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fMRI evidence for word association and situated simulation in conceptual processing

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ABSTRACT

The LASS theory proposes that Language and Situated Simulation both play central roles in conceptual processing. Depending on stimuli and task conditions, different mixtures of language and simulation occur. When a word is processed in a conceptual task, it first activates other linguistic forms, such as word associates. More slowly, the word activates a situated simulation to represent its meaning in neural systems for perception, action, and mental states. An fMRI experiment tested the LASS account. In a first scanning session, participants performed the property generation task to provide a measure of conceptual processing. In a second scanning session a week later, participants performed two localizer tasks measuring word association and situated simulation. Conjunction analyses supported predictions of the LASS theory. Activations early in conceptual processing overlapped with activations for word association. Activations late in conceptual processing overlapped with activations for situation generation. These results, along with others in the literature, indicate that conceptual processing uses multiple representations, not one. Furthermore, researchers must be careful drawing conclusions about conceptual processing, given that different paradigms are likely to produce different mixtures of language and simulation. Whereas some paradigms produce high levels of linguistic processing and low levels of simulation, other paradigms produce the opposite pattern.

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1. Introduction

Theories of cognition often assume that one type of representation underlies knowledge. Traditionally, most theories assume that amodal symbols represent knowledge in memory (e.g., Collins and Loftus, 1975; Fodor, 1975; Newell and Simon, 1972; Pylyshyn, 1984). More recently, theories have adopted statistical representations (e.g., McClelland et al., 1986; Rumelhart et al., 1986; Rogers and McClelland, 2004). Most recently, theories have proposed that knowledge is grounded in modal simulations (e.g., Allport, 1985; Barsalou, 1999, 2008; Damasio, 1989; Glenberg, 1997; Martin, 2001, 2007; Pulvermüller, 1999; Thompson-Schill, 2003), while other theories have proposed that knowledge is grounded in linguistic context-vectors (e.g., Burgess and Lund, 1997; Landauer and Dumais, 1997).

In this article, we provide functional Magnetic Resonance Imaging (fMRI) evidence that multiple systems—not one—represent knowledge. We focus on two types of representation that have

strong empirical support: linguistic representations in the brain's language systems, and situated simulations in the brain's modal systems. Although we focus on these two types of representation, we do not exclude the possibility that other types are important as well. In particular, we believe that statistical representations play central roles throughout the brain, and that they underlie linguistic and modal representations. At this point, we are somewhat skeptical that completely amodal representations exist in the brain, for both theoretical and empirical reasons (Barsalou, 1999, 2008; Simmons and Barsalou, 2003), but we are open to compelling arguments otherwise.

1.1. The LASS theory

Increasing empirical evidence suggests that conceptual processing relies heavily on both Language And Situated Simulation (LASS). The following two sub-sections present the linguistic and simulation components of the LASS theory in turn (For further detail, see Barsalou et al. in press).

1.1.1. Linguistic processing

When a word is perceived, the linguistic system becomes engaged immediately to categorize the linguistic form (which could

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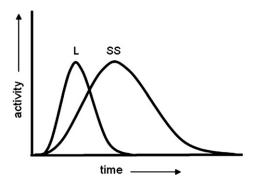


Fig. 1. Hypothesized contributions from the language system (L) and the situated simulation system (SS) during conceptual processing according to the LASS theory. When a word is presented as a cue, word form contributions from the language system precede those from the simulation system. The height, width, shape, and offset of the two distributions are assumed to vary. In response to different words, all these parameters are likely to change (e.g., SS activity could be more intense than L activity). The two distributions in this figure illustrate one of infinitely many different forms that activations of the L and SS systems could take.

be auditory, visual, tactile, etc.). As Fig. 1 illustrates, we assume that the linguistic system and the simulation system both become active initially, but that activation in the linguistic system peaks first. Based on the content addressability and encoding specificity principles, the information in memory most similar to the cue is the first information to become active (e.g., Tulving and Thomson, 1973). Because representations of linguistic forms are more similar to presented words than are simulations of their referents, representations of linguistic forms peak earlier.

Once a word is recognized, associated linguistic forms are generated as inferences, and as pointers to associated conceptual information. In the experiments described shortly, the generation of linguistic forms is realized as the simple process of word association, where a cue word elicits other words associated with it (e.g., "bird" elicits "house", "robin," and "nest"). It is essential to note that word association is the simplest possible form of the linguistic processing that could occur during conceptual processing. Much more complex processing occurs, as phrases and syntactic structures become active. We do not address these more complex forms of linguistic processing here, but assume that they can be central to conceptual processing.

Once associated linguistic forms are generated, they support a variety of superficial strategies (e.g., Glaser, 1992). As described later, much work shows that associations between words can be sufficient to produce correct responses on conceptual tasks—the activation of conceptual information is not necessary (e.g., Barsalou et al., in press; Glaser, 1992; Kan et al., 2003; Solomon and Barsalou, 2004). Consistent with linguistic context theory (e.g., Burgess and Lund, 1997; Landauer and Dumais, 1997), samples of associated words become active that provide linguistic context for the presented word. Once linguistic context becomes active, it supports many tasks and implements many basic effects.¹

These linguistic strategies appear to be relatively superficial (Glaser, 1992). Rather than providing deep conceptual information, these strategies are shallow heuristics that make correct performance possible with minimal processing effort. When linguistic forms and associated statistical information are sufficient for adequate performance, no retrieval of conceptual information is nec-

essary. This does not mean that these strategies are insignificant, given their obvious heuristic value (cf. Gigerenzer, 2000). Nevertheless, attributing conceptual depth to these heuristics mischaracterizes them and obscures other important mechanisms that provide deeper conceptual processing.

Much research on lexical processing is consistent with this proposal. In the lexical decision task, activation of a word's meaning is shallow when it is read in the context of non-words that violate rules of phonology and orthography. In this context, discriminating words from non-words can be based on linguistic form alone, such that meaning need not be accessed. Conversely, when non-words satisfy phonological and orthographic rules, words must access meaning deeply. In this context, linguistic forms no longer discriminate words from non-words, such that meaning must be retrieved to verify that a stimulus is a word (e.g., James, 1975; Joordens and Becker, 1997; Shulman and Davidson, 1977; Stone and Van Orden, 1993; Yap et al., 2006). Similarly, the large literature on depth of processing shows that phonemic orienting tasks produce shallower activation of meaning than semantic orienting tasks (e.g., Craik, 2002; Craik and Lockhart, 1972; Craik and Tulving, 1975; Lockhart, 2002; Morris et al., 1977). Broadly speaking, many findings support the proposal that linguistic forms can be processed superficially.

1.1.2. Situated simulation

After the linguistic system begins to recognize the presented word, the word's representation begins to activate associated simulations in the brain's modal systems. As associated linguistic forms become active, they too, may begin to activate simulations that contribute to the word's meaning. By "simulation" we mean that the brain simulates the perceptual, motor, and mental states active during actual interactions with the word's referents (e.g., Allport, 1985; Barsalou, 1999, 2008; Damasio, 1989; Glenberg, 1997; Martin, 2001, 2007; Pulvermüller, 1999; Thompson-Schill, 2003). If, for example, the word is "cat," then simulations reenact neural states that represent how cats look, sound, and feel, how one interacts with cats, and how one feels emotionally around them.

We further assume that these simulations tend to be situated, preparing agents for situated action (e.g., Barsalou, 2003b, 2005b, in press-b; Barsalou et al., 2003; Yeh and Barsalou, 2006). Rather than representing the meaning of a word generically, simulations tend to represent them in a situated manner. According to this view, simulations of "cat" do not typically represent cats generically, but instead represent specific cats in particular situations, where a situation is a setting that contains agents, objects, actions, events, and mental states. We further assume that these simulations are often activated automatically and quickly (e.g., within 200 ms of word onset; Pulvermüller et al., 2005).

