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Right Hemisphere Activation of Joke-Related Information:
An Event-Related Brain Potential Study

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ABSTRACT

Two studies tested the hypothesis that the right hemisphere engages in relatively coarse semantic coding that aids high-level language tasks such as joke comprehension. Scalp-recorded event-related brain potentials (ERPs) were collected as healthy adults read probe words (CRAZY) preceded either by jokes or non-funny controls (Everyone had so much fun jumping into the swimming pool, we decided to put in a little water/platform.) Probes were related to the meaning of the jokes, but not the controls. In experiment 1a, with central presentation, probes following jokes (related) elicited less negative ERPs 300-700 ms post-onset (N400) than did probes following non-funny controls (unrelated). This finding suggests related probes were primed by the jokes. In addition, unrelated probes elicited a larger anterior positivity 700-900 ms than did related, as irrelevant stimuli impacted control processes invoked by task demands. In experiment 1b, probes (CRAZY) were preceded only by sentence-final words from jokes (water) or controls (platform). No ERP effects were observed in experiment 1b, suggesting the N400 priming effect and the anterior positivity observed in experiment 1a reflect semantic activations at the discourse level. To assess hemispheric differences in semantic activations, in experiment 2, ERPs were recorded as participants read probe words presented in their left and right visual fields (LVF/RVF). Probes elicited a smaller N400 component when preceded by jokes than controls. This N400 priming effect was larger with presentation to the LVF, suggesting joke-relevant information was more active in the right hemisphere. The anterior positivity was observed with RVF but not LVF presentation, suggesting an important role for the LH in controlled retrieval in language comprehension.

Keywords: jokes, N400, hemispheric asymmetry, right hemisphere, language, divided visual field

Over the past two decades, increased interest in language-related hemispheric asymmetries has given rise to the view that the two halves of the brain process semantic information in different, perhaps complementary ways (Beeman & Chiarello, 1998). Research with callosotomy patients indicates that in spite of its impoverished speech output, the isolated right hemisphere (RH) has the ability to recognize words (Baynes & Eliassen, 1998; Baynes, Tramo, & Gazzaniga, 1992; Gazzaniga & Sperry, 1967; Zaidel, 1990). Moreover, when left hemisphere (LH) damage causes linguistic deficits, homologous RH areas can sometimes be recruited to assume the compromised functions (Blasi et al., 2002; Buckner, Corbetta, Schatz, Raichle, & Petersen, 1996; Calvert et al., 2000; Staudt et al., 2002).

Though RH lesions rarely result in severe linguistic impairment, injury to the RH has been linked to subtle semantic and pragmatic processing deficits, including difficulty understanding the meaning of idioms (Van Lancker & Kempler, 1987), indirect requests (Stemmer, 1994; Stemmer, Giroux, & Joanne, 1994), and jokes (Brownell, Michel, Powelson, & Gardner, 1983). Similarly, neuroimaging studies of healthy adults indicate that the RH is particularly important for high-level language comprehension (Bookheimer, 2002). For example, an event-related functional magnetic resonance imaging study that compared the comprehension of semantic jokes to a non-joke baseline revealed increased activation in RH Brodmann's area 21, as well as areas 21 and 37 in the LH (Goel & Dolan, 2001).

Other research with neurologically intact participants using the divided visual field (DVF) paradigm has revealed different patterns of priming effects with presentation to the right visual field (left hemisphere) and the left visual field (right hemisphere). Several studies have found, for example, that the RH shows facilitation to distantly related meanings, while the LH exhibits priming effects exclusively by close associates (Beeman et al., 1994; Burgess & Simpson, 1988; Chiarello, Burgess, Richards, & Pollock, 1990). The present studies addressed whether putative hemispheric differences in semantic activation might be relevant to joke comprehension.

Joke Comprehension

Perhaps because verbal joking is a fairly common event, we often underestimate its complexity. Joke comprehension is a high-level language task that depends on our ability to flexibly apply background knowledge in order to make inferences both about what has been said and what is coming next (Coulson, 2000). For example, given “A thoughtful wife has pork chops ready when her husband comes home from—” most people would expect “work” to follow (Coulson & Kutas, 2001). However, if a friend were telling you a joke and actually ended the sentence with “fishing,” you would likely have no trouble understanding and chuckle politely. The word “fishing” here cues the listener (or reader) to make dramatic changes in her representation of the scenario. Rather than a stereotypical wife tending to the needs of her husband, we have a mischievous wife who anticipates her husband will come home empty-handed. Known as frame-shifting, this semantic reanalysis process reorganizes existing information into a new frame or schema retrieved from long-term memory (Coulson, 2000; Coulson & Kutas, 2001).

As noted above, joke comprehension deficits have been observed in patients with RH lesions, especially when there is damage to the anterior portion of the frontal lobe (Brownell et al., 1983; Shammi & Stuss, 1999). One attempt to link the deficits observed in RHD patients to hemispheric asymmetries evident in healthy adults is Beeman’s coarse coding hypothesis (Beeman et al., 1994; Beeman & Chiarello, 1998). 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 include contextually irrelevant information, they might nonetheless be important for the comprehension of figurative language such as that needed to understand jokes. Because jokes frequently require the integration of novel information, the reinterpretation of a word or phrase, and the reinterpretation of the scenario depicted by the

preceding context, diffuse RH activation might provide additional information that makes joke processing easier. Similarly, reduced access to these diffuse semantic activations in RH damaged patients could result in joke comprehension deficits.

The Present Study

To test whether RH involvement in joke processing involves the activation of information crucial for understanding jokes, we measured event-related brain potentials (ERPs) elicited by laterally presented probe words that were preceded either by a joke, or by a non-funny control. Since all jokes turned on the last word of the sentence, control sentences were formed by replacing the sentence final word with a “straight” ending. For example, the straight ending for the joke “Everyone had so much fun diving from the tree into the swimming pool, we decided to put in a little water,” was “platform.” Probes (such as CRAZY) were designed to be related to the meaning of the joke, but unrelated to the meaning of the straight control.

