from 75 to 175 ms after the onset of lateralized stimuli at four electrode sites where N1 is known to be prominent (T5, T6, O1, and O2) (Federmeier & Kutas, 1999, 2002). The N1 was larger over RH electrode sites with LVF/RH presentation, and larger over LH electrode sites with RVF/LH presentation (Visual Field × Hemisphere $F(1, 15) = 9.13$, $P < 0.01$). As evident in Fig. 1, this N1 reversal was more pronounced at temporal than occipital electrode sites (Visual Field × Hemisphere × Posteriority $F(1, 15) = 14.4$, $P < 0.01$). In addition, with LVF/RH presentation the N1 peaked 120 ms post-onset over RH sites, and 147 ms over LH sites; with RVF/LH presentation, the N1 peaked 118 ms over LH sites, and 141 ms over RH sites (Visual Field × Hemisphere $F(1, 15) = 13.48$, $P < 0.01$). The larger amplitude and earlier peak latency of the N1 over the hemisphere contra-lateral to visual field of presentation suggests that DVF presentation did indeed lead to the increased participation of the opposite hemisphere.

3.4. Expected versus unexpected sentence completions: N400 effect

Because relatively few investigators have recorded ERPs to laterally presented words in sentence contexts (Federmeier & Kutas, 1999), initial analyses were aimed at replicating the well-known effect of expectedness on the N400 component. To this end we compared ERPs elicited by words in the filler condition (expecteds), such as “Our new green car blocked the narrow DRIVEWAY,” with words in the nonjoke condition, such as “A replacement player hit a home run with my BALL.” As noted in Section 2, the cloze probability of the expecteds was 80.8%, while the cloze probability of the nonjoke endings was only 2.1%. Expected endings were more likely to be produced by participants on a sentence completion (cloze) task, but the words in both conditions were matched for average word length and frequency of occurrence. An index of the difficulty of lexical integration, N400 amplitude, is typically greater for low (unexpected) than high (expected) cloze probability words (Kutas et al., 2000; Kutas & Hillyard, 1984).

N400 amplitude was assessed by measuring the mean amplitude of ERPs 300–500 ms after the onset of the sentence-final word in the two different types of sentences. As in previous studies (Kutas & Van Petten, 1994), relative to the expected condition, nonjoke sentence completions

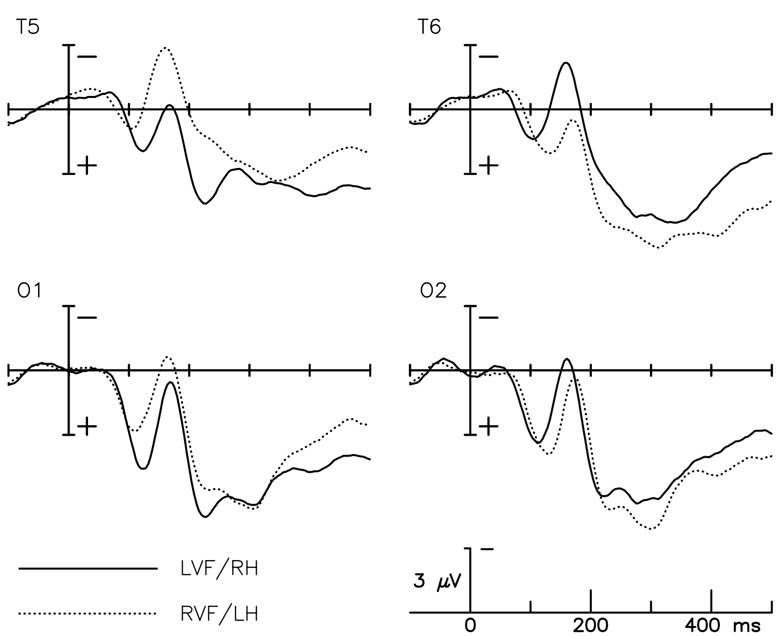

Fig. 1. Visual potentials. The N1 component is the negative (upward) deflection in the waveform peaking approximately 130 ms after the onset of the stimulus evident at temporal electrodes T5 (over the LH) and T6 (over the RH) and occipital electrodes O1 (LH) and O2 (RH). When stimuli are presented to the right visual field (dotted line), the N1 is larger over LH electrode sites. Stimuli presented to the left visual field (solid line) elicit an N1 that is larger over RH electrode sites. This reversal in the lateral asymmetry of the N1 as a function of visual field of presentation indicates the DVF paradigm worked as intended to selectively stimulate the contra-lateral hemisphere.