Finally, we assume that simulations represent deep conceptual information, unlike linguistic representations, which we view as more superficial. We similarly assume that basic symbolic processes such as predication, conceptual combination, and recursion result from operations on simulations. Barsalou (1999, 2003a, 2005a, in press-a) describes how simulation mechanisms can implement symbolic operations. We further assume that linguistic mechanisms are not capable of implementing these operations on their own, given that they simply manipulate linguistic forms, not their meanings. Nevertheless, linguistic mechanisms play important roles in controlling the simulation system during symbolic operations (Barsalou, in press-a; Barsalou et al., in press).

1.1.3. Mixtures of language and situated simulation

Different mixtures of the language and simulation systems appear to underlie a wide variety of tasks. When superficial linguistic processing is sufficient to support adequate task performance, processing relies mostly on the linguistic system and little on

¹ It is important to note, however, that it is not always clear whether linguistic contexts cause these effects or are merely correlated with them. Because linguistic contexts are correlated with conceptual information, such as the information contained in situated simulations, apparent effects of linguistic context could actually be due to correlated conceptual information. More work is needed to resolve this issue. A likely possibility is that both factors contribute to conceptual processing effects.

simulation (Glaser, 1992; Kan et al., 2003; Solomon and Barsalou, 2004). Conversely, when linguistic processing cannot support adequate performance, the simulation system provides the required conceptual information. Depending on task conditions, conceptual processing may mostly depend on linguistic processing or simulation. Under many conditions, both may contribute significantly. When mixtures of the two systems occur, we do not assume that they operate independently. As linguistic forms become active initially, they activate simulations. Once a simulation becomes active, words that refer to its space–time regions and the objects within them become active.

In general, we assume that language provides a powerful system for indexing simulations, and for manipulating simulations in language and thought (Barsalou, 1999, 2003a, 2005a, in pressa). As the two systems interact, one may dominate momentarily, followed by the other, perhaps cycling many times, with both systems being active simultaneously at many points.

1.1.4. Caveats

Our accounts of the "linguistic system" and the "simulation system" so far include simplifications that must be qualified. First, we do not assume that these systems are modular, given that each is highly complex and draws on many processes distributed throughout the brain. Additionally, many of these latter processes probably contribute to other systems besides language and simulation (e.g., vision and motor processes contribute to perception and action, respectively).

Second, we do not assume that each system takes the same rigid form across situations. Instead, we assume that each system is dynamical, drawing on different configurations of processes in different situations (Barsalou et al., in press). We also do not assume that only one form of simulation occurs in the brain. Instead, we believe that the brain implements diverse forms of simulation across different cognitive processes (Barsalou, 2008).

Third, when referring to the "linguistic system" in this article, we mean the system that processes linguistic forms, not the system that represents linguistic meaning. As described earlier, we assume that meaning is primarily represented in the simulation system. In other theoretical contexts, the "linguistic system" would obviously include the representation of meaning. Because we contrast linguistic forms and linguistic meaning in this article, we use the "linguistic system" for the former and the "simulation system" for the latter. For example, we assume that the linguistic system represents the linguistic form "apple," whereas the visual, somatosensory, motor, auditory, smell, taste, and affective modalities produce situated simulations to represent its meaning.

Thus, "linguistic system" and "simulation system" are simplifications that allow us to focus on mechanisms of interest, in particular, linguistic forms vs. situated simulations. Again, this usage should not be taken as a commitment to rigid modular systems, nor to mean that the linguistic system is unrelated to the simulation system.

1.2. Evidence for the LASS theory

Longstanding evidence supports mixtures of language and simulation in conceptual processing (for a review, see Barsalou et al., in press). Over the past 40 years, Paivio's (1971, 1986) Dual Code Theory has generated an impressive body of empirical support for the presence of linguistic and perceptual representations across many areas of cognition. As Paivio (1986) reviews in detail, evidence for two systems has accumulated in developmental psychology, where modal systems develop earlier than the linguistic system. Evidence for two systems has accrued in the individual differences literature, with different individuals relying more on one system than the other. Evidence for two systems has accrued in

the literatures that address episodic memory, semantic memory, and language comprehension. Because of the substantial empirical support that Dual Code Theory has accumulated, LASS' central assumption that cognition relies on the constant interplay between a linguistic system and a simulation system appears on solid ground.

Glaser (1992) modified Dual Code Theory in various ways, most notably proposing that the linguistic system can perform relatively superficial processing independently of the conceptual system—what he called the Lexical Hypothesis. In support of the Lexical Hypothesis, Glaser cited extensive evidence from priming and interference tasks, with both words and pictures, showing that subjects bypass the conceptual system when superficial linguistic information is adequate for producing correct responses. Additionally, Glaser concluded that words access the linguistic system first, prior to accessing conceptual information. Glaser's revision of Dual Code Theory with the Lexical Hypothesis yields an account that is nearly identical to the LASS Theory (see Barsalou et al., in press, for further details).

Solomon and Barsalou (2004) provided evidence for the LASS theory in the property verification paradigm. On each trial, participants received an object concept (e.g., *CAT*), followed by a property (e.g., *fur*), and indicated whether the property was true or false of the object. Two different groups of participants received the same 100 true trials (e.g., *CAT-fur*). The groups differed, however, in the types of false trials received. For one group, the 100 false trials contained objects and properties that were completely unassociated, as determined by prior scaling (e.g., *CHERRY-card*, *BRIEFCASE-wick*). For the other group, the 100 false trials were the same objects and properties re-paired such that each pair was highly associated (e.g., *BANANA-monkey*, *OTTER-river*).²

This false trial manipulation modulated participants' strategy for verifying properties on true trials. When the false trial materials were unassociated, participants used the linguistic system to verify properties, as indicated by both reaction times and regression analyses. Essentially, participants assessed whether the object and property words on a trial were associated—information contained in the linguistic system. If these words were associated, participants could respond true because concept and property words were always associated on true trials. If, however, these words were unassociated, participants could respond false, because concept and property words were always unassociated on false trials. Because associativeness covaried with response, participants could use associativeness information in the linguistic system to respond correctly.

Conversely, when the object and property words on false trials were associated, participants could not use the presence of an association between words as a cue for responding, because the object and property words were always associated on both true and false trials. Instead, participants had to access information about the conceptual relations between objects and properties. As shown by regression analyses, this conceptual information was obtained from simulations, given that perceptual variables, such as property size, were the best predictors of reaction times and errors.

Using fMRI, Kan et al. (2003) replicated the Solomon and Barsalou experiment, observing activation in the visual system for the associated false condition but not for the unassociated false condition. As in the behavioral study, the associated false trials blocked the use of linguistic information and forced the use of simulation to verify properties.

Santos et al. (in preparation) explored predictions of the LASS theory in the property generation paradigm. On each trial, partici-

² These related pairs are false because the property had to be a part of the object, not merely associated with it.

pants received the word for a concept (the cue) and generated properties verbally (responses). In Experiment 1, participants were asked to generate word associates to each cue. In Experiment 2, participants were asked to generate properties typically true of a concept's instances. In both experiments, LASS predicted that the linguistic system and the simulation system should both contribute to the responses that participants produce. Initially, responses should come from the linguistic system, with responses later coming increasingly from the simulation system. The results of both experiments confirmed these hypotheses.

Specifically, the responses most likely to be generated early were linguistically related to the cue. Linguistically related responses included words from lexicalized compound expressions (e.g., "bee" \rightarrow "hive"). Linguistically related responses also included words that were phonologically related to the cue (e.g., "self" \rightarrow "selfish"), morphologically related (e.g., "bumpy" \rightarrow "lumpy"), and other classic forms of linguistic relation such as synonyms and antonyms. Based on theories of the lexicon, it is likely that all of these relations would be stored in the lexical system.

Conversely, the responses most likely to be generated later described aspects of situations, such as setting information (e.g., "bee" \rightarrow "flowers", "golf" \rightarrow "sunshine"), mental states (e.g., "golf" \rightarrow "boring"), and physical properties of objects (e.g., "bee" \rightarrow "wings"). All of these responses describe things that could occur in a situated simulation of a cue word's meaning (e.g., simulating a bee in a garden). Across both experiments, these types of responses tended to occur later than linguistically-related responses, consistent with the LASS theory.