Note that this paradigm differs somewhat from our previous research on joke comprehension which compared ERPs elicited by the critical words in jokes and non-funny controls (Coulson & Kutas, 2001; Coulson & Lovett, 2004). Rather than measuring on-line processing of the jokes themselves, ERPs to probes index the extent to which joke-relevant information is active in the brain. In this paradigm, the jokes and the control sentences serve as “primes” that facilitate the processing of contextually relevant probes. For this reason, the amplitude of the N400 component of the ERPs was the dependent variable of interest.

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; Osterhout & Holcomb, 1995). Because probes were related to the meaning of the jokes, but unrelated to the meaning of the control sentences, probes would be expected to elicit larger amplitude N400 when they followed control sentences than when they followed jokes. This hypothesis was tested in experiment 1a, where participants read

centrally presented probes preceded either by jokes or by straight controls. Our goal was to establish priming specifically for probes related to the discourse-level reanalysis, or frame-shifting, triggered by joke-final words. In order to rule out N400 priming effects due to relationships between probes and the last word of each type of sentence, experiment 1b compared ERPs elicited by centrally presented probes preceded either by the last word of the jokes or the straight controls.

[INSERT FIGURE 1]

Experiment 2 assessed hemispheric differences in the activation of joke-related information by recording ERPs as participants read lateralized probe words primed either by the jokes or non-funny controls (see figure 1). Parafoveal presentation of probe words was intended to affect which hemisphere received the initial information from the stimulus, and to increase that hemisphere's participation in stimulus processing. If hemispheric differences in semantic activation are relevant for joke comprehension, visual field (VF) of presentation might be expected to modulate ERP effects observed in experiment 1a.

The coarse coding hypothesis, for example, suggests that the wide semantic fields in the RH provide information important for understanding jokes. If this is the case, probe words related to jokes should be easier to process with left visual field (LVF) than right visual field (RVF) presentation. In the present study, greater RH activation of joke-relevant information would be indexed by larger N400 relatedness effects with presentation to the LVF than the RVF. Alternatively, similar-sized N400 relatedness effects in the two VFs would suggest either that hypothesized differences in semantic activation do not exist, or that they are not relevant to joke comprehension.

EXPERIMENT 1

RESULTS

Participants in experiment 1 performed almost perfectly on the delayed naming task, presumably because the probe words were presented in the center of the screen. As a result, accuracy rates on the delayed naming task were not analyzed. In contrast, accuracy rates on the comprehension questions that followed the sentential stimuli in experiment 1a were less than perfect, although participants answered most of the questions correctly (77%, s.d.=5%). Performance on comprehension questions was the same for sentences that ended as jokes and sentences that had straight endings ($F < 1$).

ERPs to centrally presented probes following sentence and word primes, respectively, can be seen in figure 2. N400 amplitude was assessed by measuring the mean amplitude of ERPs 300-700 ms after the onset of the probe words (Van Petten, 1995). Repeated measures analysis of variance (ANOVA) with factors context (sentence/word), relatedness (related/unrelated) and electrode (28 levels) indicated a marginally significant interaction between context, relatedness, and electrode ($F(27,405)=2.19$, $p=0.067$), suggesting that the size and scalp distribution of the N400 effect was not identical across conditions. Further analyses of data restricted to medial electrode sites revealed a significant interaction between context, relatedness, and hemisphere ($F(1,15)=6.26$, $p<0.05$), reflecting a right-lateralized relatedness effect for probes preceded by sentence- but not by word- primes. A similar interaction between context, relatedness, and hemisphere was observed in the analysis of data collected from lateral electrode sites ($F(1,15)=7.06$, $p<0.05$). Significant interactions between context, relatedness, and electrode site were also observed between 700-900 ms post-probe onset ($F(27,405)=6.8$, $p<0.001$). ERPs elicited by probes preceded by sentence-primes are analyzed below under the heading experiment 1a, and probes preceded by word-primes are analyzed under the heading experiment 1b.

[INSERT FIGURE 2]

Experiment 1a: Sentence Primes

In the sentence condition, probes following jokes (related) elicited less negative ERPs 300-700 ms post-onset than did probes following non-funny controls (unrelated), as suggested by a reliable interaction between relatedness and electrode site ($F(27,405) = 5.75, p < .05$). In keeping with the typical distribution of the N400 component (Kutas, Van Petten, & Besson, 1988), the relatedness effect was largest over posterior sites (Midline: Relatedness x Posteriority $F(5,75)=5.75, p<0.01$; Medial: Relatedness x Posteriority $F(6,90)=5.36, p<0.05$), and slightly larger over the RH (Medial: Relatedness x Hemisphere $F(1,15)=7.09, p<0.05$; Lateral: Relatedness x Hemisphere $F(1,15)=6.25, p<0.05$).

In the latter part of the epoch, relatedness effects differed over anterior and posterior scalp regions in polarity. Over posterior sites, unrelated probes continued to elicit more negative ERPs than did the related probes. Over pre-frontal and frontal sites, unrelated probes elicit greater positivity beginning approximately 600 ms post-onset, and continuing until the end of the epoch. Analysis of data measured 700-900 ms post-probe onset thus revealed a reliable interaction between relatedness and electrode site ($F(27, 405)=10.68, p<0.0001$). Follow-up analyses at midline ($F(5,75)=11.64, p<0.0001$) and medial ($F(6, 90)=14.63, p<0.0001$) electrode sites revealed interactions between relatedness and posteriority, reflecting the frontal distribution of the positivity to unrelated stimuli, and the posterior distribution of the negativity. Analysis also suggested an interaction between relatedness and hemisphere due to the larger negative-going effect over RH sites (Medial: $F(1,15)=9.34, p<0.01$; Lateral: $F(1,15)=9.27, p<0.01$).

Experiment 1b: Word Primes

Probes that followed single word primes elicited ERPs typical of visually presented language stimuli – namely, N1 and P2 visual potentials followed by the N400. A late positive-going response was also observed beginning approximately 600 ms post-onset over frontal and pre-frontal sites. However, the relatedness factor did not affect the amplitude of the ERPs measured 300-700 ms (Relatedness $F(1,15)=2.36, n.s.$; Relatedness x Electrode $F(27,405)<1$) or 700-900

ms (Relatedness $F(1,15)<1$; Relatedness x Electrode $F(27,405)<1$) post-onset. This null result is not surprising, given that relatedness judgments depend upon the relationship between probe words and the meaning of the sentences (though caution is always warranted in the interpretation of a null result).

