



Close, but no garlic: Perceptuomotor and event knowledge activation during language comprehension



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ABSTRACT

Recent research has shown that language comprehension is guided by knowledge about the organization of objects and events in long-term memory. We use event-related brain potentials (ERPs) to determine the extent to which perceptuomotor object knowledge and event knowledge are immediately activated during incremental language processing. Event-related but anomalous sentence continuations preceded by single-sentence event descriptions elicited reduced N400s, despite their poor fit within local sentence contexts. Anomalous words sharing particular sensory or motor attributes with contextually expected words also elicited reduced N400s, despite being inconsistent with global context (i.e., event information). We rule out plausibility as an explanation for both relatedness effects. We show that perceptuomotor-related facilitation is not due to lexical priming between words in the local context and the target or to associative or categorical relationships between expected and unexpected targets. Overall our results are consistent with the immediate and incremental activation of perceptual and motor object knowledge and generalized event knowledge during sentence processing.

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Introduction

Long-term memory encompasses knowledge about how we perceive and interact with objects (e.g., the taste, color, and texture of a cake), as well as which objects and participants are likely to cohere into particular events (e.g., a large white multi-tiered cake is likely to co-occur with music, dancing, and a group of well-dressed guests). Language comprehension is driven in part by rapid access to these aspects of real-world knowledge. Consider the following passage:

My date was taking me to a romantic Italian restaurant for dinner tonight. I was worried that afterward I might reek of _____ so I brought gum.

We know what kinds of things are likely to be found at romantic Italian restaurants. Although these entities may not be referred to in the text, we can draw on our knowledge of events to narrow down the set of likely continuations in the second sentence. The text also refers to a perceptual property of the upcoming word's referent—in this case a strong odor. When asked to fill in the missing word, most respondents draw on both event and perceptuomotor knowledge to arrive at “garlic”. Similarly, when people are asked to list features of “axe”, for example, they provide both perceptuomotor properties (“is heavy”) and situational properties (“is used by lumberjacks”) (McRae, Cree, Seidenberg, & McNorgan, 2005). Clearly, comprehenders can access their knowledge about objects and events in these offline tasks. What is less clear, and what is the focus of this study, is when and to what extent these aspects of real-world knowledge are accessed during online language comprehension.

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Object and event knowledge may be accessed and represented in a similar fashion. Behavioral work suggests that both event and object concepts are organized according to categorical and part-based taxonomies wherein certain levels (e.g., the basic level) are more privileged than others with respect to categorization, goodness of example, and inference (Rifkin, 1985; Rosch, Mervis, Gray, Johnson, & Boyesbraem, 1976; Schank & Abelson, 1977; Zacks & Tversky, 2001). Neuroimaging studies suggest that accessing knowledge about a particular object or recalling an episode both involve partial reactivation of encoding states. Reading object names can produce activations in neural systems that overlap with those involved in perceiving and acting upon those same objects (Binder & Desai, 2011; Martin, 2007), and recalling a memory of a previously experienced event can involve reactivating the neural representations that were active during the event (Buckner & Wheeler, 2001; Polyn, Natu, Cohen, & Norman, 2005). Such partial reactivation (sometimes also called simulation) may be involved in language comprehension (Bower & Morrow, 1990; Chow et al., 2014; Glenberg, Meyer, & Lindem, 1987; Speer, Reynolds, Swallow, & Zacks, 2009; Zwaan, 2004; Zwaan & Radvansky, 1998). For example, comprehending stories containing descriptions of participant-object interactions was associated with activity in brain regions known to be involved in actually experiencing events similar to the fictional depicted events (Speer et al., 2009). Taken together, these findings suggest that object knowledge and event knowledge both reside in a long-term memory network that can revisit encoding states formed during previous perceptual, linguistic, or endogenous mental experiences.

Semantic memory structure and language processing

The relatedness between concepts rapidly influences word processing during language comprehension. Kutas and Hillyard (1980) showed that the amplitude of a negative-going ERP component peaking around 400 ms following word onset (i.e., the N400 component) reflects the degree of semantic appropriateness of a word in a particular sentence context—decreasing in amplitude for “transmitter”, “waterfall”, and “cup” respectively in, “He took a sip from the _____.” Kutas and Hillyard (1984) found that the N400 was reduced for anomalous words that were nonetheless related to an expected (but unseen) word in context. Therefore, semantic memory structure appears to have a relatively immediate influence on language processing. Related things, however, are not necessarily similar. These N400 relatedness effects were based on participants’ relatedness ratings, and thus the extent that these effects specifically index conceptual similarity remains unknown. The referents of “Labrador retriever” and “leash” are not physically similar, but these words and their referents are highly related given our knowledge about dogs. Conversely, Labradors and golden jackals are rarely experienced in the same physical or linguistic setting, but are nonetheless very similar, belonging to a common category (the genus *canis*).

Categories are informative cues to physical similarity. Discrete verbal categories often are used to study semantic

similarity under the assumption that category members have greater feature overlap than members of different categories (Rosch et al., 1976), and the assumption that feature overlap is proportional to semantic similarity (Tversky, 1977). The N400 is sensitive to category structure in single word and sentence contexts (Federmeier & Kutas, 1999; Fischler, Bloom, Childers, Roucos, & Perry, 1983; Heinze, Munte, & Kutas, 1998; Kounios & Holcomb, 1992; Polich, 1985). Federmeier and Kutas (1999) used category structure to study semantic memory use in language comprehension, reasoning that exemplars from the same basic-level category should possess more shared semantic features than exemplars from a different basic-level (but same superordinate) category. They presented sentences (e.g., “They wanted to make the hotel look more like a tropical resort. So along the driveway they planted rows of . . .”) that were completed either by a within-category coordinate (“pines”) or a between-category coordinate (“tulips”) of the expected completion (“palms”). They showed that the within-category exemplars elicited a smaller N400 than the between-category exemplars. At least two aspects of semantic memory structure could be responsible for this effect. Murphy (2002) concluded that this result directly reflects the use of categories in sentence comprehension. This interpretation is consistent with these data, but not uniquely supported by them. Federmeier and Kutas proposed that sentence context can be used to activate physical, functional, and situational knowledge (rather than category information *per se*) about an upcoming word. The N400 facilitation effect for within-category exemplars was taken to reflect greater similarity between conceptual representations. Online influences of graded semantic similarity also are supported by a visual world eye-tracking study (Huettig & Altmann, 2005) in which participants heard spoken language and simultaneously viewed images depicting objects referred to by the speaker. The probability of fixating a categorically related competitor of the expected object was significantly correlated with the items’ semantic similarity as determined from feature production norms (McRae et al., 2005).