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here elicited a broadly distributed negative-going response that was largest over centroparietal electrode sites, consistent with the distribution of the N400 component (Expectedness $F(1, 15) = 9.82$, $P < 0.01$; Expectedness × Electrode Site $F(28, 420) = 6.12$, $P < 0.001$, $e = 0.14$). Visual field of presentation also had an overall effect on the amplitude of the ERPs, as words presented to the right visual field (RVF/LH) elicited a more positive response (Visual Field $F(1, 15) = 22.76$, $P < 0.001$). Moreover, visual field modulated the topography of the ERPs in a way that suggested increased participation of the contra-lateral hemisphere. That is, LVF presentation resulted in increased amplitude of ERPs recorded over right temporal sites, while RVF presentation resulted in increased amplitude of ERPs recorded over left temporal sites (Visual Field × Electrode $F(28, 420) = 6.42$, $P < 0.001$). However, we observed no interaction between expectedness and visual field (all F values <1), suggesting the amplitude of the N400 expectedness effect was equivalent with presentation to the RVF/LH and to the LVF/RH.

3.5. N400 joke effects

To examine N400 joke effects across visual fields, we first computed ERP difference waves by subtracting ERPs elicited by experimental stimuli (joke and nonjoke endings) from those elicited by the expected condition presented to the same visual field (as in previous studies utilizing the DVF paradigm; Federmeier & Kutas, 1999, 2002). The use of difference waves was intended to cancel out standing topographic differences between ERPs to words presented in the left and right visual fields. Panel A in Fig. 2 shows difference waves for jokes (a replacement player hit a home run with my GIRL) and nonjokes (a replacement player hit