DISCUSSION

The goal of experiment 1 was to show that our joke-related probes were primed more by the jokes than by the non-funny controls, and further that this priming was due to sentence- or discourse-level information rather than lexical relationships between the probes and sentence-final words. Non-funny controls were designed to prompt essentially the same discourse-level representation as jokes with the exception of information activated by the reanalysis needed to get the joke. Consequently, the same probe words could be considered related to jokes, but unrelated to controls. N400 relatedness effects can thus be seen as indicating that jokes activated information important for comprehending the humor.

As predicted, unrelated probes elicited larger amplitude N400 components than did related probes in experiment 1a (sentence primes), but not in experiment 1b (word primes). Similarly, unrelated probe words elicited a larger positivity 700-900 ms over anterior scalp sites in experiment 1a, but not in experiment 1b. Because the joke and the control sentences in experiment 1a were identical until the final word, and those words were used as the primes in experiment 1b, ERP effects observed in 1a but not in 1b reflect sensitivity to sentence- and/or discourse-level processing, rather than to lexical associations. Related probes elicited lower amplitude N400 because they were primed by the meaning of the jokes, but not by the non-funny control stimuli. Further, we speculate that the unrelated probes elicited a larger frontal positivity because they were not relevant to the meaning of preceding sentence primes.

Experiment 2 tested whether relatedness effects were modulated by VF of presentation. As in experiment 1, ERPs were recorded as healthy adults read sentence primes, presented one word at

a time in the center of a computer monitor. Shortly after the offset of the sentence final word, a probe was briefly flashed in either the LVF or the RVF. Participants named the probe when cued by a prompt that appeared 2 seconds after its onset, and answered true/false comprehension questions about the sentence primes (see figure 1). If hemispheric differences in semantic activation affect joke comprehension, the VF manipulation would be expected to modulate the size of the N400 relatedness effect.

EXPERIMENT 2

RESULTS

Volunteers correctly named an average of 71% (s.d.=2%) of the probe words. Probes presented to the RVF (80%, s.d.=1%) were named more accurately than those presented to the LVF (62%, s.d.=1%), as suggested by a VF effect in the analysis ($F(1,15)=114$, $p<0.0001$). This outcome may be attributed to superior reading abilities in the LH, and suggests the lateralized presentation of the stimuli resulted in the increased participation of the hemisphere opposite the VF of presentation. There was no main effect of relatedness on accuracy, nor was there a reliable interaction between VF and relatedness ($F's<1$).

Accuracy scores on the comprehension questions that followed the probes suggested participants understood most of the sentences. VF of probe presentation did not affect accuracy scores ($F<1$), but analysis suggested a non-significant trend towards better comprehension of sentences with joke (84%, s.d.=2%) than straight (79%, s.d.=2%) endings ($F(1,15)=3.7$, $p=0.08$).

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, 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 75-175 ms after the onset of lateralized stimuli at 4 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 presentation, and larger over LH electrode sites with RVF presentation (VF x Hemisphere $F(1,15) = 12.85$, $p < .05$). As evident in figure 3, this N1 reversal was more pronounced at temporal than occipital electrode sites (VF x Hemisphere x Posteriority $F(1, 15) = 8.21$, $p < .05$). The larger amplitude of the N1 over the hemisphere contra-lateral to the VF of presentation suggests that DVF presentation led to the increased participation of the opposite hemisphere.

[INSERT FIGURE 3]

N400: The N400 component was assessed by measuring the mean amplitude of ERPs elicited between 300 and 700 ms post-stimulus. Repeated measures ANOVA revealed a main effect of Relatedness ($F(1, 15) = 6.64$, $p < .05$) qualified by an interaction between Relatedness, VF, and Electrode Site ($F(28, 420) = 2.17$, $p < .05$). Unrelated probes elicited more negative ERPs than did related probes, especially over posterior electrode sites where N400 tends to be largest. The three-way interaction results because this relatedness effect was larger and more broadly distributed with presentation to the LVF than the RVF (see figures 4 and 5). This interaction motivated separate analyses of data associated with presentation to each VF.

[INSERT FIGURE 4]

[INSERT FIGURE 5]

Presentation to the LVF resulted in more negative ERPs to unrelated than related probes from 300-700 ms post-onset, as indicated by main effects of relatedness at the midline ($F(1, 15) = 11.88$, $p < .01$), medial ($F(1,15) = 11.17$, $p < .01$), and lateral ($F(1,15) = 5.03$, $p < .05$) electrode sites. Consistent with the distribution of the N400 component (Kutas et al., 2000), the negativity was largest over central and parietal electrode sites (Midline: Relatedness x Posteriority $F(6, 90)$, $p < .01$; Medial: Relatedness x Posteriority $F(6,90) = 15.5$, $p < .01$), and was slightly larger over RH electrode sites (Medial: Relatedness x Hemisphere $F(1,15) = 3.38$, $p = .08$; Lateral $F(1, 15) = 5.34$, $p < .05$).

With RVF presentation, unrelated stimuli elicited more negative ERPs 300-700 ms than related stimuli over posterior electrode sites, and less negative ERPs than related stimuli over frontal sites. The analyses revealed no main effect of relatedness, but rather reliable interactions between relatedness and the factor indexing the location of electrode sites along the anterior-posterior axis (Midline: $F(6,90) = 18.23, p < .0001$; Medial $F(6,90) = 11.33, p < .001$; Lateral $F(3, 45) = 11.81, p < .01$). Consistent with the scalp distribution of the N400, the negative-going relatedness effect was largest over posterior RH electrode sites (Medial: Relatedness x Hemisphere $F(1, 15) = 8.03, p < .05$; Lateral: Relatedness x Hemisphere $F(1,15) = 5.74, p < .05$; Lateral: Relatedness x Hemisphere x Posteriority $F(3, 45) = 5.88, p < .01$). However, the presence of less positive ERPs to unrelated than related probes over frontal electrode sites differs from the typical N400 effect.