In the above studies, facilitation for related anomalies could be due to one or more of several different aspects of semantic similarity. For example, the related anomaly “drink” and target “eat” in Kutas and Hillyard’s (1984) sentence, “The pizza was too hot to eat/drink/cry,” share perceptuomotor information (actions that involve the mouth and elicit gustatory sensations) and situational information (eating and drinking are more likely to co-occur than eating and crying). Federmeier and Kutas’s (1999) stimuli incorporate several different similarity relationships between category coordinates, and vary in the degree to which the sentence context directs attention to specific knowledge types. Some exemplars were selected from biological categories (e.g., “palms/pines/tulips”) from which physical similarity can be inferred directly from the structure of a phylogenetic tree. All three exemplars share properties common to plants (e.g., grows, relies on photosynthesis), but the within-category exemplars additionally share physical properties common to trees (e.g., size, hardness). The within-category exemplars also possess greater situational similarity; e.g., planting trees

typically requires more labor and equipment than planting flowers. Other sets of exemplars are similar on some kinds of knowledge but dissimilar on others (e.g., “The snow had piled up on the drive so high that they couldn’t get the car out. When Albert woke up, his father handed him a shovel/rake/saw”). All three targets are broadly congruent with a specific action (grasping), and whereas the within-category exemplars, shovel and rake are more physically similar than either is to saw, snow shovels and rakes are typically used during very different situations associated with different locations, weather, and clothing. These examples highlight several ways in which concepts can be related, and in which sentence context can highlight particular types of knowledge.

Perceptuomotor knowledge activation during language processing

We have seen that semantic memory structure exerts an immediate influence on neural activity during language processing, and that category-related effects may be driven by different mixtures of semantic similarity. Distributed feature-based models of semantic memory (Masson, 1995; McRae, deSa, & Seidenberg, 1997; Plaut, 1995) correctly predict that semantically similar concepts can prime one another in the absence of other forms of association (Lucas, 2000; McRae & Boisvert, 1998; Thompson-Schill, Kurtz, & Gabrieli, 1998). Several studies have addressed the more specific question of whether object concepts facilitate processing of other object concepts that share specific perceptuomotor features.

Eye-tracking studies employing the visual world paradigm have shown that people are more likely to fixate a competitor with the same shape as an otherwise unrelated target (Dahan & Tanenhaus, 2005; Rommers, Meyer, Praamstra, & Huettig, 2013). Rommers, Meyer, and Huettig (2013) employed a picture target-absent version of the visual-world paradigm, where participants heard constraining sentences (e.g., “In 1969 Neil Armstrong was the first man to set foot on the moon”) and viewed four pictures 500 ms before the target word (e.g., “moon”) was spoken. Participants were more likely to make anticipatory eye movements to pictures that had similar shapes as the target word’s referent (e.g., “tomato”), suggesting that shape information was activated despite no reference to shape and the irrelevance of shape information to the task. People are faster to recognize a picture of an object in a particular orientation (vertical/horizontal) when preceded by a sentence that implies that orientation (“John put the pencil in the cup/drawer”), despite the irrelevance of orientation to the task (Stanfield & Zwaan, 2001; Zwaan & Pecher, 2012). Similarly, people are faster to recognize a picture of an eagle shown with wings outstretched versus folded after reading “The ranger saw the eagle in the sky” (Zwaan & Pecher, 2012; Zwaan, Stanfield, & Yaxley, 2002). Priming evidence for the routine activation of object color knowledge is less consistent, with some studies reporting facilitation (Zwaan & Pecher, 2012) and others reporting interference (Connell, 2007). Beyond visual knowledge, at least one study has demonstrated that knowledge about

object manipulation is routinely activated (e.g., “piano” primes “typewriter”) despite the absence of directed attention to the shared feature of manipulability (Myung, Blumstein, & Sedivy, 2006). Whereas the above studies are consistent with the routine activation of perceptuomotor knowledge during language comprehension, other studies are not. Yee, Ahmed, and Thompson-Schill (2012) found color priming (e.g., “emerald” primes “cucumber”) only when participants first performed a Stroop task that directed their attention to color. Pecher, Zeelenberg, and Raaijmakers (1998) found visual shape priming (e.g., “cherry” primes “ball”) only when participants first judged whether the stimuli denoted flat or oblong objects. Rommers, Meyer, and Huettig (2013) and Rommers, Meyer, Praamstra, et al. (2013) found no effect of orientation, and found that shape information influenced performance in only a subset of tasks (but see Zwaan, 2014). Kellenbach, Wijers, and Mulder (2000) found that the N400 was reduced for targets preceded by primes denoting objects with similar shapes (e.g., “button” primes “coin”) during lexical decision, but that this priming effect was absent in the behavioral response times. Overall, these studies suggest that a number of specific types of perceptuomotor knowledge (size, shape, orientation, color, manipulability) can be activated during language processing but that these activations may require directed attention to the particular knowledge type.

Fewer studies have examined the nature of perceptuomotor knowledge activation as language unfolds in more natural settings. Self-paced reading studies suggest that perceptuomotor information is available as soon as possible in the sentence (Sato, Schafer, & Bergen, 2013; Taylor & Zwaan, 2008; Zwaan & Taylor, 2006). Zwaan and Taylor (2006) asked participants to turn a knob either clockwise or counterclockwise to advance to the next word region of sentences that implied a particular direction of motion (e.g., “To quench / his / thirst / the / marathon / runner / eagerly / opened / the / water bottle”). They showed that reading times were faster when the direction of manual motion matched the implied motion of the critical verb (e.g., turning the knob counterclockwise to advance beyond “opened”). Sato et al. showed that comprehenders are faster to verify pictures denoting an object (e.g., shirt) in the shape (e.g., vertical, hanging) implied by a location (e.g., outdoors) before they receive the verb (e.g., dried) that specifies what shape the object should take.

Electrophysiology provides converging evidence for perceptuomotor knowledge activation during incremental comprehension. Chwilla, Kolk, and Vissers (2007) presented Dutch passages to set up events, followed by sentences containing critical words indexing either a novel but sensible action or a novel but incongruent action (e.g., “The boys found a canoe in the spare room. With this, they wanted to go canoeing on the canal whatever the costs. The fact that they could not find the paddles did not lead them to make up their mind. According to the boys, you do not at all need them. They let the canoe into the water and paddled with Frisbees/pullovers”). They found N400 reductions to the sensible condition (“Frisbees”), concluding that action affordances are

immediately generated for novel situations and that simulating a novel action (e.g., paddling with Frisbees) occurs with the same ease as simulating familiar actions. A different possibility, however, is that participants preactivated relevant conceptual features (e.g., hardness, surface area), and upon presentation of “Frisbees”, which shares more physical features with oars than either does with pullovers, the N400 reflected facilitated processing. Rommers, Meyer, and Huettig (2013) and Rommers, Meyer, Praamstra, et al. (2013) showed that beginning after about 200 ms, both anomalies “tomato” and “rice”, for example, elicited larger N400s than the expected “moon” in, “In 1969 Neil Armstrong was the first man to set foot on the _____”). They also found that after 500 ms the shape-related anomaly “tomato” elicited a smaller negativity than the anomaly. This shape-related ERP effect is substantially later than Kellenbach et al.’s (2000) shape-related N400 priming effect, and the category-related N400 effects found in written word (Federmeier & Kutas, 1999) and spoken word (Federmeier, McLennan, De Ochoa, & Kutas, 2002) studies. Rommers, Meyer, and Huettig (2013) and Rommers, Meyer, Praamstra, et al. (2013) suggests a number of possible reasons for the late effect including that “shape information might not receive the same degree of priority as semantic category information in facilitating the processing of unexpected words” (p. 444). However it is unclear whether the facilitated processing reported in previous studies reflects category information *per se*, or greater overlap of other types of semantic features (which can vary independently of category structure). It is also unclear to what extent Rommers et al.’s relatively late finding reflects the immediate activation of shape-related knowledge.