Barsalou et al. (in press) review additional findings that support the LASS theory not described here. Together all of this evidence is consistent with the view that conceptual processing reflects both language and simulation, with linguistic information tending to become available first.

1.3. Overview and predictions

The experiment reported here used fMRI to test a priori predictions of the LASS theory. Each participant performed two scanning sessions one week apart. In the first scanning session, participants performed the property generation task, which was the task of primary interest. Property generation—also known as feature listing is used widely as a means of assessing conceptual representations (e.g., Hampton, 1979; Rosch and Mervis, 1975). Researchers have assumed that the properties generated for a concept reflect its underlying conceptual content, typically represented as amodal symbols. Based on the LASS theory, however, we predicted that the properties generated first for a concept would tend to come from the linguistic system, and then to come increasingly from situated simulation. More specifically, the results of Santos et al. (in preparation) suggest that the first properties produced should often be word associates. As a simulation becomes active to represent the cue word's meaning, however, later properties should reflect content of the simulation. Specifically, participants should scan across the simulation and describe space-time regions that contain agents, objects, settings, actions, events, mental states, etc.

In each run of the property generation task, participants generated properties for concepts in a blocked design. At the start of each trial within a block, the word for a concept was presented, and the participant generated typical properties as they came to mind for 15 s. This duration was based on the results of Santos et al.'s (in preparation) Experiment 2, where participants typically produced properties fluently for about 15 s. Participants did not verbalize the properties out loud but generated them implicitly

to themselves. At the end of each run, participants recalled out loud the properties that they had generated.

In the second scanning session a week later, participants performed two localizer tasks in a blocked design: a word association localizer to identify brain areas underlying word association, and a situation generation task to identify brain areas underlying situated simulation. On each word association trial, participants received a cue and produced word associates to themselves for 5 s. This duration was based on the results of Santos et al.'s (in preparation) Experiment 1, where participants typically produced word associates fluently for about 5 s. On each situation generation trial, participants imagined a situation that contained a referent of the cue word and described it to themselves for 15 s. This duration was based on the results of Chaigneau and Barsalou (in preparation), where participants typically described a situation fluently for about 15 s. Because trial duration could not be the same for word association (5 s), situation generation (15 s), and property verification (15 s), care was taken to control blocks across tasks, making them the same in all other respects (see Section 2). Again, participants recalled their responses out loud after the localizer run.

Based on the LASS theory, we predicted that the word association localizer would activate left-hemisphere language areas, especially left inferior frontal gyrus (Broca's area). Conversely, we predicted that the situated simulation task would activate bilateral posterior areas associated with mental imagery and episodic memory. Of primary interest was the relation of localizer activations to activations during the critical task, property generation. According to the LASS theory, regions activated in the word association localizer should become active early during property generation, whereas regions activated in the situation localizer should become active late in property generation.

To test this hypothesis, we divided each 15 s trial for property generation into two 7.5 s blocks, thereby creating an early property generation period and a late property generation period. Using conjunction analyses, we then assessed whether activations from the word association localizer occurred primarily during early property generation, and whether activations from the situation localizer occurred primarily during late property generation, as the LASS theory predicts.

Fig. 2 illustrates these predictions along with predictions from alternative accounts. As Panel A illustrates, the LASS theory assumes that both linguistic processing and simulation begin immediately. However, linguistic processing peaks during the first half of the generation period, whereas simulation processing peaks in the second half. Specifically, the LASS theory assumes that the executive system focuses initially on information in the linguistic system, because linguistic information is available initially (due to encoding specificity) and because implicit verbal responses are requested. As the availability of responses from the linguistic system decreases, the executive system turns to the simulation system as an alternative source of responses. Over time, the linguistic system is more active during the first half of the generation period, whereas the simulation system is more active during the second half. Because the executive system extends the activity of each system over many seconds, using it as a source of responses, differences in the processing activity during each half are large enough for fMRI to detect (given fMRI's relatively low temporal resolution).

Panel B of Fig. 2 illustrates the predictions for the alternative account that the linguistic and simulation systems operate fully in parallel from the onset of the cue word, with properties generated from both systems at equal rates. If this account is correct, then linguistic processing should not be more active in the first 7.5 s generation period than in the second 7.5 s period; analogously, simulation activity should also not differ between the two periods. The predictions in Panel B also hold for an additional account that only a single system generates properties. If so, then early vs. late

 $^{^3}$ $X \rightarrow Y$ means that Y was a response produced in response to cue X.

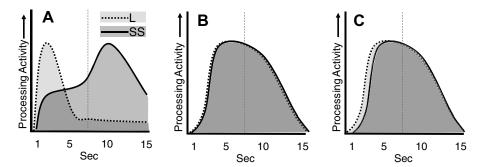


Fig. 2. Different predictions for contributions from the linguistic system (L) and the situated simulation system (SS) during the 15 s property generation trials. *Panel A.* Predictions for the account that the executive system primarily produces responses from the L system for the first 7.5 s and then produces responses from the SS system for the second 7.5 s period. *Panel B.* Predictions for the account that the L and SS systems operate fully in parallel (and also for the account that only a single system produces properties). *Panel C.* Predictions for the account that contributions from the L system only precede contributions from the SS system only for a second or two. The height, width, shape, and offset of the two distributions are assumed to vary. In response to different word cues in different task contexts, all parameters are expected to change (e.g., SS activity could be more intense than L activity). The two distributions in each panel illustrate one of infinitely many different forms that activations of the L and SS systems could take.

processing should not be differentially associated with neural activity that reflects language vs. simulation.

Finally, Panel C of Fig. 2 illustrates the predictions for the alternative account that the linguistic system produces more properties for the first second or two, but that both systems produce properties at equal rates thereafter. If this account is correct, then again linguistic processing should not be greater in the first 7.5 s period than in the second. Although simulation does not start as early as in Panel B, the difference in simulation activity across the two halves should not differ noticeably (given the low temporal resolution of fMRI). If a significant simulation difference does occur, this account still predicts no difference for linguistic processing across the two halves.

2. Methods

2.1. Participants and design

Ten right-handed, native English-speaking volunteers from the Emory University community participated in the scanning study (five females and five males; ages ranging from 18 to 45 years). Prior to scanning, all participants completed a health questionnaire. None of the participants indicated a history of neurological problems or conditions contraindicated for participation in magnetic resonance imaging. In accordance with protocols prescribed by Emory University's Institutional Review Board, all participants read and signed an informed consent document describing the procedures and possible risks.

Participants were scanned on two occasions one week apart (plus or minus a day or so). In the first session, participants performed the property generation task. In the second session, participants performed the word association and situation generation tasks. Each participant provided one replication of a complete within-subjects design. Versions of the experiment materials were counter-balanced between participants so that each cue word occurred in every task but only occurred once for each participant.

2.2. Materials

The same 60 cue words used in Santos et al. (in preparation, Experiment 2) were used here. These cues represented diverse concepts, including common objects (e.g., car, bee), events (e.g., calculate, throw), mental states (e.g., guilty, guess), abstract concepts (e.g., self, extension), properties (e.g., green, sweet), and brand names (e.g., Tylenol, Microsoft). Because these cues were drawn from diverse word groups, it is unlikely that any observed activations reflect common semantics in a specific domain. Instead, these activations are likely to reflect forms of general processing common across concepts, such as word association mechanisms and simulation mechanisms.⁴

The 60 cue words were divided quasi-randomly into two groups of 30 words balanced for stimulus factors. The five subjects assigned to Version 1 of the materials received one 30-word group for property generation in the first scanning session, and received the second 30-word group for word association and situation generation in the second scanning session. The other five subjects who received Version 2 had the opposite assignment of word groups to sessions. In the second session, different lists for each 30-word group were constructed so that every word occurred in both the word association and situation generation tasks.