Analysis from 700-900 ms: An omnibus ANOVA of mean amplitude of ERPs measured 700-900 ms post-stimulus onset revealed an interaction between Relatedness and Electrode Site ($F(28, 420) = 9.37, p < .0001$), as well as a trend toward an interaction between Relatedness and VF ($F(1, 15) = 3.76, p = .07$). As can be seen in figure 4, LVF presentation resulted in a continuation of the N400 relatedness effect, as ERPs to unrelated probes were more negative than were ERPs to related ones (Midline: $F(1, 15) = 4.82, p < .05$; Medial: $F(1, 15) = 4.9, p < .05$). As in the previous time window, the negativity was largest over posterior scalp regions (Midline: Relatedness x Posteriority $F(6, 90) = 5.6, p < .01$; Medial: Relatedness x Posteriority $F(6, 90) = 2.85, p = .07$). In contrast, RVF presentation resulted in a positive-going response to unrelated probes over pre-frontal and frontal electrode sites, and a small negative-going response over more posterior sites (Midline: Relatedness x Posteriority $F(6, 90) = 18.54, p < .001$; Medial: Relatedness x Posteriority $F(6, 90) = 12.47, p < .001$; Lateral: Relatedness x Posteriority $F(3, 45) = 10.78, p < .01$).

DISCUSSION

As in experiment 1, related probes in both VFs elicited less negative ERPs than unrelated 300-700 ms post-onset. This finding suggests semantic activations in both hemispheres supported the priming of joke-related information. Moreover, this N400 priming effect was larger with presentation to the LVF than the RVF, suggesting joke-relevant information was more active in the RH. Larger LVF effects result both from relatively more positive ERPs to related probes, and more negative ERPs to unrelated probes.

With RVF presentation, unrelated probes also elicited more positive ERPs over frontal electrode sites in the latter part of the epoch. This effect was largely absent with LVF presentation. Although a hint of a positive-going response is evident in the waveforms collected from pre-frontal sites (see figure 4), the LVF positivity is much smaller and less broadly distributed than observed with RVF presentation; it appears to begin later and end earlier than with RVF presentation, and was not statistically significant. The functional significance of the anterior positivity is discussed more extensively below.

GENERAL DISCUSSION

The present study was aimed at evaluating whether hemispheric differences in semantic activation affect joke comprehension. In experiment 1a, ERPs were recorded as healthy adults read centrally presented probe words (e.g. CRAZY) preceded either by a joke (e.g. “Everyone had so much fun diving from the tree into the swimming pool, we decided to put in a little water,”) or by a control sentence with a straight ending (e.g. “Everyone...a little platform.”). Probes were related to the meaning of the jokes but unrelated to the meaning of the control sentences.

Relative to the unrelated probes, related probes elicited a smaller N400, suggesting semantic integration of joke-relevant information was easier after the jokes. Further, relative to related probes, unrelated probes elicited a more positive-going ERP response over frontal electrode sites, the anterior positivity. As discussed below, we suggest that the anterior positivity indexes the

brain's recognition (either implicit or explicit) of the contextual irrelevance of the unrelated probes.

In experiment 1b, ERPs were recorded as participants read centrally presented probe words from experiment 1a. The primes, however, were single words – sentence-final words from the joke stimuli and their controls from experiment 1a (e.g. water-CRAZY, platform-CRAZY), as these were the single word in the sentence contrasts that differed. In this experiment, “unrelated” probes (primed by the last word of the control sentences) elicited similar amplitude N400 as the “related” probes (primed by the last word of the jokes). The anterior positivity was also unaffected by “relatedness” (prime type) in this experiment. Thus priming of joke-relevant information observed in experiment 1a depends on a message-level interpretation of the sentential primes rather than lexical priming between sentence-final words in the joke and the joke-related probes.

In experiment 2, probe words primed either by jokes (related) or controls (unrelated) were presented in participants' left and right VFs. Consistent with predictions of the coarse coding hypothesis, LVF presentation did indeed result in larger N400 relatedness effects in experiment 2 (see figure 5). Over posterior sites, ERPs to related probes were more positive with LVF than RVF presentation, and ERPs to unrelated probes were more negative, suggesting joke-related information was more active in the RH than the LH in this time window.

Unfortunately, this interpretation is clouded by the presence of a partially overlapping anterior positivity that occurred with presentation to the RVF but not the LVF. Summation of a positive- and a negative- going response could easily result in the apparent attenuation of the RVF N400 effect. However, the presence of an overlapping anterior positivity in the RVF condition cannot explain our finding that ERPs to related probes measured 300-700 ms post-onset over posterior midline electrodes were more positive with presentation to the LVF than RVF. This latter result can be interpreted as indicating the RH found the related probes to be less

surprising than did the LH, assuming more positive ERPs in the N400 latency window index ease of lexical integration. Of course, inferences from an amplitude comparison between VFs (even in the within-subjects design employed here) are open to question.

Taken at face value, however, the larger N400 relatedness effect with LVF presentation suggests that joke-relevant information was more active in the RH. This result is consistent with other research in the DVF priming paradigm that indicates semantic activations in the RH are important for high-level language comprehension tasks. For example, solution-relevant information for linguistic insight problems is more active in the RH than the LH (Beeman & Bowden, 2000). Like jokes, insight problems involve the reinterpretation of deliberately ambiguous information and are accompanied by a sudden feeling of “getting it.” Further, in a study of inferences drawn during story comprehension, probe words related to predictive inferences (e.g. LAUNCH after “The shuttle sat on the ground in the distance,”) showed priming only with presentation to the LVF, suggesting RH semantic activation supports predictive inferencing in story comprehension (Beeman, Bowden, & Gernsbacher, 2000).