Event knowledge activation during language processing

In parallel with the reviewed lines of research on perceptuomotor knowledge activation, researchers have, to a more limited extent, probed the activation of event knowledge during sentence comprehension. In particular, several ERP studies have demonstrated that real-world knowledge about situations and events is routinely activated during comprehension (Sanford, Leuthold, Bohan, & Sanford, 2011; Otten & Van Berkum, 2007; Metusalem et al., 2012). In particular, Metusalem et al. presented event-related but locally contextually incongruent sentence continuations, and established that event knowledge never explicitly referred to in the text is nonetheless activated during incremental comprehension. For example, participants read passages like, “Elizabeth was standing at the intersection waiting for the light to change. All of a sudden she saw a car barrel through the red light. A moment later, she heard a terrible _____ come from down the street.” Although both incongruent continuations “policeman” and “conductor” elicited larger amplitude N400s than the most probable continuation “crash”, N400 amplitude to “policeman” was reduced relative to that of “conductor”. Although neither continuation is well suited to the local context, “policeman” is part of our general knowledge about car accidents, and thus may be easier to process by virtue of the generalized event information activated in

long-term memory by the context. We utilized this “related anomaly” design to investigate the activation of event knowledge alongside perceptuomotor knowledge during online sentence processing. The evidence presented earlier suggested that both object knowledge and event knowledge are activated by partially re-enacting the encoding states formed during experiences. Using the ERP technique and including event-related and perceptuomotor-related anomalies in the same sentence frames will allow us to better address the extent to which comprehenders are accessing these types of knowledge as soon as they are available.

Present study

We use ERPs to determine the extent to which perceptuomotor knowledge and event knowledge are activated immediately during incremental language processing. Rather than isolating a single knowledge type (e.g., shape, manipulability), we include several different perceptuomotor modalities: visual, haptic, auditory, olfactory, gustatory, and motor. Participants view an introductory sentence that establishes a situation (e.g., “My date was taking me to a romantic Italian restaurant for dinner tonight.”) Next, they view a serial visual presentation (SVP) sentence that directs their attention to specific perceptual or motor-related information associated with an upcoming noun (e.g., “I was worried that afterward I might reek of _____ so I brought gum.”) On any given passage, participants receive one of four conditions: the expected (highest cloze probability) continuation or one of three anomalous continuations. The expected continuation (“garlic”) is congruent with the event information (garlic is a standard ingredient in Italian cooking) and with the perceptuomotor information. The unrelated continuation (“ice”) is incongruent with both the event and the perceptuomotor information. The perceptuomotor-related continuation (“tobacco”) is not closely associated with the event but is congruent with the perceptuomotor information (one can also reek of tobacco). The event-related continuation (“napkins”) is congruent with the event introduced in the context sentence, but incongruent with the perceptuomotor information.

We expect that all three anomaly conditions will elicit robust N400s in comparison to the expected condition. The event-related condition is a conceptual replication of Metusalem et al. (2012), and thus an intermediate amplitude N400 (statistically distinguishable from the expected and unrelated conditions) would constitute converging evidence that generalized situational knowledge is active during incremental comprehension despite an incongruent local linguistic context. The most novel condition in this study, the perceptuomotor-related continuation, will aid in determining the extent to which knowledge about perceptual and motor object properties is activated despite a poor fit to the global or message-level context. Observing a reduced N400 to perceptuomotor-related words would suggest that, along with event-related knowledge, individuals’ knowledge about perceptual and motor object properties is available rapidly to contribute to the incremental

construction of mental representations during sentence comprehension.

Event-related Potential Experiment

Method

Participants

Thirty-two right-handed (Oldfield, 1971) undergraduates (17 women; ages 18–30) were recruited from the University of California, San Diego. The experiment was undertaken only with the understanding and written consent of each participant. Participants were awarded course credit and/or compensated at \$7/hour at the end of the experiment. Participants had normal or corrected-to-normal vision, and were native English speakers with no significant exposure to other languages before 7 years of age. Participants reported no major neurological or general health problems, and no psychoactive medication use.

Materials

Experimental stimuli consisted of 136 sentence pairs. The first sentence provided an event or situational context. The second sentence established an expectation for a noun referring to an entity with a particular perceptual or motor characteristic, and contained one of four possible continuations: (expected) the most expected word that was congruent with both the situation context and the perceptuomotor expectation; (event-related) a contextually anomalous word that was related to the situation introduced in sentence one but incongruent with the perceptuomotor expectation; (perceptuomotor-related) a contextually anomalous word that was unrelated to the situation context but congruent with the perceptuomotor expectation; or (unrelated) a contextually anomalous word that was both unrelated to the situation context and incongruent with the perceptuomotor expectation.

We constructed passages wherein the first sentence introduced an event or situation, and the second sentence established an expectation for a specific noun referring to an entity with a particular perceptuomotor characteristic. The second sentence was designed to provide no specific details about the situation, and therefore to license numerous plausible continuations if it were presented in isolation, without the preceding context sentence. The most expected continuations were determined from the results of an online cloze task conducted on 148 sentence pairs. Forty English-speaking undergraduates at UCSD provided completions for 74 passages, and the remaining 74 passages were the second sentences presented in isolation; an additional 40 participants completed the same task for the opposite pairing of sentences. Participants provided the word(s) that they believed should appear in the critical position in each sentence (marked with a blank line), with the post-critical word portion of the sentences truncated. Given that expectations for a specific orthographic form were not of critical interest, we combined the cloze probabilities of words we considered to be direct synonyms of the most commonly listed word in each case (e.g., for one particular sentence, a minority of responses of “Kleenex”

were replaced with “tissue”, which was the most common answer). Cloze probability for a specific word in a specific sentence was computed as the proportion of participants that completed that particular sentence with that particular word. Twelve stimuli were excluded due to low mean cloze probabilities (<0.25) or because the highest cloze target was a compound word (e.g., “hot dog”). The remaining 136 experimental sentence pairs had best completions that ranged in cloze probability between 0.26 and 1.0 (see Table 1 for descriptive statistics). An expected continuation was always the word with the highest cloze probability in that context.

