The Neural Organization of Spatial Thought and Language

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ABSTRACT

The cognitive neuroscience of semantics has focused largely on object knowledge. By contrast, spatial semantics, especially as related to language, has received little attention. Spatial thought and language gives our semantic system a rich texture by introducing relational thinking and greater levels of abstraction than is evoked by object semantics. This article describes the neural instantiation of spatial thought and language based on imaging and lesion studies. We underscore two functional-anatomical organizational principles. First, perceptual and conceptual representations have a parallel organizational structure within the nervous system. Lateral temporal cortices are important for manners of motion, action representations, and action verbs. More dorsal regions are important for paths of motion, locative representations, and prepositions. Second, posterior perceptual representations serve as points of entry for more anterior and centripetally located peri-Sylvian conceptual and linguistic representations.

KEYWORDS: Spatial language, spatial representations, verbs, prepositions, thought

Learning Outcomes: As a result of this activity, the reader will be able to (1) demonstrate an understanding about the neural interface of spatial and linguistic representations, (2) define manner and path aspects of motion, and (3) identify the patterns of brain damage associated with deficits in spatial language.

How is space perceived and conceived when communicating using language? Implicit in this question is the view that language is not a completely autonomous cognitive module. Rather, language is informed and constrained by nonlinguistic information.[1–3] The relationship among percepts, concepts, and language may not be straightforward.[4] However, it is also not likely to be arbitrary.[5–15] Spatial representations entail many domains, such as

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spatial attention, working memory, imagery, navigation, and reaching. Slobin[16,17] suggested that "thinking for speaking" is different than thinking for other purposes (also see[18]). This article focuses on thinking about space specifically for speaking. We concentrate on the neural underpinnings of spatial representations in the service of spoken language. We show that spatial perception and language have a parallel neural organization. Furthermore, we present evidence suggesting that motion is processed with a concrete to abstract gradient along the posterior to anterior lateral temporal lobe.

A GENERAL FRAMEWORK

Objects in space have intrinsic and extrinsic properties. Intrinsic properties refer to the object itself, whereas extrinsic properties refer to the object in relation to an external referent. Additionally, objects can have static or dynamic properties (see Table 1). Thus investigations of intrinsic properties of objects in their static form would be the study of object knowledge (such as shape, color, etc.). Empirical investigations in semantics have mostly focused on knowledge of objects in this static sense. In neuropsychology, the findings of category-specific naming and recognition deficits have led to vigorous discussions of the implications of these observations for how the nervous system compartmentalizes object knowledge.[19–28] By contrast, investigations of objects in their dynamic or relational aspects have been sparse.

Intrinsic motion can be operationally considered motion without an external referent. This category includes various manners of motion that constitute actions. Some manners of motion may be internal to an object. That is, parts of an object might move in relation to itself, as in "wriggling" or "rotating." Other manners of motion might also convey translational motion, such as "running." The movement even in this case is not anchored to a specific external referent. Thus the concept of "run" implies translational movement, but specifying its path requires giving it an external referent by saying something like "runs across the meadow" (see[29,30] for related ideas in developmental studies).

Table 1 A General Framework for the Study of Semantics

	Intrinsic	Extrinsic
Static	Object, proper	Locative relations
Dynamic	Manner of motion	Path of motion

Extrinsic spatial information is often discussed in the context of different reference frames.[31–35] Object-centered frames are distinguished from viewer and environment reference frames (also described as allocentric as distinct from egocentric and geocentric). Neurophysiological studies suggest that neurons within posterior parietal cortices integrate visual information with eye, head, and body position to give rise to these reference frames.[36–40] Static locative relationships, such as those depicted by "on" or "under," describe an object (the figure) in relation to something else (the ground). The external referent for locative relations may be another object, the viewer, or the environment itself. Consistent with the neurophysiological studies, classic neuropsychological studies implicate parietal cortices in judgments of static spatial relations.[41] However, this remains an area in great need of study, especially in the context of language. More generally, aspects of movement and actions through space (and time) cohere together to form events that fundamentally structure how we think of the world in a dynamic sense. We are only beginning to understand how the representation of events are organized and how they relate to language.[42]

THE IMPORTANCE OF SPATIAL LANGUAGE

Confining the study of semantics to understanding objects leaves us with an impoverished view of how we think about the world. Thinking about space gives our mental lives depth and texture by uncovering relational thinking and levels of abstraction inherent in spatial language. Verbs establish thematic roles, such as who is doing what to whom in a sentence. Thus the verb "push" implies that someone is doing the pushing and that something is being pushed. By coordinating the argument structure of a sentence, verbs organize a set of possible relations being communicated. Similarly, prepositions describe relationships of two or more objects. For example, the preposition "in" implies two objects in a specific spatial configuration. This shift of focus away from concrete perceptual attributes of objects and to their relations delivers enormous cognitive flexibility and generativity.[43]