RH Semantic Activations

Our finding that joke-related probe words elicited different ERP effects with presentation to the left and right VFs suggests hemispheric differences in semantic activation are indeed relevant to joke comprehension. Further, the larger N400 priming effect with LVF presentation is consistent with the coarse coding hypothesis that RH semantic activation is less specific than that in the LH. However, this leaves open the precise nature of the differences between semantic activation in the two hemispheres.

The most straightforward interpretation of the coarse coding hypothesis – sensitivity to associative relationships – appears not to be supported by existing data. If the RH activates a wider array of information, somewhat irrespective of its contextual relevance, one would expect it to be less affected than the LH by differences in associative strength between words. However,

in a DVF priming study that compared how associative strength affected the size of priming effects, Coney found a similar function with both LVF and RVF presentation (Coney, 2002).

Rather than semantic distance, *per se*, we suggest that such hemispheric differences reflect RH coding of thematic and relational information. RH damaged patients have greater difficulty than those with LH damage at recalling the theme of stories they have read (Hough, 1990). Further, neuroimaging research with healthy adults also suggests the importance of RH temporal lobe activity in processing thematic information. In a story comprehension task using materials modeled after the classic Bransford & Johnson study, St. George and colleagues report greater RH temporal lobe activation when thematic information was *not* provided for ambiguous paragraphs than when thematic information was provided by the inclusion of titles for the paragraphs (St. George, Kutas, Martinez, & Sereno, 1999).

One chief source of evidence for the coarse coding hypothesis comes from an experiment in which centrally presented trios of words served as “summation primes” for a weakly related lateralized target (Beeman et al., 1994). For example, “cry, foot, glass” served as summation primes for the target “CUT”, and as direct primes for the target “LAUGH” which was semantically related to one of the prime words. Accuracies on a naming task indicated that, relative to unrelated items, both hemispheres benefited from both sorts of primes. However, there was a RVF advantage for the direct primes, and an LVF advantage for summation primes. Beeman and colleagues argue that these findings suggest the RH benefits from the summed activation of shared features within a set of semantic fields. Note, however, that the features of “foot” and “glass” do not intersect. Rather, glass can be construed as an instrument that induces a change of state in a patient, such as a foot. These considerations point to the possibility that the RH “appreciates” the relational structure that links summation primes.

Summation priming may result because the RH preferentially activates stored knowledge about typical situations when glass, feet, and crying might co-occur, while the LH is more

sensitive to syntactic cues that overtly specify the same types of complex relations. Like Beeman's summation triads, jokes require the listener to access non-overtly encoded information 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. Thus, hemispheric differences in semantic activation might explain hemispheric differences in joke comprehension.

Neural Basis of Semantic Activation Differences

These findings raise the issue of the anatomical and physiological causes of observed hemispheric differences. Previously, hemispheric differences in semantic activation have been linked to greater connectivity in the RH (Beeman & Chiarello, 1998). Research indicates a greater extent of dendritic branching in language areas of the RH and LH (Jacobs, Batal, Lynch, Ojemann, G., Ojemann, L.M., & Scheibel, 1993; Jacobs, Schall, Scheibel, 1993), and a higher density of interneurons (Hutsler & Gazzaniga, 1995). Similarly, there is more interconnectivity in the RH, both at the level of individual neurons, and at the level of cortical columns (Hutsler & Galuske, 2003). The wider spacing of cortical columns in posterior language regions in the LH could be conducive to coding for more distinct features, while RH cortical columns are less functionally differentiated (Galuske, Schlote, Bratzke, & Singer, 2000; Hutsler & Galuske, 2003).

Asymmetries in cortical microcircuitry could thus give rise to less distinctive coding in RH posterior language regions, and might make them more suited for coding abstract, relational features. Indeed, the very definition of an abstract feature is a property shared by superficially different exemplars. The concept *fruit*, for example, is more abstract than *apple*, and different exemplars of apples share more perceptual features than do different exemplars of fruits. Similarly, understanding the relational concept *taller* involves abstracting over multiple comparisons of people, buildings, and other objects of varying sizes and shapes.

Alternatively, differences in semantic activation might be related to hemispheric 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, 1986; Fink, 1996; Van Kleeck, 1989; Yamaguchi, 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.

Anterior Positivity

Perhaps the most striking VF effect in the present study was not the N400 priming effect, but the anterior positivity. Compared to related probes, unrelated probes elicited more positive ERPs over frontal recording sites. One possible interpretation of this effect is that it stems from the demands of the delayed naming task. Note however, that the absence of relatedness effects in experiment 1b suggests the anterior positivity reflects sensitivity to context rather than the naming task per se. Participants named the same words in 1a and 1b (and in related and unrelated conditions), but the unrelated probes were only viewed as unrelated when they followed the sentences in 1a.

With central presentation, the anterior positivity was larger over LH electrode sites, consistent with a generator in LH prefrontal cortex. A LH generator is also supported by the fact that the positive-going relatedness effect begins earlier with RVF than central presentation (400 vs. 600 ms post-onset), and is absent with LVF presentation. A LH generator for this effect is consistent with neuroimaging research that reveals left inferior frontal activation in tasks targeting long-term memory encoding and retrieval, working memory, and speech generation (Buckner, 2003; Duncan & Owen, 2000). More relevantly, areas in the anterior portion of the left inferior pre-frontal cortex have been shown to increase in activation as a function of semantic distance between words (Roskies, Fiez, Balota, Raichle, & Petersen, 2001; Wagner, Pare-

Blagoev, Clark, & Poldrack, 2001). Relatedness effects on the anterior positivity may thus reflect activity in brain regions associated with selective retrieval of information from semantic memory.

On this account, contextually unrelated probes place more demands on control processes that gate the retrieval of relevant information in language comprehension. Consistent with this interpretation, DVF priming studies indicate the RH is less effective than the LH at suppressing contextually irrelevant information (Burgess & Simpson, 1988; Faust & Gernsbacher, 1996). Given the role of the left inferior pre-frontal cortex in controlled retrieval processes (Buckner, 2003; Wagner et al., 2001), the exclusively RVF elicitation of the anterior positivity may reflect an important role for the LH in the selection of relevant and the suppression of irrelevant information (Beeman et al., 2000). Consequently, while joke-relevant information might be more active in the RH, LH selection processes may be required for the full appreciation of a joke.