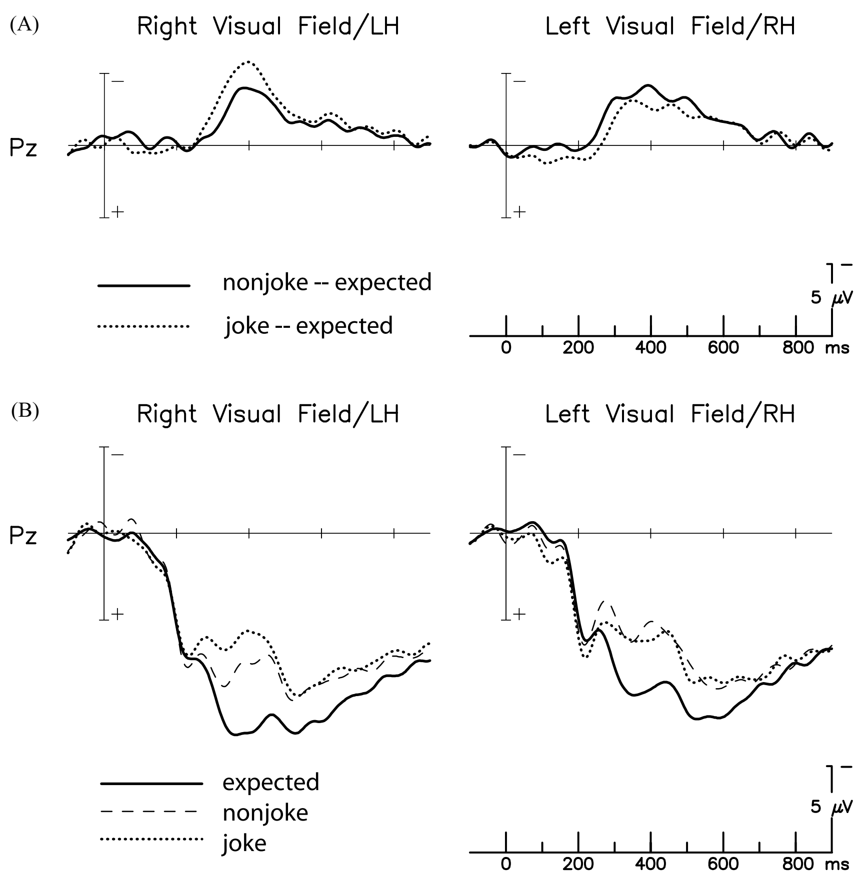

Fig. 2. N400 joke effect. Panel A shows ERP difference waves recorded at a midline parietal electrode site (Pz) where N400 tends to be prominent. ERPs elicited by the last word of sentences that ended as expected ("Our new green car blocked the narrow DRIVEWAY") were subtracted from ERPs elicited by the last word of sentences in each of the two experimental conditions in order to visualize the N400 effect for joke endings ("A replacement player hit a home run with my GIRL") (dotted line) and straight endings ("A replacement player hit a home run with my BALL") (solid line). The N400 effect is the negative (upward) deflection peaking approximately 400 ms after stimulus onset. For stimuli presented to the right visual field (LH), jokes elicited a larger N400 than did straight endings suggesting that the jokes were more difficult to process. For stimuli presented to the left visual field (RH), the amplitude of the N400 elicited by joke and straight endings did not reliably differ. Panel B shows ERPs elicited by the last word of sentences that ended as expected (solid line), with unexpected straight endings (dashed line), and with joke endings (dotted line). Regardless of visual field of presentation, ERPs for expected endings are more positive (less negative) than for the two unexpected ending types in the latency range of the N400 (300–500 ms post-onset). Although right visual field presentation led to ERPs that were more positive overall than those elicited with left visual field presentation, the N400 difference between expected and unexpected straight endings was the same in both visual fields. The visual field manipulation affected the amplitude of the N400 elicited by jokes. RVF/LH presentation led to larger N400 for joke than straight endings; LVF/RH presentation did not.

a home run with my BALL). Panel B shows the raw waveforms for expected completions, joke endings, and nonjoke endings.

Overall analysis of ERP difference waves measured 300–500 ms post-onset indicated that the N400 joke effect differed as a function of visual field (Ending × Visual Field × Electrode Site $F(28, 420) = 2.43$, $P < 0.05$, $e = 0.19$). More focused analyses of ERPs collected at midline, dorsal, and lateral electrode sites all suggested the interaction reflects the different effects of visual field of presentation on an N400 joke effect evident over centro-parietal and posterior temporal electrode sites (Midline: Ending × Visual Field × Anteriority $F(6, 90) = 4.74$, $P < 0.01$; Dorsal: Ending × Visual Field × Anteriority $F(5, 75) = 3.55$, $P < 0.05$; Lateral: Ending × Visual Field × Anteriority $F(4, 60) = 4.69$, $P < 0.05$, $e = 0.35$; Ending × Visual Field × Hemisphere × Anteriority $F(4, 60) = 7.19$, $P < 0.05$, $e = 0.32$).

Follow-up analyses of ERPs elicited by joke and nonjoke endings in each visual field indicated the ending-type manipulation affected the amplitude of the N400 elicited by stimuli presented to the RVF/LH but not the LVF/RH. When presented to the RVF/LH, jokes elicited more negative ERPs over centro-parietal electrode sites (Midline: Ending × Anteriority $F(6, 90) = 4.72$, $P < 0.05$, $e = 0.40$; Dorsal: Ending × Anteriority $F(5, 75) = 3.26$, $P < 0.05$, $e = 0.40$). Analysis of RVF/LH ERPs collected from lateral electrode sites revealed that while a small joke effect was evident over RH scalp sites, it was only evident over the most posterior temporal LH site (T5) (Lateral: Ending × Hemisphere $F(1, 15) = 9.37$, $P < 0.01$; Ending × Hemisphere × Anteriority $F(4, 60) = 4.47$, $P < 0.05$, $e = 0.40$). By contrast, when presented to the LVF/RH, N400 elicited by jokes was equivalent in amplitude to that elicited by the straight endings (Midline: all $F < 1$; Dorsal: all $F \leq 1.09$). Analysis of ERPs collected from lateral sites (with LVF/RH presentation) revealed an interaction between Ending, Hemisphere, and Anteriority ($F(4, 60) = 5.91$, $P < 0.05$, $e = 0.33$) that apparently results because ERPs to jokes were more negative than to nonjokes over a single electrode site (F7).

Timing of the N400 effect was assessed by measuring the peak latency of the difference waves at the midline parietal electrode site Pz. The N400 effect peaked at 391 ms post-stimulus onset. These latency values were subjected to repeated measures ANOVA with factors Ending and Visual Field. Analysis suggested N400 peak latency was affected by neither factor ($F < 1$). Onset of the N400 was assessed by again measuring the difference waves at electrode site Pz in order to determine the latency at which this component reached 10% of its peak amplitude. Measured in this way, the average N400 onset latency was 288 ms post-stimulus onset. Repeated measures ANOVA revealed no indication that either Ending or Visual Field affected the onset latency of the N400 ($F < 1$).

3.6. Late effects

As in previous ERP studies of joke comprehension (Coulson & Kutas, 2001; Coulson & Lovett, 2004), the N400 was followed by two effects in the 500–900 ms post-stimulus interval: more negative ERPs to jokes than nonjokes over left anterior site F7, and more positive ERPs to jokes over dorsal and midline electrode sites. We assessed effects in the late interval in the same manner as the N400 by measuring difference waves formed by subtracting ERPs elicited by words in the expected condition from those elicited by each category of experimental stimuli (joke and nonjoke endings) presented to the same visual field. This subtraction was intended to cancel out standing topographic differences due to visual field of presentation, while still allowing us to observe topographic differences in ERPs to jokes and nonjokes. Thus the mean amplitude of these difference waves was measured between 500 and 900 ms after stimulus onset and subjected to repeated measures ANOVA.