The perceptuomotor-related continuations, like the expected continuations, denoted objects that were salient with respect to a specific perceptuomotor property referenced in Sentence 2. We selected these continuations in large part by consulting object attribute norms in which participants rated objects on several perceptual and motor attributes (Amsel, Urbach, & Kutas, 2012). For example, consider passage (2) below:

(2) *Felicia didn't want a traditional diamond engagement ring. Instead she was hoping for a brilliant green...*

The second sentence sets up an expectation for an object that is both vividly colored and specifically green. Among the ratings collected in the Amsel et al. (2012) norming study was, “how vivid (intense) is the color of this object?” The average ratings for the expected continuation “emerald” and the perceptuomotor-related continuation “banner” were 7.1 and 6.5 respectively on a scale of 1 (“Not at all vivid”) to 8 (“Extremely vivid”), suggesting that paired with a congruent color (green), the second sentence presented in isolation could license either continuation. Many of our perceptuomotor-related continuations were selected in part by consulting the Amsel et al. norms, and we used their seven modalities to construct items for this condition. Among the 136 experimental scenarios 25 referred to a color or brightness property, 27 to a particular action affordance (e.g., grasping), 14 to perceived motion, 21 to a haptic or pain experience, 16 to smell, 17 to sound, and 16 to taste. Perceptuomotor expectations were referenced with a variety of word types, including transitive and intransitive verbs, adjectives, and nouns. One advantage of including incongruent words related to expected continuations by several different kinds of perceptuomotor (as well as situational) knowledge is the decreased likelihood that participants will recognize the manipulation. For example, 60% of the anomalous targets in Rommers, Meyer, and Huettig (2013) and Rommers, Meyer, Praamstra, et al. (2013) were unrelated to the expected condition, and the remaining 40% were designed to relate specifically by shape information.

Following Metusalem et al. (2012) we selected event-related continuations that were related to the event or situation context introduced in sentence one, but not explicitly mentioned in either sentence. Continuations were selected in part by asking a group of research assistants to verbally list salient elements of the situations and events after listening to an experimenter read each context sentence. Our design also required satisfaction of the additional constraint that the continuation be a poor

Table 1
Stimuli characteristics. Entries are means and standard deviations.

Condition	Cloze	Cloze (SVP)	S1-to-target (LSA)	S2-to-target (LSA)	Target Length	Target Frequency	Target Ortho. N
Expected	.78 (.18)	.10 (.15)	.20 (.06)	.20 (.07)	5.9 (1.8)	28.4 (45.6)	5.3 (6.4)
Perceptuomotor-related	.0006	.02 (.07)	.14 (.06)	.17 (.07)	5.9 (1.9)	28.7 (79.5)	5.1 (6.1)
Event-related	.0007	<.0001	.18 (.06)	.17 (.07)	5.9 (1.7)	28.1 (73.1)	5.2 (5.6)
Unrelated	<.0001	<.0001	.16 (.06)	.18 (.07)	5.9 (2.0)	28.7 (34.2)	5.2 (5.9)

fit to the perceptuomotor modality referenced in Sentence 2, specifically a poor fit to the perceptuomotor expectation (e.g., "... bright green gorillas"; "... reached for his pair of zebras").

For the anomalous unrelated condition we selected continuations that were both unrelated to the event/situation context and a poor fit to the perceptuomotor modality referenced in Sentence 2.

The critical words in Sentence 2 were all sentence-medial, with a minimum of two sentence-final words following them. Simple yes/no comprehension questions followed approximately one third of our experimental stimuli to ensure that participants were reading for comprehension. Finally, we included 34 medium to high constraint filler passages, all containing highly expected words. The structure of the fillers varied more than the experimental items in that they were not constrained to set up a particular event context and were not constrained to include any reference to perceptuomotor information. Their inclusion increased the proportion of non-anomalous items to 40% across the experiment.

Following these procedures we determined whether or not the continuations from each condition were matched on mean word frequency (SUBTL frequency: Brysbaert & New, 2009), length, and number of orthographic and phonological neighbors. We selectively replaced continuations from each of the anomalous conditions until all conditions were matched (see Table 1). We created four experimental lists to ensure that each participant saw each passage only once (all participants saw every filler passage). The full stimulus set was divided into the four subsets that were matched as much as possible on the four item characteristics mentioned above (the p value associated with the one-way ANOVA was $>.4$ for all 16 combinations of item characteristics by list).

Next, we assessed the likelihood that the three unexpected conditions could be primed by words in the local context (SVP sentence). We used latent semantic analysis (LSA; lsa.colorado.edu) based on the *TASA General reading up to 1st year College* corpus to estimate the degree of semantic similarity between each word in the SVP sentence and the target word. For every passage we computed the cosine between each of four targets and each word in the SVP sentence. These values were averaged to form a mean semantic similarity score for each condition in each sentence. Unsurprisingly, the LSA scores for the expected targets ($M = .20$, $SD = .07$) were significantly higher than the perceptuomotor-related continuations ($M = .17$, $SD = .07$), event-related continuations ($M = .17$, $SD = .07$), and unrelated ($M = .18$, $SD = .07$) continuations ($ps < .05$). Importantly, the perceptuomotor-related and event-related conditions did not significantly differ from the

unrelated condition ($ps > .20$). This pattern of results was unchanged following analyses based on the immediately preceding word or two words prior to the target. Therefore any lexical priming influences of the words immediately preceding the targets are not likely to differ across the three unexpected conditions.

Finally, we assessed the degree to which the unexpected targets were associatively related to the expected target according to the Nelson free association norms (Nelson, McEvoy, & Schreiber, 2004). Of the 136 passages, the Nelson norms contained 109 expected continuations as cues. We determined the forward association strength from the expected continuations to each of the unexpected continuations for each sentence (i.e., proportion of participants who provided that target for that cue), and averaged these proportions across conditions. The mean association strengths for the perceptuomotor-related, event-related and unrelated continuations were zero, .004 (1 out of 250 participants), and .0006 (3 out of 5000 participants) respectively. Of the 109 stimuli included here, six of the event-related continuations and one of the unrelated continuations were provided as targets for the expected continuations by at least one participant in the Nelson ratings. Most importantly, there was no evidence that the perceptuomotor-related continuations were associatively related to the expected continuations, despite their shared perceptuomotor attribute.