METHODS

Experiment 1

Participants. 16 adults from the UCSD community (8 men) aged 18-36 were either paid \$24 or awarded credit for cognitive science or psychology course requirements in exchange for their participation. All were healthy, right-handed, monolingual English speakers. Handedness was assessed via the Edinburgh inventory (Oldfield, 1971). Average laterality quotient was +71.

Materials. Experimental stimuli were constructed from jokes found in published anthologies and deemed by the experimenters to require frame-shifting for their comprehension. In all jokes, the “punch-word” was the last word of the sentence. Jokes that fit these criteria were normed in an off-line cloze (sentence completion) task administered to a minimum of 45 people. Results of the

cloze task enabled us to choose non-funny “straight” endings for the sentences that matched joke endings for length (6.8 characters), frequency (46.8 per million), and cloze probability (2.5%). Straight endings were chosen so as to be consistent with the frame or schema evoked by the first part of the sentence, in contrast to joke endings which prompted frame-shifting. The sentence constraint of experimental stimuli – operationalized as the cloze probability of the most common response for each item on our cloze task – varied from 7% to 96%, and averaged 35%.

Probe words were selected so as to be related to the humorous inferences prompted by the jokes, and unrelated to the thematic content of the straight controls. Relatedness between probe words and the two types of sentence primes was assessed in a norming study in which 66 UCSD students (34 volunteers for list 1 and 32 for list2) rated the degree of relatedness between each probe word and one of its sentence primes. On a scale from 1-7, where 1 was unrelated and 7 was highly related, probes following jokes were rated 5.4 (s.e.=.36), while probes following straights were rated 2.9 (s.e.=.63). Although sentences with joke and straight endings differed by only one word, probes were judged to be related to the meaning of the jokes, and unrelated to the straight sentences.

Experimental stimuli consisted of 140 probes, 140 jokes, and 140 straight control sentences. Because probes were always related to jokes, and unrelated to straights, materials also included a total of 240 filler probes, primed by either 120 jokes or 120 straight controls. Filler probes matched experimental probes in word length and word frequency. Filler probes following jokes were judged as being unrelated in the norming study described above (rated 2 on our 7-point scale), while fillers following straights were judged as related (rated 5.7 on the same scale).

In experiment 1a (sentences), each participant read 70 experimental probes, half of which were preceded by jokes, half of which were preceded by straights, as well as 60 filler probes, half preceded by jokes and half by straights. The same people participated in experiment 1b (words), in which each participant read 70 experimental probes, half preceded by a sentence-final word

taken from a joke, and half by a sentence-final word taken from a straight control sentence. 60 filler probes were also included, half preceded by a sentence-final word taken from a filler joke, and half by a sentence-final word taken from a filler straight. Four lists were constructed so that no individual participant saw more than one version of any prime, but manipulations were perfectly counterbalanced across participants. Trials with sentence primes (experiment 1a) were blocked, as were trials with single word primes (experiment 1b). Sentence blocks and word blocks were interleaved.

Stimulus Presentation. All trials in experiment 1a began with a warning cross presented for 1000 ms. Sentence primes were shown one word at a time (200 ms duration and 300 ms ISI) in the center of a 19" color monitor. Probes appeared 800 ms after the offset of the sentence final word, and were shown for 200 ms. 2800 ms after the presentation of the probe word, a blue question mark appeared in the center of the screen for 3 seconds, and served as the naming prompt. Immediately following the offset of the naming prompt, a comprehension question appeared on the screen (in full) for a total of 4 seconds. Comprehension questions were either true or false statements about preceding sentence primes.

Trials in experiment 1b also began with a warning cross presented for 1000 ms. Prime words were presented for 200 ms. Probes appeared 800 ms after the offset of prime, and were shown for 200 ms. 2800 ms after the presentation of the probe word, a blue question mark appeared in the center of the screen for 3 seconds, and served as the naming prompt.

Procedure. Participants were seated in a comfortable chair at a distance of 37" from the monitor. In experiment 1a, 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 at all times on a fixation point just below the centrally presented words. After the probe word appeared, they were to read it silently without moving their eyes, and then say it aloud when the blue question mark appeared, or to say "No," if they had been unable to read it. When the comprehension probe appeared, they were to

press “Yes” if it supported the preceding sentence, and “No” if it contradicted it. (Response hand was counterbalanced across participants.) In experiment 1b, they were told that they would be reading two words in a row and they should read the second word out loud when the blue question mark appeared, or to say “No,” if they had been unable to read it. There were no comprehension questions in this part of the experiment.

Electroencephalogram (EEG) Recording. EEG, sampled at 250 Hertz, was collected from 29 tin electrodes arranged in an expanded version of the 10-20 system (Nuwer et al., 1998), referenced to the left mastoid. ERPs were re-referenced off-line to an average of the signal collected from the left and right mastoid electrodes. Blinks and eye movements were monitored via an electrode beneath the right eye and one electrode at each of the outer canthi (the electro-oculogram, EOG). Average artifact rejection rate in experiment 1a (sentence primes) was 12% (sd=8%). Average artifact rejection rate in experiment 1a (word primes) was 19% (sd=17%). The EEG and EOG were recorded and amplified with a set of 32 bioamplifiers from SA Instruments, with half-amplitude cut-offs at .01 and 40 Hertz, and digitized on a PC. Informed consent was obtained and all procedures conformed to ethical requirements of the University of California, San Diego.

Data Analysis. Mean accuracy on the comprehension questions was assessed with repeated measures ANOVA with relatedness as the sole factor. Because nearly every probe on the naming task was named correctly, naming accuracy was not analyzed. Mean amplitude of ERPs was measured 300-700 ms and 700-900 post-probe onset. These values were initially subjected to repeated measures ANOVA with factors Context (Sentence/Word), Relatedness (Related/Unrelated), and 28 levels of electrode site. In individual analyses of experiment 1a and 1b, respectively, the Context factor was not included. Reliable interactions between the experimental variable and electrode site were followed up with three sorts of analyses: Midline (using channels FPz, FCz, Cz, CPz, Pz, and Oz), Medial (using channels FP1, F3, FC3, C3, CP3, P3, O1 and their LH counterparts), and Lateral (F7, FT7, TP7, T5 and their LH counterparts).