Overall analysis confirmed that jokes elicited more positive ERPs in this time window than nonjokes (Ending × Electrode $F(28, 420) = 3.44$, $P < 0.05$, $e = 0.13$). Subsequent analysis of ERPs collected from midline and dorsal electrode sites indicated the Ending effect was mainly evident over frontal electrode sites (Midline: Ending × Anteriority F(6,90), $P < 0.01$, $e = 0.38$; Dorsal: Ending × Anteriority $F(5, 75) = 4.03$, $P < 0.05$, $e = 0.37$). Measurements at lateral electrode sites indicated ERPs to jokes were approximately 0.5 μV more negative than nonjokes over left anterior electrode site F7, but more positive (again by approximately 0.5 μV) over left temporal sites (Lateral: Ending × Hemisphere × Anteriority $F(4, 6) = 10.02$, $P < 0.0001$, $e = 0.68$).

Left-lateralized joke effects at lateral electrode sites can be considered different from the joke effect evident over anterior midline sites, and the bilaterally symmetric effect over dorsal sites. While effects at the midline and dorsal sites reflect more positive ERPs to jokes than nonjokes, effects at lateral sites are driven mainly by more negative ERPs to jokes. However, none of these effects differed as a function of visual field (Overall: all $F < 1$; Midline: all $F < 1$; Dorsal: all $F < 1$; Lateral: all $F < 1$).

Fig. 3 shows ERPs elicited by joke and nonjoke endings in each visual field. The sustained anterior negativity to jokes is evident at electrode site F7, while the anterior positivity to jokes is evident at sites F3 and F4. Although the overall analysis revealed no interactions between ending and visual field, inspection of the figure suggested that the anterior positivity was more asymmetric with LVF presentation. Post hoc RVF and LVF analyses were thus conducted on data recorded at electrodes F3, FC3, F4, and FC4 (where the anterior positivity was largest). The mean amplitude of the difference waves described above were measured between 500 and 900 ms and subjected to repeated measures ANOVA with factors Ending, Hemisphere (left versus right

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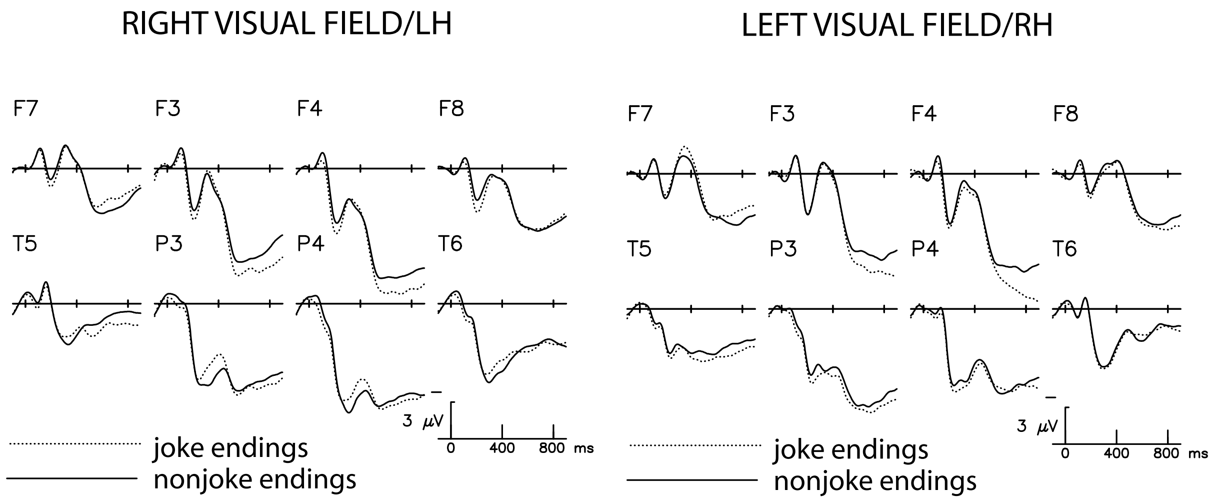

Fig. 3. Joke effects. Grand average ERPs elicited by sentences that ended as jokes (dotted) or with nonjoke endings (solid) presented to the right and left visual fields at frontal, temporal, and parietal electrode sites. The anterior negativity is evident 500–900 ms at site F7, while the anterior positivity is evident at F3 and F4 in the same interval. Different N400 joke effects in the right (present) and left (absent) visual field can be seen at parietal sites P3 and P4.

hemisphere electrode sites), and Anteriority (frontal versus fronto-central).