2.3. Procedure

2.3.1. Pre-scan practice and instruction

Immediately prior to the first scanning session, participants practiced performing the property generation task out loud, so that they would have a good sense of how to perform it in the scanner. On each practice trial, participants received a cue word (not used in the main experiment) and generated properties according to the instruction, "What characteristics are typically true of X?" where X was the cue word. Participants were carefully instructed that there were no correct answers, and that they should produce whatever characteristics came to mind, as they came to mind.

At the end of the practice session, participants also received instructions about what to expect in the scanner. In particular, they were told that they would not be allowed to speak out loud but should try to perform the task similarly by generating properties to themselves implicitly. Participants were reminded that they would perform a second scanning session the following week, but were not told about the word association and situation generation tasks. Instead, they were simply told that the task would be different.

2.3.2. Property generation scan

During the first scanning session, subjects first performed one practice run, followed by five critical runs. Every run contained three property generation blocks lasting 30 s each. As Fig. 3 illustrates, every property generation block contained two trials lasting 15 s. Across runs, every participant generated properties for 30 of the 60 cue concepts used in the experiment (6 concepts in each of five critical runs). Every run also included three lexical decision blocks mixed in with the property generation blocks, along with rest periods. The lexical decision blocks were included as fillers and are not considered further. Overall, each run lasted 4 min and 45 s.

"Properties?" appeared for 5 s at the start of each property generation block indicating that a pair of property generation trials was about to begin. The first concept word was then presented. During the subsequent 15 s period, the participant silently generated properties according to the instructions practiced earlier, "What characteristics are typically true of X?" After 15 s, a second concept word appeared, for which participants also generated properties silently. Participants were directed to continue generating properties for each entire 15 s period.

Following each scanning run, participants received the six cue words from the property generation trials that they had just completed and recalled their proper-

⁴ Based on the results of Santos et al., the 60 cue words were grouped into three levels based on whether a cue produced a high, medium, or low number of linguistic responses (e.g., responses that reflected a compound continuation, shared morphological root, a phonological similarity, a etc.). The different versions of the 60 cue words presented to different participants were carefully controlled so that equal numbers of cues from each level occurred in all three tasks for each participant.

⁵ During each 30 s lexical decision block, participants received letter strings and indicated whether each was a word or not. Prior to each lexical decision block, "Lexical?" appeared for 5 s, indicating that a block was about to begin. Six letter strings were then presented individually for 5 s each, half words, and half non-words. None of the word strings were the same as the words for the cue concepts.

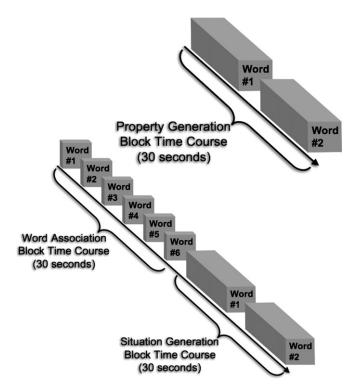


Fig. 3. Schematic representations for the three types of task blocks. In the first scanning session, subjects performed property generation task blocks, with each block containing two 15 s property generation trials. On each trial, subjects read a stimulus word and then silently generated characteristics that are typically true of the word's referent. In a second scanning session one week later, subjects performed two functional localizer tasks: word association and situation generation. In each word association block, subjects read six words presented for 5 s each and silently generated associated words that came to mind immediately. In each situation generation block, subjects read two words presented for 15 s each, imagined a situation that contained what the word means, and silently described the situation.

ties out loud. This procedure encouraged subjects to perform the property generation task during the previous scan.

2.3.3. Localizer scan

A week after the first scanning session (plus or minus a day or so), participants returned to perform the word association and situation generation tasks. Again, participants practiced the two tasks outside the scanner beforehand. During practice on each word association trial, participants received a cue word (not used in the main experiment) and generated responses out loud according to the instruction, "For the following word, what other words come to mind immediately?" During practice on each situation generation trial, participants received a cue word (not used in the main experiment) and generated responses out loud according to the instruction, "For the following word, imagine a situation that contains what the word means and then describe it?" Participants were again instructed that there were no correct answers, and that they should produce whatever responses came to mind, as they came to mind.

During the second scanning session, participants performed a single run that included four word association blocks and three situated generation blocks mixed together. Analogous to the first scanning session, each block lasted 30 s, with block order counterbalanced across participants. As Fig. 3 illustrates, each word association block contained six concepts presented for 5 s each, and each situation generation block contained two concepts presented for 15 s each. As in the first session, 30 s lexical decision blocks were mixed into the critical run as fillers but not analyzed further. Overall, the run in the second session lasted 7 min and 40 s.

The 30 cue words not used for a participant in the first scanning session were used in the second scanning session, with 24 assigned to the word association task, and 6 to the situation generation task. A short practice run of one word association, one situation generation, and one lexical decision block preceded the critical run, using different concepts from those in the critical run.

"Word Associates?" appeared for 5 s at the start of each word association block indicating that six word association trials were about to begin. A concept word was then presented. During the subsequent 5 s period, the participant silently generated word associates according to the instructions practiced earlier, "For the following word, what other words come to mind immediately?" After 5 s, another concept word appeared, for which participants also generated word associates silently. Participants continued this procedure until they had generated word associates for all six concept words in the block. Participants were directed to continue generating word associates for each entire 5 s period.

"Situation?" appeared for 5 s at the start of each situation generation block indicating that a pair of situation generation trials was about to begin. A concept word was then presented. During the subsequent 15 s period, the participant silently generated responses according to the instructions practiced earlier, "For the following word, imagine a situation that contains what the word means and then describe it?" After 15 s, a second concept word appeared, for which participants also generated properties silently. Participants were directed to continue describing a situation for each entire 15 s period.

2.3.4. Factors held constant across the three tasks

As described earlier, trial length differed between tasks, based on the results of previous research (15 s for property verification, 5 s for word association, and 15 s for situation generation). Trial length could not be set at 15 s for word association because participants use other strategies to generate responses after 5 s.

To minimize differences associated with trial length, all other aspects of the three tasks were made as comparable as possible. First, every word occurred in each task, such that the cues used to generate responses were held constant. Second, block length was also held constant across tasks, always 30 s. Third, visual presentation was made as comparable as possible across tasks. In the word association blocks, each word was on the screen for 4850 ms followed by a blank screen for 150 ms, for a total of 5 s. In the property generation and situation generation conditions, the word on each trial appeared on the screen for 4850 ms followed by a 150 ms blank screen. The same word then reappeared for 4850 ms followed by a blank screen for 150 ms two more times for a total of 15 s. As a result, one trial in the property generation and situation generation condition had the same visual characteristics as three trials in the word association condition.

2.4. Image acquisition and analysis

Word stimuli were back-projected onto a screen located at the head of the scanner and viewed through a mirror mounted on the head coil. Stimulus presentation and response collection were controlled using Presentation software (Version 0.70, www.neurobs.com).

A 3 T Siemens Trio scanner collected fMRI data in both imaging sessions. In the first session, five critical runs of 114 gradient recalled echo EPI volumes depicting BOLD contrast were collected. In the second session, one critical run of 184 gradient recalled echo EPI volumes depicting BOLD contrast were collected. In both sessions, individual scan volumes consisted of 28 contiguous, 4-mm thick slices in the axial plane (TE = 35 ms, TR = 2500 ms, flip angle = 90°, FOV = 192 mm², 64×64 matrix, yoxel size = $3 \times 3 \times 4$ mm).

Prior to statistical analyses, image preprocessing was conducted in SPM99 (Wellcome Department of Neurology, UK; http://www.fil.ion.ucl.ac.uk). To reduce motion-related signal changes between volumes, each participant's scans were realigned and resliced using sinc interpolation. Volumes were then normalized to the Montreal Neurological Institute template brain available in SPM99, and finally smoothed in the axial plane using an 8 mm isotropic Gaussian kernel.⁷

Subsequent statistical analyses were also conducted using SPM99. For the property generation task, individual subjects' data were analyzed using the general linear model with two boxcar functions, each convolved with the standard SPM hemodynamic response function. One function modeled responses during the first 7.5 s of each property generation trial; the other function modeled responses during the last 7.5 s. Global effects were removed by proportional scaling, and the data were low-pass filtered. Condition effects for each participant were assessed for the early vs. late periods of the 15 s property generation trials. Specifically, two contrasts compared the BOLD response during the first 7.5 s of the property generation trials with the BOLD response during the last 7.5 s. One directional contrast established the brain areas having a higher BOLD signal during the first 7.5 s of property generation. A second directional contrast established the brain areas having a higher BOLD signal during the last 7.5 s.