Where appropriate, the Huhyn-Feldt correction (Huynh & Feldt, 1978) has been applied. We report corrected p-values, but the original degrees of freedom have been maintained for clarity.

Experiment 2

Participants. 16 adults from the UCSD community (8 men) aged 18-25 were either paid \$24 or awarded credit hours for course requirements in exchange for their participation in the study. All were right-handed, monolingual English speakers with normal visual acuity and no history of neurological disorder. Handedness was assessed via the Edinburgh inventory (Oldfield, 1971). Participants' average laterality quotient was +75.

Materials. Materials were the same as the sentences used in experiment 1a. Each participant read 140 experimental probes, half of which were preceded by jokes, and half by straights, along with 120 filler probes, half preceded by jokes and half by straights. In each condition, (experimental related and unrelated, filler related and unrelated) half of the probes appeared in the participant's left visual field, and half in her right. Four lists were constructed so that while all manipulations were counterbalanced across participants, no individual participant saw more than one version of any prime or probe.

Stimulus Presentation and Procedure. Stimulus presentation was identical to that employed in experiment 1a, except that probe words were not presented centrally. Left visual field probes were presented so that their right-most character was 2 degrees of visual angle to the left of the center of the monitor. Right visual field probes were presented so that their left-most character was 2 degrees of visual angle to the right of the center of the monitor. Simultaneous with the onset of the lateralized probe, a fixation cross appeared in participants' center of gaze. As in experiment 1, the session began with a brief practice block. In experiment 2, 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 probe presentation, wait until prompted by the blue question mark to name the probe, and answer the comprehension

questions with a button-press). Experimenters monitored participants' eye movements on-line via the EOG. When participants moved their eyes during probe presentation, data collection was paused and the experimenter re-explained the instructions.

EEG Recording. EEG recording parameters were identical to experiment 1. The average artifact rejection rate was 15% (sd=14%).

Data Analysis. Mean accuracy on the naming task (scored in terms of percent correct) was assessed with repeated measures ANOVA with factors Visual Field (LVF/RVF) and Relatedness (Related/Unrelated). Accuracy on comprehension probes (also scored in terms of percent correct) was subjected to a similar analysis. Mean amplitude of ERPs was measured 300-700 ms and 700-900 post-probe onset. These values were initially subjected to repeated measures ANOVA with factors Visual Field (LVF/RVF), Relatedness (Related/Unrelated), and 29 levels of electrode site. Reliable interactions between either of the experimental variables and electrode site were followed up with three sorts of analyses: Midline (using channels FPz, Fz, FCz, Cz, CPz, Pz, and Oz), Medial (using channels FP1, F3, FC3, C3, CP3, P3, O1 and their LH counterparts), and Lateral (F7, FT7, TP7, T5 and their LH counterparts). In these analyses, the Posteriority factor indexes the position of electrodes along the anterior/posterior axis of the scalp. Where appropriate (i.e. medial and lateral analyses), the Hemisphere factor indexes the electrodes' location on the participant's head (over the LH or over the RH). In the analyses described above, the term Hemisphere always refers to electrode location and never refers to the Visual Field factor. Other aspects of the analyses were the same as in experiment 1.

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FIGURES

Figure 1. Sample Trial

Figure 2. Relatedness Effects with Word and Sentence Primes

Figure 3. N1 Visual Potentials

Figure 4. Relatedness Effect in Right and Left Visual Fields

Figure 5. Relatedness Difference Waves (Unrelated minus Related)

+

The

The replacement player
hit a homerun with my girl.

girl

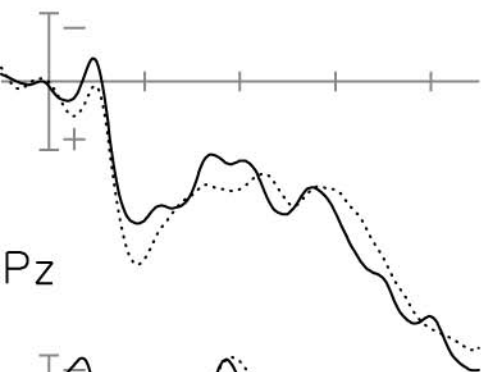
infidelity +

?

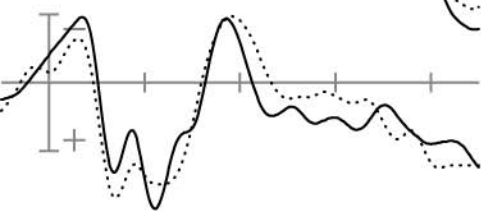
Someone else slept
with my girlfriend.

WORD PRIMES

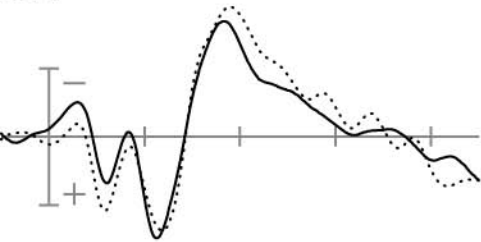
FPz



Pz

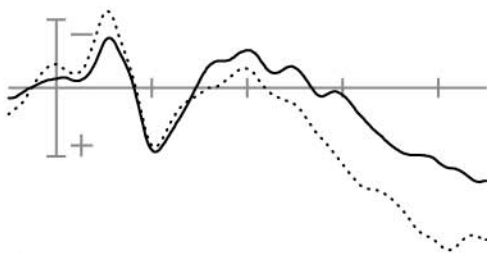


Oz

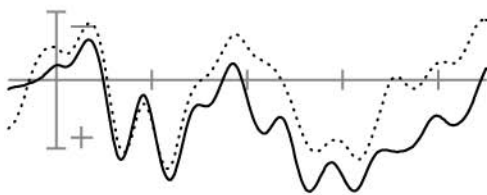


SENTENCE PRIMES

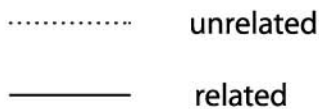
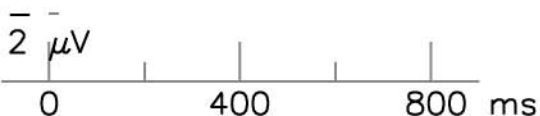
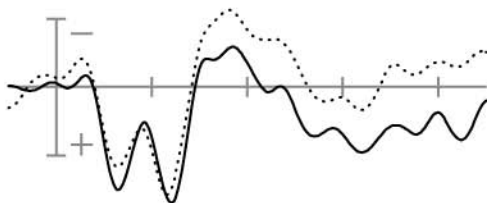
FPz