Analysis of RVF data revealed a marginal 1.1 μV Ending effect larger at the more anterior electrode sites (Ending $F(1, 15) = 3.45$, $P < 0.09$; Ending × Anteriority $F(1, 15) = 3.49$, $P < 0.09$), and no sign of lateralized effects ($F < 1$). Analysis of LVF data revealed a slightly more robust 1.3 μV Ending effect, larger at the more anterior electrode sites (Ending $F(1, 15) = 3.85$, $P < 0.07$; Ending × Anteriority $F(1, 15) = 7.37$, $P < 0.05$). Unlike the bilaterally symmetric joke effects in RVF data, in LVF data joke effects were approximately 0.5 μV larger over RH electrode sites (Ending × Hemisphere $F(1, 15) = 2.32$, $P = 0.15$). Though somewhat equivocal, these findings suggest the anterior joke positivity was slightly right-lateralized with LVF presentation, and bilaterally symmetric with RVF presentation.

4. Discussion

Right hemisphere involvement in joke comprehension is supported both by neuroimaging data from neurologically intact individuals (Goel & Dolan, 2001) and evidence of joke comprehension deficits in patients with unilateral lesions to the RH (Shammi & Stuss, 1999). One attempt to link the deficits observed in RHD patients to hemispheric asymmetries evident in healthy adults is the coarse coding hypothesis (Beeman et al., 1994). According to this hypothesis, words in the RH are represented by means of wide semantic fields, while words in the LH are represented via a narrow range of features relevant to the immediate discourse context. Although coarse RH semantic activations would predictably activate irrelevant information they might be particularly important for the comprehension of figurative language such as that needed to comprehend jokes.

To test the relevance of findings in the DVF priming literature to the semantic component of joke comprehension, the present study evaluated the event-related brain response to laterally presented "punch words" to one-line jokes in comparison to equally unexpected nonjoke endings for the sentences. The N400 component of the ERPs was of particular interest, because the amplitude of this component can be used as an index of the difficulty of lexical integration. In previous studies of joke comprehension, joke endings have been known to elicit larger N400s than nonjoke controls (Coulson & Kutas, 2001). In the present study, jokes presented to the RVF/LH elicited larger amplitude N400 than the straight endings, suggesting that the joke endings were more difficult to integrate. However, when presented to the LVF/RH, the joke and straight endings elicited N400s of equal amplitude – as if the RH found joke endings no more difficult to integrate than straight endings. Assuming that integration difficulty results from initial differences in semantic activation, these findings are consistent with the suggestion that semantic activations in the two hemispheres differ from one another, and moreover that semantic activation in the RH facilitates joke comprehension.

4.1. Coarse coding hypothesis

If, as posited by the coarse coding hypothesis, the LH activates a narrower range of features than the RH in response to linguistic input, lexical integration of the "punch word" of a joke might be expected to be more difficult with presentation to the RVF/LH than the LVF/RH. The observed modulation of the N400 joke effect by visual field of presentation thus supports the coarse coding hypothesis.

Presumably these differences affect joke comprehension because getting a joke involves retrieving information from semantic memory in order to understand the connection between one's initial interpretation and the construal implied by the joke's punch-line. For example, in the joke "The replacement player hit a home run with my girl," the reader must reinterpret information about a baseball game by accessing information about romance. Understanding this joke involves apprehending the parallels between the literal home run in baseball and the metaphorical one in romance, as well as the parallelism with respect to the *replacement* player's role in the athletic endeavor and the romantic one.

Hemispheric differences in semantic activation might be related to greater connectivity in the RH. Beeman and Chiarello (1998), for example, point to hemispheric differences in the ratio of gray to white matter (Gur et al., 1980) and to the observation of more dendritic branching in the RH pyramidal cells (Scheibel et al., 1985). Work by Jacobs and colleagues (Jacobs et al., 1993a; Jacobs, Schall, & Scheibel, 1993b) indicates a greater extent of dendritic branching in language areas of the RH than the LH, and a higher density of interneurons (Hutsler, 1995). Hemispheric differences in semantic representation might also be related to differences in attentional bias, as studies of visuo-spatial processing suggest the RH is superior in tasks that require the direction of attention to global (whole object) aspects of stimuli, while the LH is better at attending to local (object features) aspects (Delis, Robertson, & Efron, 1986; Fink et al., 1996; Van Kleek, 1989; Yamaguchi, Yamagata, & Kobayashi, 2000). Such biases might affect the way that information is encoded into memory, which in turn might affect the way it is retrieved during inferential aspects of language comprehension.