Data for the word association and situation generation tasks were also analyzed at the single subject-level using the general linear model, once again with two boxcar functions, each convolved with the standard SPM hemodynamic response function. In this case, however, one function modeled responses during word association blocks, and the other modeled responses during situation generation blocks.

⁶ The lexical decision blocks had the same structure as those in the first scan session and did not repeat any critical cue words.

⁷ Anatomical scans from individual participants were not used to normalize images, given use of the MNI EPI template.

Two contrasts compared the BOLD response for word association trials with the BOLD response for situation generation trials. One directional contrast established the brain areas having a higher BOLD signal for word association. A second directional contrast established the brain areas having a higher BOLD signal for situation generation.

Contrast images from the individual contrasts were analyzed in second-level random effects analyses. Using one-sample t-tests, the following contrasts were assessed: (1) early property generation > late property generation; (2) late property generation > early property generation; (3) word association > situation generation; and (4) situation generation > word association.

To avoid Type II errors that could lead to missing important areas of overlap in the more conservative conjunction analyses to follow, all of the above contrasts used relatively liberal criteria for determining significance. Specifically, a significance threshold of p < .005 was used for the individual contrasts, with a spatial extent threshold of at least five contiguous functional voxels. Using these criteria also provided a broad sense of the areas potentially relevant for each task.

The activation maps from these contrasts were then used in the following conjunction analyses to test hypotheses of the LASS theory: (1) early property generation > late property generation masked by word association > situation generation; (2) late property generation > early property generation masked by situation generation > word association. Two additional conjunction analyses were conducted in which LASS does not predict activations: (3) early property generation > late property generation masked by situation generation > word association; (4) late property generation > early property generation masked by word association > situation generation. Again, a significance threshold of p < .005 was used, with a spatial extent threshold of at least five contiguous functional voxels.

By their nature, the conjunction analyses used more conservative statistics than the independent contrasts. Specifically, conjunction analyses between the activation maps for the early vs. late property generation and word association vs. situation generation have low probabilities of observing chance activations, because it is unlikely that property generation activations will co-occur in the same voxels as localizer activations. In addition, specific patterns of co-occurrence were predicted during different temporal periods within the property generation task for theoretical reasons, further decreasing the likelihood that these activations occur by chance. Finally, a spatial extent threshold of at least five contiguous functional voxels was again applied to all conjunction analysis maps to further reduce chance activations

3. Results

3.1. Initial analyses

3.1.1. Word association vs. situation generation

Generating word associates activated brain regions previously implicated in language processing. In particular, word association, relative to situation generation, activated two regions of the inferior frontal gyrus bilaterally. The lateral inferior frontal gyrus exhibited stronger and spatially more extensive activity on the left (e.g., Broca's area) than on the right, as did the more medial inferior frontal gyrus cluster (see Table 1). Three other areas commonly observed in language tasks were also active. First, the premotor cortex was active only in the left hemisphere. Second, the cerebellum was activated bilaterally, but with greater activity on the right than the left. Finally, word association activated a portion of the left inferior temporal gyrus previously implicated in word form processing (Cohen et al., 2002). Activations not so clearly related to language include bilateral activations in the orbitofrontal cortex, putamen, and thalamus, and unilateral activations in the left middle occipital and superior parietal gyri, left temporal pole, left brainstem, and on the right in the supplementary motor area, insula, caudate, calcarine cortex, and cingulate gyrus.

Generating situations activated brain regions previously implicated in mental imagery, episodic memory, and the processing of locations. Relative to word association, generating situations activated regions in the cuneus, precuneus, and posterior cingulate gyrus, as well as in the retrosplenial cortex (Table 2). More laterally in the parietal cortex, activity was observed in the right posterior angular gyrus and the right posterior superior temporal sulcus. In addition, situation generation produced activation in the left anterior middle temporal gyrus, and bilaterally in the superior temporal

Table 1Activated brain regions in the word association > situation generation contrast

Side/Location	MNI coordinate	MNI coordinates (X, Y, Z)			
L inferior frontal gyrus	-39	24	-12	4.18	.001
L inferior frontal gyrus	-48	36	-6	4.74	.001
L inferior frontal gyrus	-51	18	-3	5.56	<.001
L inferior frontal gyrus	-51	39	6	5.96	<.001
L inferior frontal gyrus	-57	12	12	5.83	<.001
R inferior frontal gyrus	54	12	18	4.22	.001
L precentral gyrus	-42	3	30	5.73	<.001
L cerebellum	-9	-69	-42	7.14	<.001
L cerebellum	-27	-60	-30	5.43	<.001
L cerebellum	-9	-54	-12	7.96	<.001
R cerebellum	15	-87	-33	5.04	<.001
R cerebellum	27	-69	-30	6.52	<.001
L inferior temporal gyrus	-45	-48	-18	6.89	<.001
L OFC	-18	15	-15	6.77	<.001
L OFC	-33	33	24	6.28	<.001
R OFC	21	18	-15	6.57	<.001
L putamen	-24	0	9	5.22	<.001
R putamen	24	3	9	4.98	<.001
L thalamus	-15	-9	3	4.20	.001
L thalamus	-12	-18	12	5.50	<.001
R thalamus	18	-15	-3	4.27	.001
L middle occipital gyrus	-24	-96	0	6.14	<.001
L superior parietal	-24	-69	48	7.34	<.001
L temporal pole	-54	6	-6	4.93	<.001
L brainstem	-9	-15	-18	5.94	<.001
Midline supplementary motor area	0	0	69	3.98	.002
R supplementary motor area	15	6	72	4.81	<.001
R insula	48	18	-3	5.15	<.001
R caudate	12	18	-3	4.15	.001
Midline calcarine cortex	0	-93	6	4.11	.001
R cingulate gyrus	12	21	39	3.99	.002
R cingulate gyrus	-9	18	42	3.95	.002

Table 2Activated brain regions in the situation generation > word association contrast

Side/location	MNI coordina	MNI coordinates (X, Y, Z)			р
L cuneus	-12	-72	24	4.18	.001
L cuneus/precuneus	-21	-69	18	5.83	<.001
L precuneus	-6	-57	54	5.53	<.001
L precuneus	-12	-42	57	4.07	.001
R precuneus	3	-69	27	8.96	<.001
R precentral gyrus	39	-12	42	5.87	<.001
L posterior cingulate	-9	-30	51	3.78	.002
L retrosplenial cortex	-9	-45	21	4.49	.001
R angular gyrus	48	-72	33	7.21	<.001
R posterior superior temporal sulcus	48	-60	12	6.90	<.001
L middle temporal gyrus	-45	-3	-21	4.68	.001
L superior temporal gyrus	-51	0	-15	4.85	<.001
L superior temporal gyrus	-42	-21	-3	4.20	.001
L superior temporal gyrus	-54	-15	9	5.82	<.001
L superior temporal gyrus	-54	-30	15	4.06	.001
R Heschel's/superior temporal	51	-18	9	4.13	.001
Midline medial prefrontal cortex	0	54	-6	5.53	<.001
L superior frontal gyrus	-24	51	-3	4.95	<.001
R superior frontal gyrus	18	36	39	5.34	<.001
L middle frontal gyrus	-24	45	27	3.78	.002
L middle frontal gyrus	-27	27	45	4.76	.001
L postcentral gyrus	-63	-9	-30	10.57	<.001
R insula	42	-6	-9	4.60	.001

Note. L = Left; R = Right.

ral gyrus. Generating situations also activated several prefrontal regions, including the ventral medial prefrontal cortex, the ventral superior frontal gyrus on the left, the dorsal aspect of the superior frontal gyrus on the right, and the left middle frontal gyrus. Finally, the left postcentral gyrus and the right insula were also activated.