Procedure

Participants sat in an armchair in a dimly lit, sound-attenuated, electromagnetically shielded chamber. Passages were read on a CRT computer monitor located approximately 112 cm in front of the participants' eyes. Participants were instructed to "read each passage as you normally would read any text", and were informed that there would be comprehension questions about the text's meaning following some trials. Importantly, the experimenter never mentioned the perceptuomotor or event-related aspects of the critical anomalies. The first sentence was presented in the center of the screen in its entirety, and participants were told to press a button to advance to the second sentence only after they had read and understood the first sentence. They were instructed to refrain from blinking and to be as still as possible once they advanced to the second (SVP) sentence of each pair. They were told that they could resume blinking only after the final word (which was always presented with a period) disappeared from the screen. The words of the SVP sentence were presented near the center of the screen directly above a central fixation square, one word at a time with a 500 ms stimulus onset asynchrony divided into a 200 ms stimulus duration and a 300 ms inter-stimulus interval.

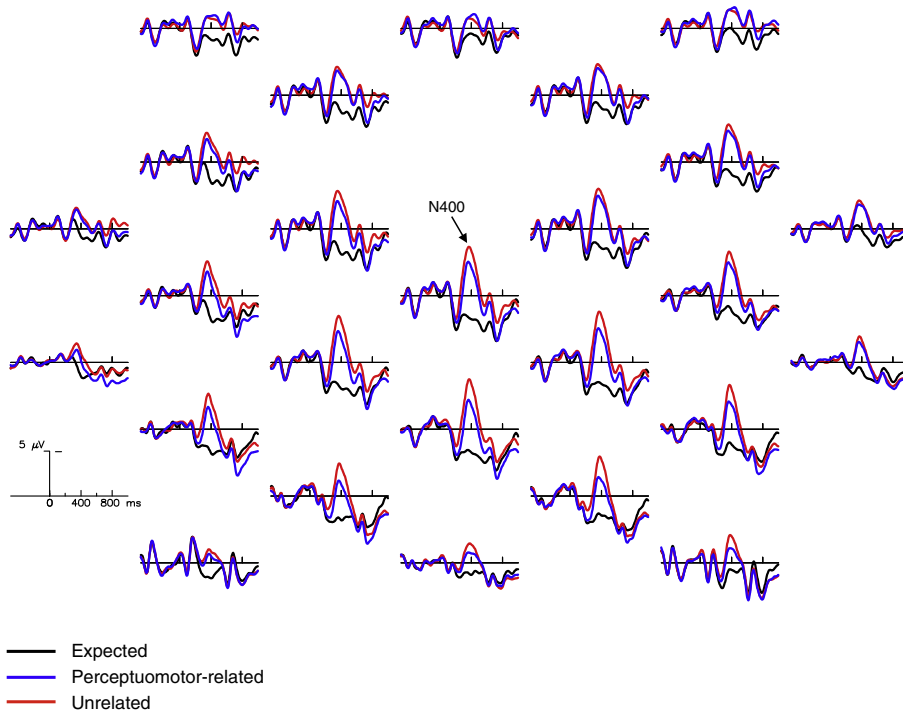


Fig. 2. ERPs to perceptuomotor-related continuations are shown alongside ERPs to expected targets and unrelated continuations. The perceptuomotor-related N400 reduction is clearly visible at several centro-parietal sites.

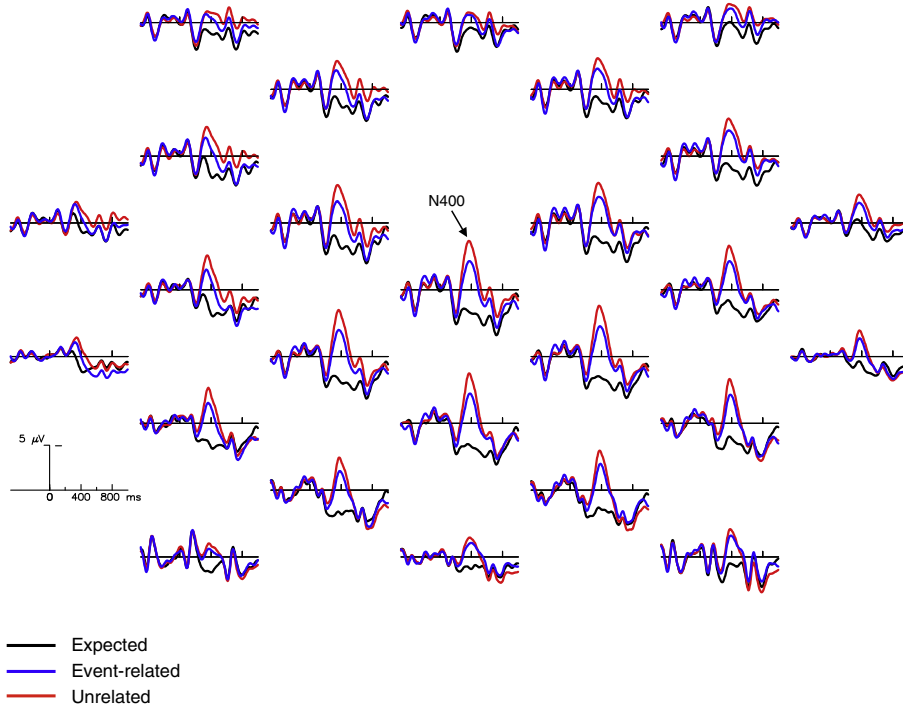


Fig. 3. ERPs to event-related continuations are shown alongside ERPs to expected targets and unrelated continuations. The event-related N400 reduction is clearly visible at several centro-parietal sites.

Table 2

Pearson's correlation coefficients between individual difference measures and N400 measures. No correlations are statistically significant after Holm-Bonferonni correction.

	Letter fluency	Category fluency	Digit span	Print frequency
Unrelated N400	0.19	−0.11	0.52	0.03
Event-related N400	0.10	−0.02	0.44	−0.28
Expected N400	0.16	0.20	0.17	−0.03
Perceptuomotor-related N400	0.22	0.02	0.32	−0.02
Unrelated N400 effect	0.02	−0.30	0.33	0.05
Event-related N400 effect	−0.05	−0.19	0.23	−0.21
Perceptuomotor-related N400 effect	0.09	−0.18	0.19	0.01

comparison of the perceptuomotor-related and event-related conditions revealed a significant interaction between condition and anteriority, $F(3,87) = 5.7$, $p = .01$, characterized by larger negativities for perceptuomotor-related versus event-related targets at prefrontal, frontal, and parietal sites, and the opposite pattern at occipital sites. In other words, the N400 reduction for the perceptuomotor-related condition was more pronounced than for the event-related condition at occipital sites, but more pronounced for the event-related reduction than the perceptuomotor-related reduction at frontal sites.