4.2. Predictive/integrative model

Results of the present study are also consistent with the model of hemispheric differences in semantic activation posed by Federmeier and Kutas (1999). According to this model, the LH uses a *predictive* strategy, in which sentential context is used to pre-activate semantic features of likely upcoming words. The RH, in contrast, is hypothesized to use an *integrative* strategy, in which features of the currently processed word are compared with those active in the contextual representation. The LH is thus able to preactivate concepts predicted by the sentence context, while the RH, by contrast, is better suited for integrating currently activated concepts with overlapping features from previously activated ones. In this predictive/integrative view, both hemispheres are proposed to draw upon message level representations of the discourse in progress, but the RH is argued to exhibit less sensitivity to categorical relations between active semantic features.

The predictive and integrative strategies would be expected to work equally well for the contrast between expected and nonjoke endings, consistent with our observation of similar-sized N400 expectedness effects with LVF and RVF presentation. However, because joke endings are not consistent with the frame evoked by the sentence context, the integrative strategy might be expected to actually out-perform the predictive strategy on the jokes. Indeed, larger amplitude N400 for jokes than nonjokes with RVF presentation suggests that the left hemisphere found joke endings more difficult to integrate. Overall, results of the present study were parallel to those reported by Federmeier and Kutas (1999): similar-sized expectedness effects in both VFs, but more subtle discrimination between low-cloze endings with RVF presentation.

4.3. Hemispheric differences in time course of semantic activation

Besides proposals above about differences in the nature of semantic activation in the two hemispheres, DVF priming studies have also been argued to support hemispheric differences in processing speed (Burgess & Simpson, 1988). The processing hypothesis is supported by a hemi-field priming study of ambiguous words presented in isolation. By varying the stimulus onset asynchrony (SOA) between the prime and the target words, Burgess and Simpson (1988) were able to establish that while dominant meanings are processed similarly, the rise time for subordinate meanings is slower in the RH. Further, when the prime target SOA was 750 ms, the subordinate meaning had been inhibited in the LH, but was still active in the RH.

In fact, Burgess and Lund have argued that observed hemispheric asymmetries in priming can be explained by a slower rate of semantic activation in the RH (Burgess & Lund, 1998). Using a high-dimensional model of semantic memory based on word co-occurrence statistics in a corpus of 160 million English words, the researchers calculated semantic distances between ambiguous words and their dominant and subordinate targets. They then conducted computational simulations of lexical activation in both hemispheres, assigning lower values to the weights representing activation onset and decay rate for the RH. The results of the model replicated the human pattern of sustained priming for subordinate targets in the RH and not the LH at long SOAs. Their simulations show how modest differences in the activation onset and decay of the very same semantic representation could lead to differential priming effects across the two hemispheres (Burgess & Lund, 1998).

A continuous on-line measure of processing ERPs allow for fine-grained temporal distinctions (Van Petten, Coulson, Rubin, Plante, & Parks, 1999) that can test the suggestion that the time course of semantic activation differs across the hemispheres. Rather than relying on indirect measures of the time course of semantic activation, for example, by varying SOA in order to observe the effect of that manipulation on reaction time, ERP methodology allows the researcher to observe differences in the time course of processing directly, by comparing the onset and offset of ERP effects of interest. As can be seen in Fig. 2, the onset of N400 effects is virtually identical in both VFs – approximately 200 ms post-stimulus onset. Moreover, our measurements of onset and peak latency suggested that the timing of these effects was the same regardless of ending or VF of presentation. Our failure in the present study to find differences in the onset and peak latencies of N400 effects argues against the suggestion that the observed hemispheric asymmetry in joke processing results *purely* from hemispheric differences in the onset of semantic activation. However, caution is always warranted in the interpretation of a null effect.

4.4. Divided visual field presentation

One potential objection to these findings might be that the DVF paradigm employed in the present study does not effectively index the contribution of each of the cerebral hemispheres. Because participants were neurologically intact adults, one would expect that after initial processing in the contra-lateral hemisphere, the information would rapidly be distributed to both hemispheres. However, a number of factors suggest that the VF manipulation did serve to shift the balance of the two hemispheres in the processing of the stimuli. Among other things, these include effects of VF on the delayed naming task, on the amplitude of the visual N1 potentials, and on the scalp topography of ERPs in later intervals.

In the delayed naming task employed in the present study, a full 2.5 s intervened between the presentation of the stimulus and the participants' response – considerably longer than in previous studies, and, indeed, considerably longer than is required for inter-hemispheric transfer. Nonetheless, para-foveal presentation clearly produced differences in the processing of the stimulus. The observation here of an RVF advantage on the delayed naming task thus indicates that the DVF presentation worked as intended to increase participation of the contra-lateral hemisphere.