3.1.2. Early vs. late property generation

As described earlier, the early phase of conceptual processing during property generation was designated as the first 7.5 s of each trial, and the late phase was designated as the last 7.5 s. Similar to word association, the early stages of property generation activated

Table 3Brain regions activated in the early property generation > late property generation contrast

Side/location	MNI coordinates (X, Y, Z)			Peak t	р
L inferior frontal gyrus	-45	36	6	5.22	<.001
L inferior frontal gyrus	-54	27	12	3.79	.002
L inferior frontal gyrus	-39	27	15	4.56	.001
L inferior frontal gyrus	-45	33	24	4.25	.001
L orbitofrontal cortex	-3	45	-18	6.72	<.001
L orbitofrontal cortex	-21	30	-18	6.58	<.001
L superior frontal gyrus	-6	57	3	4.76	.001
L superior frontal gyrus	-15	57	27	6.84	<.001
L superior frontal gyrus	-3	42	30	4.56	.001
L superior frontal gyrus	-3	45	51	5.11	<.001
L superior frontal gyrus	-18	33	54	6.22	<.001
R superior frontal gyrus	6	63	3	4.35	.001
L precentral gyrus	-54	-6	42	6.89	<.001
L precentral gyrus	-30	-15	54	4.09	.001
L precentral gyrus	-30	-6	54	3.68	.003
R cerebellum	27	-72	-33	4.27	.001
R cerebellum	6	-57	-39	3.76	.002
Midline cerebellum	0	-45	-21	8.86	<001
L middle temporal gyrus	-54	-39	-9	3.58	.003
L middle temporal gyrus	-51	-48	-3	4.46	001
L precuneus	-3	-57	18	6.78	<.001
L calcarine cortex	-12	-51	3	4.56	.001
L caudate	-15	15	0	4.73	.001
L supplementary motor area	-3	9	60	8.36	<.001
L anterior cingulate gyrus	-12	33	-15	8.37	<.001
R anterior cingulate gyrus	6	30	-12	7.18	<.001

Note. L = Left; R = Right.

brain regions implicated in language processing. Relative to the later 7.5 s half of the property generation period, the early 7.5 s half activated three frontal regions: left inferior frontal gyrus (e.g., Broca's area), left orbitofrontal cortex (OFC), and bilateral superior frontal gyrus (Table 3). In addition, early property generation was characterized by activity in the left premotor cortex and right cerebellum, as well as more medially in the cerebellar vermis. Unilateral left hemisphere activations were also observed in the middle temporal gyrus, the inferior aspect of the precuneus, the calcarine cortex, the caudate, and the supplementary motor area. Finally, bilateral activity was observed in the anterior cingulate.

Relative to early property generation, the later half of property generation activated a large area of parietal and temporal cortex. Although the peak voxel was located in the left precuneus, this single large cluster stretched from medial regions in the precuneus and posterior cingulate gyrus, laterally into the inferior parietal, angular, and posterior superior temporal sulcus (Table 4). In frontal regions, the right inferior, middle, and superior frontal gyri, as well as the lateral OFC, were also active in the later half of property generation. In contrast, no left frontal regions were active during the late property generation period. Several other regions were active exclusively in the right hemisphere late during property generation. These included the Rolandic operculum and temporal pole. Exclusively on the left, the lingual, fusiform, and middle occipital gyri, inferior parietal cortex, and insula were active. The caudate and putamen were active in the right hemisphere, and the thalamus was active bilaterally.

3.2. Critical analyses

As described earlier, the LASS theory makes specific predictions about the time course of property generation (Fig. 2, Panel A). Specifically, LASS predicts that when a word activates a concept, the linguistic system responds first, producing related linguistic forms. In parallel, but slightly more slowly, the word begins to activate a situated simulation that represents the word's meaning. Because the executive system extends processing within each system over time, however, the linguistic system produces responses for one extended period, and then the simulation system produces responses for a second extended period.

Table 4Brain regions activated in the late property generation > early property generation contrast

Side/location	MNI coordinates (X, Y, Z)			Peak t	р
L precuneus	-12	-72	33	11.65	<.001
R inferior frontal gyrus	54	24	-6	6.37	<.001
R inferior frontal gyrus	54	18	6	4.67	.001
R middle frontal gyrus	45	18	39	8.77	<.001
R superior frontal gyrus	33	63	12	4.79	<.001
R superior frontal gyrus	18	54	39	4.54	.001
R superior frontal gyrus	3	36	45	14.98	<.001
R superior frontal gyrus	27	18	63	4.74	.001
R superior frontal gyrus	24	6	66	5.30	<.001
R orbitofrontal cortex	27	54	-6	5.17	< 001
R operculum	51	-18	9	4.20	.001
R temporal pole	39	9	-36	5.64	<.001
L lingual gyrus	-21	-48	-9	4.47	.001
L fusiform gyrus	-39	-15	-18	4.80	<.001
L fusiform gyrus	-30	-60	-12	5.42	<.001
L middle occipital gyrus	-42	-84	12	4.27	.001
L middle occipital gyrus	-24	-84	18	3.68	.003
L inferior parietal	-60	-51	33	3.90	.002
L inferior parietal	-39	-48	42	6.78	<.001
L inferior parietal	-51	-48	51	8.95	<.001
L insula	-39	9	-12	4.98	<.001
R caudate	6	3	9	6.56	<.001
R putamen	27	15	-6	4.17	.001
R putamen	33	6	-6	3.93	.002
L thalamus	-15	-27	12	3.96	.002
R thalamus	12	-15	18	14.09	<.001

Note. L = Left; R = Right.

If these hypotheses are correct, activations during early property generation should overlap with activations during word association. Conversely, activations during late property generation should overlap with activations during situation generation. Clearly, the time course of conceptual processing is much more fine grained than this. If the LASS theory is correct, however, there should be statistically greater likelihoods of word association during the first 7.5 s of each trial vs. statistically greater likelihoods of situated simulation during the last 7.5 s. Because the executive system extends the processing of each system in time, fMRI is capable of detecting early linguistic processing vs. late simulation processing. If this theory is not correct, then the predicted pattern in Panel A of Fig. 2 should not occur. Alternatively, if the linguistic and simulation systems become active together (Panels B and C of Fig. 2), or if there is only a single system producing responses (Panel B), then the likelihood of linguistic processing should not differ across halves of the experiment, nor should the likelihood of situated simulation.

In support of the LASS theory, activations during early property verification (Table 3) appear more similar to activations during word association (Table 1) than to activations during situation generation (Table 2). Conversely, activations during late property verification (Table 4) appear more similar to activations during situation generation (Table 2) than to word association (Table 1). It is essential, however, to assess these similarities formally. The design of the current experiment allows us to do so, using conjunction analyses between the property generation task and the localizer tasks.

3.2.1. Word association during early property generation

To assess the presence of word association during early property generation, the word association > situation generation contrast map was used as an inclusive mask on the early property generation > late property generation contrast map. This conjunction analysis identified regions of overlapping activation during word association and early property generation. As Table 5 and Fig. 4a illustrate, three regions of overlap were observed. First, and most importantly, the left inferior frontal gyrus (Broca's area) was active in both maps. More posteriorly, activity was also observed in the left precentral gyrus and in the right cerebellum.

In contrast, when the situation generation > word association contrast map was used as an inclusive mask for the early property generation > late property generation contrast map, no areas of overlap were observed. In other words, no situation generation areas were active early during early property generation.

3.2.2. Situation generation during late property generation

To assess the presence of situated simulation during late property generation, the situation generation > word association contrast map was used as an inclusive mask on the late property generation > early property generation contrast map. This conjunction analysis identified regions of overlapping activation during situation generation and late property generation. As Table 5 and Fig. 4b illustrate, three regions of overlap were observed. First, overlapping activity was observed bilaterally in the precuneus and posterior cingulate cortex. Second, overlapping activation was observed in the right posterior superior temporal sulcus.