Spatial representations also introduce abstraction to our thinking in several ways. Thinking of objects largely evokes sensory-motor attributes, such as their visual properties or their functional uses (reviewed in[44]). By contrast, the link between spatial concepts and specific sensory-motor attributes is less clear. A lion and a child may be running, but which attributes contribute to "running"? Such dynamic events are also transient. In the world, the percept cannot be returned to in the same way that one can return to a static object. Even for static locative relations, the problem remains, insofar as that the specific objects involved may vary widely. A cup may be on the table, or a monkey may be on a branch. These are very different visual percepts, and yet they share something in common. Mandler[14] notes, "Achieving this kind of abstract representation, one that ignores the concrete details of the objects involved may be required before spatial relations can be mapped onto language" (p. 251). The mapping onto language itself involves another shift in level of abstraction. This shift (an analog percept to digital language conversion) is not specific to spatial language per se, but the evanescent nature of spatial events makes the conversion less straightforward. Finally, a point to which we return later, spatial terms can be used figuratively, to describe situations in which a spatial event is not being described literally. Thus the sentence "she stands up for herself" makes use of spatial terms to convey a more abstract idea.

VISUAL MOTION: PERCEPTION AND CONCEPTION

A fundamental tenet in neuroscience is that "what" and "where" visual information are processed by ventral and dorsal processing streams, respectively.[45] Although both streams interact,[46,47] this distinction, derived from macaque neurophysiological studies, is generally confirmed in human imaging and neuropsychology.[44,48–50] In the macaque, part of this dorsal stream is area medial temporal (MT) (within the middle temporal gyrus) and area medial superior temporal (MST), which contain neurons that are selectively sensitive to motion. In human imaging studies, area MT/MST as defined functionally is usually located at the junction of the inferior temporal gyrus and the occipital gyrus.[51–54] Area MT and MST have traditionally been thought of as sensitive to low-level perception of motion and not meaningful motion as might be relevant to conception and communication. Networks dorsal to these regions, within both banks of the posterior superior temporal sulcus (pSTS), are sensitive to biological motion.[55–58]

How might the perception of motion be linked to conception and communication? We hypothesize that the nervous system organizes perception and conception along similar anatomical principles. If this hypothesis is true, then the way that language deals with motion might offer a clue to the perceptual parsing of motion as relevant to communication. It turns out that languages consistently distinguish between manner and path of motion by expressing these attributes in different constituents.[59] For example, in English, manner of motion is conveyed primarily by verbs. So *gallop*, *canter,* and *trot* describe different manners of motion. By contrast, path information in English is conveyed primarily by prepositional phrases. So the horse *gallops across* the meadow or *into* the barn or around the track. The specific link of manner of motion to verbs and paths of motion to prepositional phrases is not a universal property of language. In some languages such as Greek or Spanish, path information is conveyed in the verb and manner with an additional satellite. However, for our purposes, the important observation is that languages separate these motion attributes in different linguistic constituents.

If the parsing of motion by language is a clue to its perceptual parsing, the neural processing of manner and paths of motions should segregate. We reasoned that path information, because of its extrinsic nature, would activate brain regions more dorsally than would manner of motion. By contrast, because manner of motion is primarily related to the biomechanical properties of the object itself, it would be processed more ventrally. We tested these hypotheses by conducting a functional magnetic resonance imaging (fMRI) study.[60] In the study, we used a one-back matching block design in which conditions of interest were a "star" figure moving with different manners and paths. In some blocks, subjects attended to the path of motion and in others the manner of motion, even though the stimuli were identical across conditions. Manner and path of motion information had distinct neural signatures. Greater activation for manner than path was seen bilaterally within the posterior middle temporal gyrus (pMTG) at the junction of BA 19/37. Greater activation for path than manner was seen bilaterally in the posterior intraparietal sulcus (IPS, BA 39/7) and posterior middle frontal gyrus (pMFG, BA 8/6). The observed neural differences could not be accounted for by perceptual attributes of the stimuli because the same stimuli were used in each condition. Nor could these patterns of activation be accounted for by differences in eye movements across conditions.