Indeed, one might note that the asymmetry in the naming performance in the present study is greater than is typically observed in DVF studies. This raises the possibility that observed results might not only reflect hemispheric differences in the perceptual demands of word recognition, but also memory demands engendered by the delayed naming task. However, even with a concurrent articulatory suppression (viz. rehearsal prevention) task, the average adult can recall three syllables for up to 9 s (Peterson & Peterson, 1959). Because the demands of remembering a single word for 2.5 s with no intervening verbal stimuli are minimal, we find this explanation unlikely.

Rather, the relatively large RVF advantage we observed may reflect the fact that target words used in the present study were slightly longer (averaging almost seven characters) and less frequent (approximately 46 per million words) than words in previous studies. Further, though neither the joke nor the nonjoke endings were predictable from the preceding sentence context, words in the expected condition were. The greater contextual support for words in the expected condition would be expected to decrease the demands of word recognition for these stimuli, thus explaining greater observed accuracy for expected words over joke and nonjoke endings, as well as the relatively small RVF advantage for words in the expected conditions. Words in the two experimental conditions were equally predictable from sentence context, and thus it is not surprising that the RVF advantage was essentially the same magnitude for the joke as for the nonjoke endings.

Moreover, a number of factors besides the observed RVF naming advantage indicate that lateralized presentation of the stimulus resulted in differential involvement of the contra-lateral hemisphere. First, the visual field manipulation affected the topography of the visual potentials in the ERP as the N1 component was largest over RH scalp sites with LVF presentation, and largest over LH scalp sites with RVF presentation. Second, the visual field manipulation affected the topography of ERPs elicited in the N400 time range, 300–500 ms after the onset of the stimulus, suggesting that non-overlapping neural generators were active with RVF and LVF presentation. Finally, the visual field manipulation affected the amplitude of the N400 joke effect, suggesting that one hemisphere (the left) was sensitive to lexical integration difficulties engendered by jokes while the other was not.

Another objection to these findings might be that the absence of an N400 joke effect with LVF/RH presentation could reflect general RH "incompetence" in language processing. However, the analysis included only trials for which participants were able to correctly name the laterally presented word. Further, while the N400 joke effect was observed only in LH-initiated responses, both hemispheres were equally sensitive to expectedness, as suggested by the fact that the size of the expectedness effect on the N400 did not differ as a function of visual field of presentation. Similarly, the N400 joke effect was followed by joke effects 500–900 ms post-onset that did not differ as a function of visual field. The equal sensitivity of the two hemispheres to the N400 expectedness effect and to the later joke effects makes it less likely that the absence of an N400 joke effect with LVF/RH presentation reflects a general insensitivity to linguistic manipulations.

4.5. Late joke effects

In fact, the contrast between the impact of visual field of presentation on the N400 and the late joke effects is perhaps the most interesting finding of the present study. As noted above, two different joke effects were evident in the interval 500–900 ms post-stimulus: a bilaterally symmetric positivity over anterior midline and dorsal sites, as well as a small sustained negativity over LH electrode site F7. While visual field *did* affect the size of the N400 joke effect, it did *not* affect the size of the subsequent joke effects (see Fig. 3),

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suggesting temporal variation in the degree of joke-related lateralization.

Alternatively, the absence of interactions between visual field and the ending-type manipulation in the interval 500–900 ms post-stimulus could be a signal that the VF manipulation has “worn off,” and thus the hemispheric contributions are no longer lateralized. However, mean amplitude measurements of ERPs elicited by joke and nonjoke endings 500–900 ms post-stimulus revealed a robust interaction between visual field and electrode site.[1] Analysis of data collected from dorsal sites indicated that stimuli presented to the LVF elicited more asymmetric ERPs, especially over the fronto-central sites where the positivity was largest.[2] These findings indicate the visual field manipulation affected the scalp topography of the brain response in this interval, consistent with the suggestion that RVF and LVF stimuli continue to be processed asymmetrically.

Assuming that the visual field manipulation did promote increased contra-lateral processing even between 500 and 900 ms, then the absence of a visual field effect on either the sustained anterior joke effect or the anterior joke positivity might reflect bi-hemispheric capacity for the on-going cognitive operations. Though its functional significance is unclear, the anterior negativity has been argued to index the manipulation of information in working memory that participants perform in order to get the jokes (Coulson & Lovett, 2004). In the present study, both the anterior negativity and the anterior positivity observed in the joke/nonjoke comparison are presumed to reflect the discourse integration and inference processes important for joke comprehension. Bi-hemispheric capacity for inferential aspects of language comprehension is consistent with recent work with patients that indicates deficits with these aspects of comprehension have been associated with damage to anterior left hemisphere regions (Ferstl, Guthke, & von Cramon, 2002; Pearce, McDonald, & Coltheart, 1998), as well as right hemisphere damage (Joanette et al., 1990; Martin & McDonald, 2003; Molloy, Brownell, & Gardner, 1990).