In contrast, when the word association > situation generation contrast map was used as an inclusive mask on the late property generation > early property generation contrast map, only one word association area in the posterior thalamus was observed.

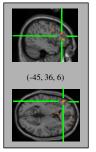
4. Discussion

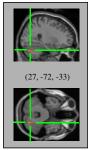
We begin by relating activations in the localizer tasks to other findings in the literature. We then review the critical results from

Table 5Word association and situation generation areas activated during early vs. late property generation

Contrast/side/location	MNI coordinates (X, Y, Z)			Peak t	р		
Early property generation > late property generation masked by word association > situation generation							
L inferior frontal gyrus	-45	36	6	5.22	<.001		
L precentral gyrus	-48	6	33	4.40	.001		
R cerebellum	27	-72	-33	4.27	.001		
Early property generation > late property generation masked by situation generation > word association							
No areas of overlap							
Late property generation > early property generation masked by situation generation > word association							
L precuneus	-6	-54	54	5.99	<.001		
R precuneus	9	-72	27	6.90	<.001		
R precuneus	6	-69	42	6.70	<.001		
R precuneus	9	-54	51	7.69	<.001		
R posterior superior temporal sulcus	51	-54	18	7.74	<.001		
Late property generation > early property generation masked by word association > situation generation							
R thalamus	9	-15	12	4.95	<.001		

A Early Property Generation > Late Property Generation Masked by Word Association > Situation Generation

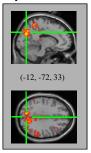


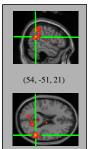


L Inferior Frontal Gyrus

R Cerebellum

B Late Property Generation > Early Property Generation Masked by Situation Generation > Word Association





Precuneus

R Temporal Sulcus

Fig. 4. Results from conjunction analyses. *Panel A.* Activations in a conjunction analysis for the early property generation > late property generation contrast, masked by the word association > situation generation contrast. *Panel B.* Activations in a conjunction analysis for the late property generation > early property generation contrast, masked by the situation generation > word association contrast.

the conjunction analysis and address their implications for the LASS theory, and for conceptual processing in general. Finally, we address the time course of conceptual processing and methodological issues raised by our findings.

4.1. Relations of the localizer activations to previous literature

Many of the activations observed in the localizer tasks here have been reported in similar tasks previously. Activations observed here for word association have been observed in related linguistic tasks. Activations observed here for situation generation have been observed in diverse tasks that assess various aspects of how people represent situations. We address each in turn.

4.1.1. Word association

Generating word associates activated the neural substrate for language. Most prominently, word association activated Broca's area in the left inferior frontal gyrus, a region commonly observed in word generation tasks (Dräger et al., 2004; Klein et al., 1995; Stippich et al., 2003).

In addition, other areas frequently observed in functional neuroimaging studies of language were active here during word association. Activity was observed in the left premotor cortex, a region implicated in the generation of object names and word finding (Duffau et al., 2003). Activity also occurred in the right cerebellum. Although the cerebellum's role in movement is well known, functional neuroimaging studies also frequently observe activity in the right cerebellum during linguistic tasks (Dräger et al., 2004; Klein

et al., 1995). Recent neuropsychological evidence suggests that the right posterior lateral cerebellum is involved in generating two-word associations, particularly for automated word associations produced during speech (Gebhart et al., 2002). Converging fMRI evidence shows that cerebellar activation contralateral to dominant cortical language areas also occurs during word generation (Jansen et al., 2004).

In summary, the pattern of activation for word association suggests that participants engaged in the linguistic retrieval and selection of verbal responses (Broca's area), as well as implicit motor movements associated with articulating words (premotor and cerebellum).

4.1.2. Situation generation

Generating a situation in which one commonly experiences an entity should engage a markedly different set of brain regions than those engaged by word association. In contrast to word association, situation generation engaged brain regions often reported active during mental imagery (e.g., Ganis et al., 2004; Kosslyn et al., 2000), episodic retrieval (e.g., Buckner and Wheeler, 2001; Cavanah and Trimble, 2006), and situational context (e.g., Barr, 2004). Specifically, situation generation activated large regions of the precuneus, posterior cingulate, and retrosplenial cortex. Many functional neuroimaging studies implicate the precuneus and posterior cingulate in mental imagery of information recalled from episodic memory, in particular, recall of autobiographical memories (Addis et al., 2004; Cabeza and Nyberg, 2000). Precuneus and posterior cingulate are central for representing contextual associations that underlie source memory (Lundstrom et al., 2003). Precuneus, posterior cingulate, and especially the retrosplenial cortex are central to interactions between episodic memory and emotion (Maddock, 1999). Lesions to retrosplenial cortex have been associated with loss of both verbal episodic memory and memory for spatial relationships (Katayama et al., 1999; Takahashi et al., 1997; Valenstein et al., 1987). In general, activation of these areas in our situation generation task suggests that our participants were imagining complex situations that may have often drawn on episodic and emotional content.

Another area active during situation generation was the lateral parietal cortex. Specifically, the right angular gyrus was active, an area associated with the coding of coordinate spatial relations (Baciu et al., 1999; Blanke et al., 2002). Because simulating a situation should often specify spatial relationships between simulated objects, it is not surprising that this area became engaged.

The right posterior Superior Temporal Sulcus (STS) was also active during situation generation. Recent imaging evidence has implicated this area in the perception of biological motion (Beauchamp et al., 2002). This further suggests that participants in our experiments represented social agents within the situations that they imagined. Similarly, situation generation also activated the ventral medial OFC, an area widely implicated in self-referential processing, person-knowledge, and evaluation of others' mental states (Mitchell et al., 2002; Schmitz et al., 2004). Again, it is not surprising that such an area would become active during situation generation, given that many of the situations imagined may have represented the mental states of self and others.

In summary, the brain areas active for situation generation have previously been associated with representing diverse aspects of situations. Brain areas become active that implement mental imagery, episodic memory, spatial context, spatial relations, motion, emotion, and mental states. This distributed pattern suggests that participants were simulating the background situations that have been widely implicated in conceptual processing (e.g., Barsalou, 2003b, 2005b, in press-b; Barsalou et al., 2003; Yeh and Barsalou, 2006).

4.2. The overlap of conceptual processing with language and situated simulation

As we just saw, the localizer tasks activated networks of brain areas that underlie linguistic processing and situation representation. Of primary interest in this experiment was the role that these networks play during property generation. According to the LASS theory, when people process a word conceptually, related linguistic forms should become active first, followed by the simulation of a situation, with executive processing extending these activations over time.

Conjunction analyses supported this account. By inclusively masking the activation maps from the early and late property generation periods with the activation maps for word association and situation simulation, we were able to identify regions of commonality between tasks. Three regions of overlap were observed between the early phase of property generation and the word association task, namely the left inferior frontal gyrus, the left precentral gyrus, and the right cerebellum. As described in the previous section, all three of these regions have previously been implicated either in language production (left inferior frontal gyrus, premotor cortex) or in generating two-word associations (right cerebellum). This overlap indicates that participants were performing a process something like word association during the early phase of conceptual processing.

Importantly, no regions of overlap were observed between the situation generation task and early property generation. This suggests that the simulation of situations did not dominate early conceptual processing. As described in the next section, this does not mean that simulations were not running during this period. Instead, it may simply mean that these simulations did not receive executive attention until later during conceptual processing.

A different set of regions overlapped between the late phase of property generation and the situation generation task, namely, bilateral precuneus, posterior cingulate, and the right posterior superior temporal sulcus. As described in the previous section, all three regions have previously been implicated in mental imagery, episodic memory, and context representation. This overlap indicates that participants were performing a process something like situation generation during the late phase of conceptual processing.

Importantly, late property generation shared only one small area with the word association localizer, the posterior thalamus. It is not clear what this overlap means, but clearly the size of the overlap between late property generation and the situation generation task is much larger—and more clearly interpretable—than the overlap between the late property generation task and the word association task.