Individual difference measures and N400 amplitude

We conducted exploratory correlational analyses of two verbal fluency measures, print frequency (i.e., sum of ART and MRT), and digit span, with N400 amplitudes and N400 expectancy effects (expected–unexpected). Although the category and letter fluency portions of the test typically are combined into a single measure and do exhibit a strong correlation in our subjects ($r = .70$), fMRI studies of healthy adults (Gourovitch et al., 2000; Mummery, Patterson, Hodges, & Wise, 1996) and left hemisphere stroke patients (Baldo, Schwartz, Wilkins, & Dronkers, 2006, 2010) demonstrate that the left temporal lobe is uniquely activated during the category fluency (versus letter fluency) task. Therefore we might expect performance on the category portion of the verbal fluency test in particular (i.e., retrieving names of category members) to predict measures of semantic access—including the N400. Table 2 contains Pearson correlation coefficients for each comparison, and does not contain any statistically significant correlations after controlling for family-wise error. We see no reliable evidence that category fluency is more associated with N400 amplitude than letter fluency, and note that digit span possesses the strongest relationships with N400 amplitudes.

Discussion

The present ERP study utilized a related anomaly paradigm which capitalized on the sensitivities of the N400 ERP component to determine when and to what extent perceptuomotor object knowledge and event knowledge are activated during incremental sentence processing. We showed that N400 amplitude was significantly reduced for words that shared perceptual or motor-related information with the expected word, and for words that were related to

the event introduced in the context-setting sentence (in comparison to unrelated anomalous words). The reduction in N400 amplitude to the novel perceptuomotor-related condition is consistent with the immediate and incremental activation of perceptual and motor-related knowledge. However, first we address a number of potential alternative explanations. One possibility is that the N400 reductions in both related anomaly conditions are caused exclusively by relatively higher propositional plausibility in comparison with the unrelated anomaly condition. On one hand, the N400 is highly correlated with predictability (i.e., cloze probability), which in turn varies with plausibility. For example, in “he liked lemon and sugar in his tea/coffee”, both completions are possible, but “tea” is more predictable because the sentence describes something that is more likely to occur in the real world—the very instructions given to participants in a plausibility ratings task. So it is unsurprising that N400 amplitude can vary inversely with plausibility (DeLong, Quante, & Kutas, 2014; Federmeier & Kutas, 1999; Kutas & Hillyard, 1984). On the other hand, the N400 also can vary dramatically in the absence of plausibility. For example, among targets that render a sentence highly implausible (e.g., thematic role violations), those that are related to the message-level context can lead to reduced or even nonexistent N400s (Kuperberg, 2007; Metusalem et al., 2012; Nieuwland & Van Berkum, 2005, 2006; Sanford et al., 2011). Rather than attempting to infer the role of plausibility in our study indirectly by appealing to past studies, we directly addressed the role of plausibility by conducting a plausibility ratings study.

Plausibility study

Method

Participants

One hundred forty-three UCSD undergraduate students who did not participate in the ERP study participated for course credit.

Materials

We obtained plausibility ratings for every experimental passage (and filler passage) used in the ERP study, as well as for the second sentence of each pair in isolation. Eight lists were constructed such that each sentence pair and each isolated second sentence only appeared once per

participant (an isolated second sentence and its corresponding sentence pair were never shown to the same participant).

Procedure

Participants viewed each sentence or sentence pair up to and including the critical target and were asked to rate each on plausibility. Following previous plausibility ratings studies (Matsuki et al., 2011; Paczynski & Kuperberg, 2012), we instructed participants to rate each sentence/pair using the integers between 1 and 7, where 1 indicated that the sentence(s) described something that was very unlikely to occur in the real world and 7 indicated that the sentence(s) described something that was very likely to occur in the real world. Each session lasted approximately 40 minutes.

Results and discussion

Unsurprisingly, sentence pairs containing expected targets were rated as highly plausible ($M = 6.2$, $SD = .62$). A by-items one-way ANOVA revealed a significant difference between full passage plausibility ratings on passages containing the three critical anomaly conditions, $F(2,405) = 53.5$, $p < .001$. Tukey HSD tests revealed that the unrelated anomalies ($M = 1.86$, $SD = 0.65$) were significantly less plausible than the event-related anomalies ($M = 2.73$, $SD = 1.07$), $p < .001$, which in turn were marginally less plausible than the perceptuomotor-related anomalies ($M = 2.98$, $SD = 1.03$), $p = .07$.

The relatively higher rated plausibility of the related anomalies in comparison with the unrelated anomalies is broadly consistent with the pattern of N400 amplitudes for these conditions. To address the possibility that plausibility could entirely account for the N400 relatedness effects we identified a subset of stimuli in each of the three anomaly conditions such that plausibility and the additional relevant variables were matched as closely as possible across conditions (Table 3). The plausibility matched item set contained 77 of the original 136 passages per condition¹

We re-analyzed N400 amplitudes for the anomaly conditions by averaging ERP amplitudes between 300 and 500 ms at the same four canonical N400 sites used earlier (MiPa, MiCe, RMCe, LMCE). If plausibility is entirely responsible for the N400 effects and is entirely confounding the apparent event and perceptuomotor-related effects, we should see no N400 amplitude differences between these conditions. Fig. 4 shows the ERPs for all three matched anomaly conditions as well as the difference waves corresponding to each facilitation effect (i.e., unrelated anomaly-related anomaly). A repeated measures ANOVA with factors of channel and condition was significant, $F(2,58) = 3.89$, $p = .03$. N400 amplitude for unrelated anomalies ($M = -3.7$, $SD = 3.4$) was significantly more negative than for both perceptuomotor-related anomalies ($M = -2.5$, $SD = 4.1$), $t(29) = 2.5$, $p = .02$, and

event-related anomalies ($M = -2.3$, $SD = 3.6$), $t(29) = 2.3$, $p = .03$. This result rules out the possibility that the observed event-related and perceptuomotor-related facilitation are entirely confounded by differences in plausibility.

We examined the relatedness effects (unrelated anomaly-related anomalies) in the plausibility matched items by conducting three 4-way ANOVAs with two levels of hemisphere, two levels of laterality, four levels of anteriority, and two levels of condition between 300 and 500 ms. The difference between the unrelated and event-related N400s interacted with laterality $F(1,29) = 4.2$, $p < .05$, whereas the difference between the unrelated and perceptuomotor-related N400s interacted both with laterality, $F(1,29) = 4.3$, $p < .05$, and anteriority, $F(3,87) = 7.4$, $p < .01$. However, a direct comparison of the perceptuomotor-related and event-related conditions did not reveal any significant interactions between condition and distributional factors, suggesting that the observed distributional differences between related anomalies in the previous analyses may have been due in part to differences in plausibility.