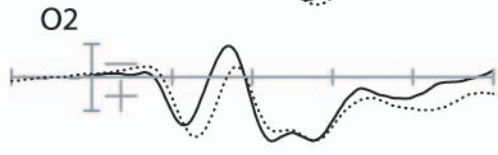
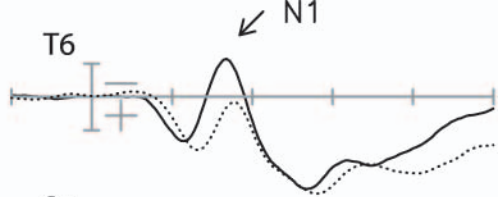
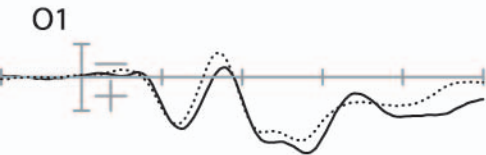
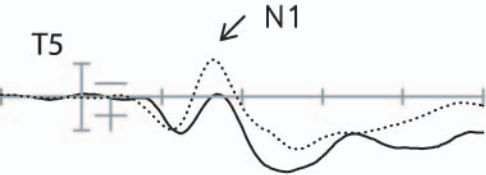


Pz



Oz

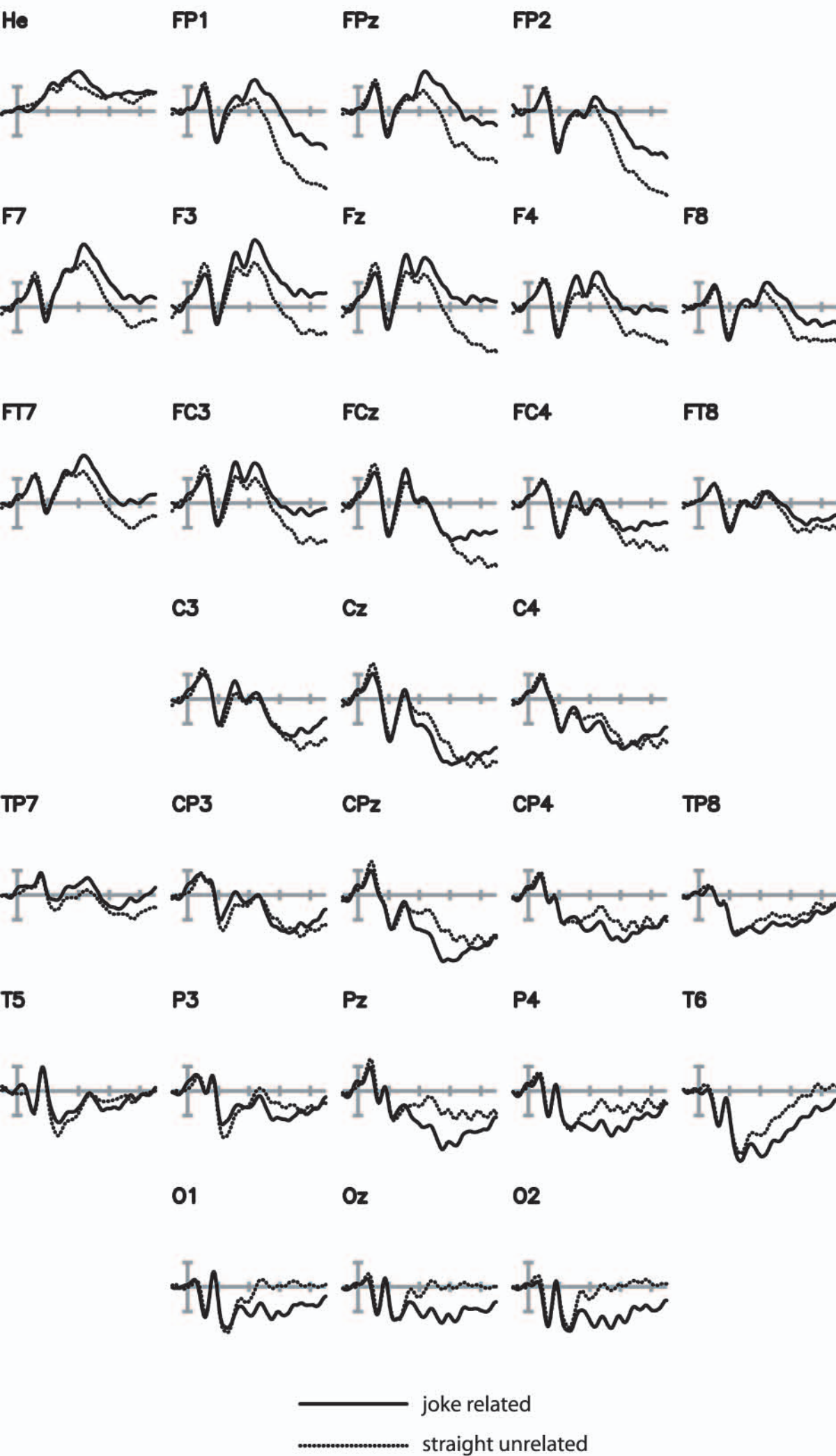




..... rvf/LH
—— lvf/RH

2 μV —
0 200 400 ms

RVF/LEFT HEMISPHERE



LVF/RIGHT HEMISPHERE