In summary, significant meaningful overlap occurred between early property generation and word association, and between late property generation and situation generation. Consistent with the LASS theory, both word association and situated simulation underlie conceptual processing, with word association occurring earlier.

It is important to note that property generation is not a precise union of the brain regions underlying word association and situation generation. Early property generation activated regions that were not observed in word association, and vice versa. Late property generation activated regions that were not observed in situation simulation, and vice versa. These differences may be just as informative as the commonalities in elucidating how the property information is retrieved in the brain. Future work is required to understand these tasks more completely.

Furthermore, the overlaps identified probably reflect shared processing mechanisms that process diverse types of concepts. Because many different types of concepts were used (e.g., objects, events, properties, mental states, brands), it is likely that activations representing the detailed content of specific concepts did not aggregate across trials into a detectable signal. Instead, only common processing across concepts was likely to have aggregated sufficiently. The regions of overlap fit this description. During early conceptual processing, overlapping areas appeared to contain mechanisms involved in the production of word forms. During late conceptual processing, overlapping areas appeared to contain mechanisms involved in the representation of imagery, episodic memory, and context.

4.3. The time course of conceptual processing

In the experiment just reported, areas that represent simulated situations were not significantly active during the first 7.5 s half of property generation. If simulations had been equally dominant as word forms from the onset of a cue word, then the activations observed should have conformed more to Panel B or C in Fig. 2 than to Panel A. The activations observed for property generation, however, conformed to Panel A. Linguistic processing dominated the first 7.5 s of property generation, and situated simulation dominated the second 7.5 s.

Several experiments reviewed earlier similarly found that linguistic processing preceded situated simulation as well. Santos et al. (in preparation) found that linguistic responses tended to initially dominate word association and property generation for at least a second or two. Solomon and Barsalou (2004) found that accessing the simulation system took over 100 ms longer than accessing the linguistic system. Furthermore, simulations are not even compulsory. Kan et al. (2003) found that the simulation system did not become active when a word association strategy was sufficient for task performance. Glaser (1992) reviews many further examples of linguistic processing preceding deeper conceptual representation, and of conceptual processing being bypassed completely.

Importantly, other work has found that simulations become active very quickly. For example, Pulvermüller and his colleagues found that motor simulations became active within 200 ms of word onset (e.g., Pulvermüller et al., 2005). As suggested earlier, however, simulations may not capture executive processing immediately. When the executive system focuses selective attention on another system as a source of information, this other system may control responses, while a simulation runs in parallel unattended.

Why might executive processing select the linguistic system first as a source of relevant information? One potential factor is that the cues in these tasks are words. When participants receive words as cues for conceptual processing, the first information activated may be related words, following the principles of contentaddressable memory and encoding specificity (e.g., Tulving and Thomson, 1973). Furthermore, having to respond with words in many of these tasks may further orient executive processing towards the language system initially. When the executive system is capable of mapping a retrieved word form directly into a response, there may be no need to go outside this system and simulate a conceptual representation. When the language system runs out of responses, however, attention may shift to the simulation system. Although the simulation system may produce simulations all along, it may only be consulted once the linguistic system stops producing information that can guide responding.

An important goal for future research is to document parallel streams of activity in the two systems, along with interactions between them. Another important goal is to articulate the executive processing strategies that control these two processing streams. How do executive strategies determine which stream to process under what conditions? When do executive strategies shift attention to a different stream? How do executive strategies make deci-

sions based on the content of the stream(s) processed? How do executive strategies generate responses from these streams?

4.4. Methodological implications

4.4.1. Conceptual processing of non-linguistic stimuli

In this article we have focused on paradigms where words serve as cues for conceptual processing. From the perspective of evolution, however, words have only played this role recently. Non-linguistic experiential states in perception, action and thought have played this role much longer (e.g., visual objects, motor movements, affective states). In our opinion, research on conceptual processing has suffered from an over-reliance on words. We suspect that the processing of non-linguistic experience continues to be more central in human cognition than the processing of linguistic forms.

How might conceptual processing differ as a function of receiving non-linguistic experiential stimuli as cues (e.g., pictures, videos)? One possibility is that simulations situating an experiential cue may precede the activation of linguistic forms. Following the principles of content addressability and encoding specificity, an experiential cue may activate a simulation faster than it activates a linguistic form, because a simulation is more similar to cue information. Such simulations may provide the extensive situational inferences documented in the literature (e.g., Barsalou, 2003b, 2005b, in press; Barsalou et al., 2003; Yeh and Barsalou, 2006).

Another possible effect of experiential input may be stronger conceptual effects. As Glaser (1992) concluded from his review, conceptual priming and interference are both much larger for picture cues than for word cues. This suggests that conceptual information resides in the simulation system. This further suggests that deeper understandings of situations may typically occur when people receive experiential cues than when they receive linguistic cues.

Linguistic structures also become active in response to experiential cues, although, again, they may become active more slowly than simulations. Much remains to be learned about the roles that linguistic activations play during the conceptualization of experience. One possibility is that linguistic structures activate simulations that are more distant than the simulations activated by experience itself. Experience may tend to activate simulations that map closely onto it, whereas linguistic structures may tend to activate simulations of situations likely to follow the perceived situation (i.e., predictions), or that precede it (i.e., explanations). Linguistic activations may also serve to draw attention towards important regions of experience relevant for situated action. As a word becomes active, it may name a region of a simulation, thereby shifting attention towards it (e.g., Estes et al., 2008).

In general, the conceptual processing of experience deserves much greater scientific examination than it has received so far. Researchers typically study words in laboratory tasks because doing so is much easier than using pictures, sounds, touches, actions, and mental states. We believe, however, this has led to distorted views of cognition, in general, and of the conceptual system, in particular. Clearly, language plays central roles in conceptual processing, as demonstrated here. Nevertheless, experience and simulations of experience play roles that are at least as central.

4.4.2. Multiple profiles for conceptual processing

As we saw in the experiment here, both language and situated simulation occur during conceptual processing. As we further saw in other research reviewed earlier, different profiles of conceptual processing arise across different task conditions (e.g., Glaser, 1992; Kan et al., 2003; Santos et al., in preparation; Solomon and Barsalou, 2004). Under some conditions, conceptual

processing relies heavily on the linguistic system. Under other conditions, conceptual processing relies heavily on simulation. Under still other conditions, conceptual processing relies on both

Various inconsistencies in the literature may reflect variable profiles in conceptual processing. For example, the potential for variable profiles provides a perspective on the controversy surrounding whether modal theories or non-modal theories best explain the literature on category-specific deficits. Whereas some lesions may primarily affect the simulation system, others may primarily affect the linguistic system (e.g., Gainotti, 2006, vs. Capitani et al., 2003). For a special issue on this debate that reflects both perspectives, see Martin and Caramazza (2003). Similarly, variable profiles in conceptual processing explain the presence of mental simulation in some neuroimaging experiments but not others (e.g., Martin, 2001, vs. Devlin et al., 2002). Depending on the specific task conditions, some experiments provide evidence for simulation, whereas others provide evidence for linguistic processing. According to the LASS theory, however, both types of findings are valid, given that each represents one form that conceptual processing takes.

Because different profiles for conceptual processing result from different task conditions, researchers must take this fact into account when designing experiments. An experiment is likely to demonstrate contributions from the linguistic system when linguistic stimuli are used, processing time is short, the task is easy, and the task can be performed primarily with information available in the linguistic system. Conversely, an experiment is likely to demonstrate contributions from the simulation system when pictures are used, processing time is long, the task is difficult, and the task requires experiential information. Glaser (1992) and Barsalou et al. (in press) provide further detail on task conditions likely to produce different profiles during conceptual processing.

Most importantly, researchers should be careful not to conclude that conceptual processing only takes one form. Given many possible mixtures of language and simulation, it does not make much sense to argue strongly for one form and to argue against others that are likely to occur under different task conditions. Instead, research on conceptual processing should attempt, first, to identify the full set of mechanisms that underlie conceptual processing, and second, to explain how these mechanisms are sampled under different task conditions to produce different profiles of conceptual processing.

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