General discussion

We found evidence that perceptuomotor and event-related knowledge are activated immediately during online language processing. We have ruled out the possibility that plausibility could entirely account for these findings. The event-related N400 effect extends the original report of Metusalem et al. (2012), who did not address the role of plausibility directly and presented additional contextual information before the critical sentence (two sentences versus our one sentence). Therefore our result shows that event-related facilitation is not a reflection of more plausible scenarios *per se*, and that relatively sparse event information (a single sentence) is sufficient. Generalized event knowledge appears to be available to facilitate language processing even when the immediate linguistic input conflicts with the message-level context, and thus may benefit comprehenders to understand discourse beyond the words actually presented (Kukona, Fang, Aicher, Chen, & Magnuson, 2011; Metusalem et al., 2012).

Alternate explanations of the perceptuomotor-related effect

The main novel contribution of our study is the perceptuomotor-related facilitation effect. We ruled out a plausibility confound, but evidence for perceptuomotor-related knowledge activation hinges on the likelihood of two additional alternate explanations. One is the possibility that the N400 reduction could be driven entirely by a subset of stimuli in which the local context led participants to expect the perceptuomotor-related continuation rather than the best continuation. In 35 out of the 136 original experimental passages at least one participant in the immediate context sentence cloze norming task provided the perceptuomotor-related continuation (rather than the best completion as determined by cloze norming on the full passages). We re-analyzed the N400 reduction in the perceptuomotor-related condition using only those 101

¹ Mean trial counts (across subjects) were very similar for re-computed anomaly conditions (perceptuomotor-related = 16.5 trials; event-related = 15.7 trials; unrelated = 16.7 trials).

Table 3

Characteristics of the plausibility-matched anomaly conditions. Entries are means and standard deviations.

Condition	Cloze	Cloze (SVP)	S1-to-target (LSA)	S2-to-target (LSA)	Target Length	Target Frequency	Target Ortho. N	Rated plausibility
Perceptuomotor-related	.0003	.03 (.86)	.13 (.06)	.16 (.07)	5.7 (1.8)	26.5 (93.5)	5.0 (5.6)	2.3 (0.5)
Event-related	.0010	<.0001	.17 (.06)	.17 (.07)	6.0 (1.6)	26.6 (82.8)	5.2 (5.9)	2.2 (1.0)
Unrelated	<.0001	<.0001	.16 (.06)	.18 (.07)	5.9 (2.1)	25.0 (35.4)	5.7 (6.3)	2.2 (0.7)

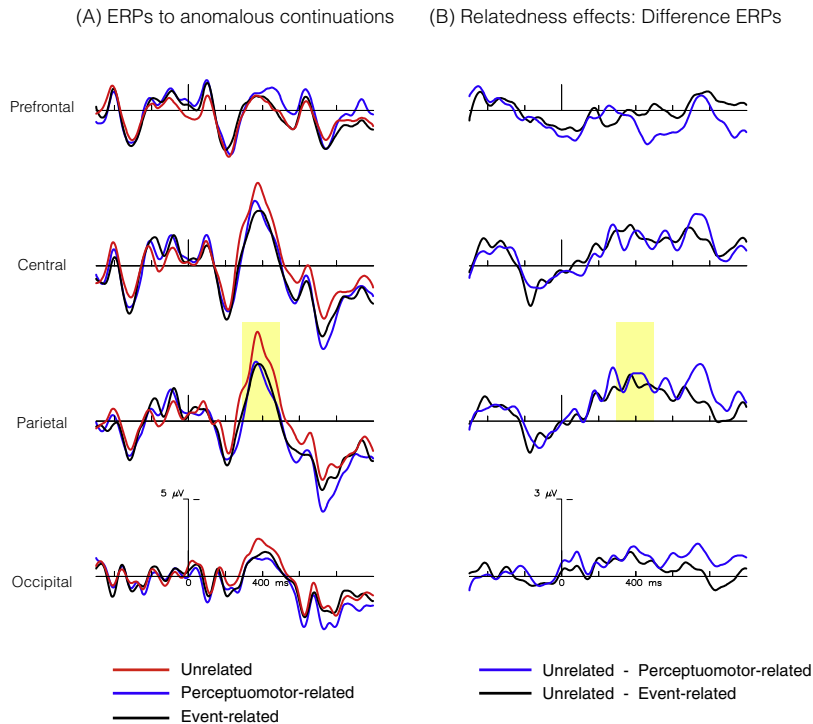


Fig. 4. ERPs for plausibility-matched anomalies. (A) Grand averaged ERPs at four midline (anterior to posterior) sites show the reduced N400s for the event-related and perceptuomotor-related conditions in comparison with the unrelated condition. (B) Grand averaged difference ERPs at the same four sites show the N400 facilitation effects. The 300–500 ms time window employed in statistical analyses is shaded in both panels.

sentences in which no participants provided the perceptuomotor-related continuation in response to the SVP sentence stem. We averaged ERP amplitudes between 300 and 500 ms at the same four canonical N400 sites and found that the N400 remained significantly smaller in the perceptuomotor-related condition ($M = -2.5$, $SD = 3.6$) versus the unrelated condition ($M = -3.9$, $SD = 3.2$), $t(29) = 4.0$, $p < .001$.

Another alternate explanation of the perceptuomotor-related effect is that it reflects category structure rather than perceptuomotor knowledge activation *per se*. Given that 55 of the 136 perceptuomotor related continuations are category co-ordinates of the expected targets (almost entirely between co-category and not within-category coordinates), the N400 reduction could potentially be due to category-related facilitation (Federmeier & Kutas, 1999) for these items only. We compared the average N400 amplitudes elicited by unrelated continuations, categorically related perceptuomotor-related continuations, and non-

categorically related continuations between 300 and 500 ms averaged across the same four canonical N400 sites. We found a significant three-way split whereby categorically related perceptuomotor-related continuations ($M = -1.5$, $SD = 4.1$) were less negative than non-categorically related perceptuomotor-related continuations ($M = -2.6$, $SD = 3.9$), $t(29) = 2.3$, $p = .03$, which in turn were less negative than unrelated continuations ($M = -3.9$, $SD = 3.2$), $t(29) = 3.2$, $p = .003$. This result suggests that the N400 is sensitive to overlapping sensory or motor object knowledge in addition to other types of semantic feature overlap shared among category members. Another possibility is that semantic memory is organized primarily by object category and then by modality (Mahon & Caramazza, 2008, 2009), in which case this result would be consistent with the independent effects of both constraints on real time language processing.