We tentatively suggest that the anterior positivity observed in the present study reflects memory retrieval processes in pre-frontal cortex. Neuroimaging studies in humans have shown that the activation of areas in prefrontal cortex is associated with retrieval tasks (Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1998). Moreover, electrophysiological work with monkeys has shown that prefrontal activity regulates the retrieval of information from inferior temporal regions (Hasegawa, Fukushima, Ihara, & Miyashita, 1998; Tomita, Ohbayashi, Nakahara, Hasegawa, & Miyashita, 1999). In the joke comprehension task employed in the present study, participants must retrieve information encountered earlier in the sentence (e.g. the REPLACEMENT player, HOME RUN), the new frame evoked by the “punch word” (e.g. “girl” evokes the romance frame), as well as the meanings the words assume in the new frame.

The sustained left anterior negativity observed in the present study resembles that reported in a similar study that compared ERPs to jokes and nonjoke control stimuli (Coulson & Kutas, 2001), although the effect in the present study was smaller. This effect was argued to index frame-shifting necessary to get a joke because it was evident in ERPs to both high and low constraint stimuli and was absent from ERPs recorded from poor joke comprehenders, i.e. people who had difficulty getting the jokes used in the study. The sustained left anterior negativity was also observed in a recent study that compared ERP joke effects in groups that differ with respect to the cerebral organization of language: left- and right- handed men and women (Coulson & Lovett, 2004). The sustained negativity was readily apparent in ERPs collected from right-handers, all of who scored very well on the comprehension questions. But while left-handers also scored extremely well on the comprehension questions, the sustained anterior negativity was either much reduced or entirely absent from their ERPs.

In fact, in the latter study, reduced joke effects at left anterior sites were accompanied by enhanced positivities in the same time window and frequency range at frontal, central and parietal electrode sites (Coulson & Lovett, 2004), suggesting a trade-off between the frame-shifting and memory retrieval operations subserved by the generators of the left anterior effect and the late positivity. Moreover, the morphology and the bilateral distribution of the anterior positivity elicited by jokes in the present sample of right-handed individuals resembled that of an ERP joke effect Coulson and Lovett (2004) observed in the left-handed women in their sample, the group most likely to exhibit bilateral language representation.

Findings of the present study (bilateral sensitivity to jokes in the late ERP effects) are consistent with the suggestion by Molloy and colleagues that different meanings available in the left and right hemispheres are ultimately coordinated by structures in pre-frontal cortex (Molloy et al., 1990). Interhemispheric connections in prefrontal cortex, along with its connections with higher order sensory cortex, would presumably support the interhemispheric communication and inhibition needed for this aspect of discourse comprehension (Molloy et al., 1990). Indeed, studies of split-brain humans (Sidtis, Volpe, Holtzman, Wilson, & Gazzaniga, 1981) and monkeys (Hasegawa et al., 1998) suggest that the anterior part of the corpus callosum has the capacity to transmit higher order semantic information associated with stimuli presented to a single hemisphere.

4.6. Summary

Jokes presented to the RVF/LH elicited larger amplitude N400 than the nonjoke endings to the same sentences. But when presented to the LVF/RH, the joke and nonjoke controls elicited equal amplitude N400. Different N400 effects

[1] VF × Electrode $F(28, 420) = 7.92$, $P < 0.0001$, $e = 0.16$.

[2] VF × Hemisphere $F(1, 15) = 32.19$, $P < 0.0001$; VF × Hemisphere × Anteriority $F(5, 75) = 10.48$, $P < 0.001$, $e = 0.34$.

as a function of VF suggest that the right hemisphere has less difficulty integrating the joke endings (which require frame-shifting), a finding consistent with hypothesized differences in meaning activations in the two hemispheres. On this view, broad semantic activation in the right hemisphere facilitates the lexical integration of joke endings.

Relative to nonjoke endings, jokes also elicited two ERP effects following the N400: a left frontal negativity and a frontal positivity, both between 500 and 900 ms. It was suggested that these effects index working memory and retrieval operations important for inferential aspects of joke comprehension. Neither of these late effects differed as a function of VF, perhaps reflecting a high degree of bilateral processing that serves to integrate information from each hemisphere in the message- or discourse-level representation. Joke comprehension deficits in RHD patients might result either from the failure to activate joke-relevant information in the RH during the initial stages of processing, or from the detrimental effect of unilateral damage on subsequent, normally bilateral, inferential processing, or both.

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