Finally, to ensure that none of the aforementioned potential confounds could account for the

perceptuomotor-related N400 reduction, we recomputed mean N400 amplitude using only those sentences from the 77 plausibility matched items in which (1) no participants provided the perceptuomotor-related continuation in response to the SVP sentence stem, (2) anomalies were not category coordinates of the expected targets, and (3) additional relevant variables were matched as closely as possible with those of the unrelated anomalies. In comparison with the plausibility matched unexpected continuations ($N = 77$) this subset of perceptuomotor-related continuations ($N = 44$) had slightly fewer letters (5.7 vs. 5.9) and orthographic neighbors (5.3 vs. 5.7), was substantially less frequent (15.5 vs. 25.0), and had lower LSA context-to-target relatedness (.16 vs. .18). Plausibility remained matched between item sets (2.2 vs. 2.2). Other than the slight difference in orthographic neighborhood, all of the other discrepancies would be expected to work against a reduced N400 for perceptuomotor-related versus unrelated anomalies. We compared the average N400 amplitudes elicited by these subsets, finding that the perceptuomotor-related condition ($M = -2.3$, $SD = 4.7$) remained less negative than the unrelated condition ($M = -3.7$, $SD = 3.4$), $t(29) = 2.4$, $p = .02$. In sum, in all of the analyses presented thus far the perceptuomotor-related condition elicited significantly smaller N400 amplitudes than the unrelated condition. Having ruled out several potential alternate explanations, we now discuss the implications of this result in more detail.

Perceptuomotor-related knowledge activation facilitates language processing

Results of previous related anomaly studies (e.g., Federmeier & Kutas, 1999; Kutas, 1993; Kutas & Hillyard, 1984) have been used to argue for expectancy-based accounts of language processing, whereby the sentence context is used to activate semantic information that can facilitate processing of the upcoming word. Federmeier and Kutas (1999) showed that this information could include shared attributes of basic level category members (e.g., the shared attributes of palm and pine trees). Kellenbach et al. (2000) provided ERP evidence for object shape knowledge activation during lexical decision, and Rommers, Meyer, Praamstra, et al. (2013) implicated object shape knowledge during auditory sentence comprehension (although the particularly late onset of their ERP effect complicates their prediction-based interpretation). Chwilla et al. (2007) did not interpret their results with respect to preactivated knowledge, but this interpretation is available. They found that the N400 was reduced to unexpected words in sentences describing affordable versus non-affordable actions (e.g., “They let the canoe into the water and paddled with Frisbees/sweaters”). Much like our subset of motor-related targets, their novel affordable action words (“Frisbee”) shared particular action affordance features with the expected words, and their sentence contexts directed the reader’s attention to that feature. Along these lines of reasoning, one interpretation of our finding is that comprehenders can spontaneously use sentence

context to preactivate knowledge about how they see, hear, taste, smell, touch, or grasp a particular object, which in turn can facilitate processing of unexpected words that refer to objects with which they have similar knowledge. Alternatively, our results (and presumably some of the above results) could reflect differences in the rapid integration of unexpected words that share certain perceptuomotor features with activated contextual information, versus unexpected words that do not. Whether our result reflects preactivation, integration, or some combination of both (e.g., Hagoort & Indefrey, 2014), an important and unanswered question remains: what is the nature of this activated perceptuomotor knowledge?

The semantic feature overlap hypothesis invoked in some earlier studies is often described using examples of verbalizable properties (e.g., “silver”, “made of steel”, “used for chopping”). However much of our object knowledge is unlikely to be verbalizable, and this is especially apparent for knowledge about non-visual properties. Consider a passage in our study that had 100% agreement on the best continuation (“David always dreaded meeting his calculus tutor, who never seemed to brush his teeth. David could barely handle the revolting smell of his breath/armpit”). The contextual information (“... never seemed to brush his teeth”) sets up a specific and reliable (at least in our cloze participants) expectation for “breath”, the perceptual experience of which is very different from that of armpits—just as the sounds of screaming and nails on a chalkboard are very different. That our perceptuomotor-related facilitation effect occurs despite these experiential differences suggests that the activated knowledge driving the effect does not consist solely of such specific perceptual information. More generally, catching a whiff either of bad breath or body odor can be revolting, and thus the knowledge of olfactory revulsion contained in each object concept could serve as a shared feature in feature-based models of semantic memory. Our N400 facilitation effect could reflect shared features at this level of specificity, or even more general conceptual overlap like whether or not *any* information about a specific modality is salient in the representation. It remains to be seen to what extent more specific experiential knowledge is accessed and used immediately during language comprehension.

Of course, the specificity of activated perceptuomotor knowledge may depend on the particular kind of knowledge. The perceptuomotor-related condition in the present study consisted of several different (usually modality-specific) knowledge types, enabling broad coverage at the expense of focusing on particular knowledge types. Although we had insufficient numbers of stimuli for systematic comparisons, visual inspection of our data broken down by modality (color, sound, taste, etc.) suggests differences in the timing and magnitude of the effects—both in the N400 time window and otherwise. Previous single word or word pair experiments also have hinted at different spatiotemporal patterns of activation for different kinds of knowledge following word onset (Amsel, 2011; Amsel, Urbach, & Kutas, 2013; Hoenig, Sim, Bochev,

Herrnberger, & Kiefer, 2008; Trumpp, Traub, Pulvermüller, & Kiefer, 2014). A systematic comparison of the magnitude and timing of perceptual, motor-related, affective, situational, and more abstract knowledge activation during more natural language processing will be important and awaits future study.

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A. Appendix

Example passages from each modality.

Modality	Sentence 1	Sentence 2	Continuation (Expected / Perceptuomotor-related / Event-related / Unrelated)
Color / brightness	Nathan loved watching the monkeys at the zoo, and if he was lucky the zookeeper allowed him to feed them	Today was his lucky day as he was given several bright yellow ... when he arrived	bananas / yolks / gorillas / dancers
Visual motion	At the archery competition I aimed and then released my bow	The spectators could only see the blur of my ... from their seats	arrow / rocket / target / texts
Sound	The counselor strummed along as we sang songs around the nightly campfire	Everyone loved the sound of his ... and his voice	guitar / clarinet / sparks / sauce
Smell	My date was taking me to a romantic Italian restaurant for dinner tonight	I was worried that afterward I might reek of ... so I brought gum	garlic / tobacco / napkins / ice
Taste	Jamie's eyes watered as she chopped the vegetables for the burgers	She knew they would taste great topped with ... and mushrooms	onions / icing / kitchen / thread
Action affordance	During the African safari, Javier thought he spotted a giraffe off in the distance	He quickly reached for his pair of ... in the back	binoculars / slippers / zebras / bubbles
Haptic / Pain	The bank robber waved his handgun and yelled for everybody to get down, but Tim stood his ground	Tim yelled in pain when his shoulder was struck with a ... and started to bleed	bullet / club / mask / fish

Finally, our finding that perceptuomotor and event knowledge are available in a common time window, and influence a common neural process, may reflect how we acquire knowledge in general. When interacting with (or simply observing) our environment, we do not often acquire knowledge about the perceivable properties of objects independently from knowledge about the situations in which they occur. The scent of sautéed garlic is not experienced haphazardly, but dependably in restaurants and kitchens. It appears that we can immediately draw upon all of this knowledge when we construct inner worlds with words, and perhaps use this knowledge to guide our expectations about words (and worlds) yet to appear.

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