ACTION PERCEPTION AND CONCEPTION

If the neural organization of perception is linked to conception, then this ventral-dorsal distinction between different aspects of motion should also apply to the conception and verbalization of actions. Thus one would predict that actions and verbs insofar as they primarily convey manners of motion (in English) should be neurally mediated by posterolateral temporal structures. In an fMRI study, we used a testing procedure in which triads of stimuli were presented and subjects matched one of two target stimuli to a test stimulus based on their similarity. For example, in the action condition, subjects might match a picture of digging to shoveling rather than sewing.[61] Object trials showed pictures of static objects. Voxels showing a main effect for the action and object matching tasks compared with a low-level perceptual baseline were identified and then queried for relative contrasts for the action-object comparison of interest. Pictures of actions activated an area bilaterally within the posterior temporal-occipital cortex involving inferior and middle temporal gyrus more than pictures of objects (see Fig. 1). These areas included voxels within area MT/MST (primarily within Broadmann area [BA] 37 and anterior BA 19). Thus, when people made semantic judgments of actions, they activated visual motion and adjacent areas even though the stimuli under consideration themselves were not moving. These findings are consistent with other findings that static images of actions activate area MT/MST and this general region is involved in processing meaningful actions.[58,62,63] As an aside, we should point out that "action" refers to manners of motion and not to actions such as reaching or skilled movements, domains that have traditionally been referred to as praxis in the neuropsychological literature[38,64–71]

As mentioned earlier, an important part of representing actions is the shift of cognitive focus away from objects themselves. The posterolateral temporal cortex appears to be critical in mediating perception and conception of actions. But do these neural circuits abstract action representations away from the specific actors involved? To address this question, we conducted an fMRI adaptation (also known as repetition suppression) experiment.[72] These experiments capitalize on the physiological observation that neural responses in specialized circuits diminish when repeatedly processing features for which the circuit is specialized.[73]

Subjects watched action movie clips and judged whether the specific action was common (typically seen at least once a week). During the first three scans, only one set of movies was presented, and each movie was repeated five times. During the last two scans, four sets of movies were presented: (1) The same set of movies used in the first three scan ("Old Actor, Old Action"), (2) a set of movies with the same people seen in the first three scans performing different actions ("Old Actor, New Action"), (3) a set of movies with different people performing the same actions seen in the first three scans ("New Actor, Old Action"), and (4) a set of movies in which both the people

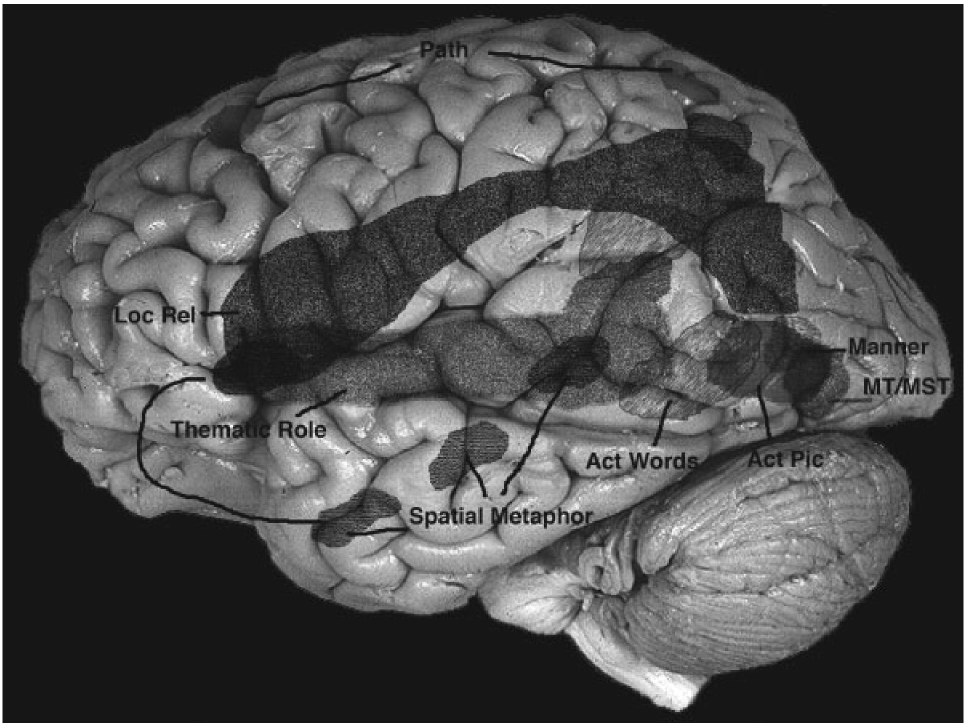

Figure 1 Cartoon of areas of the brain implicated in spatial language and thought. These areas are meant to give the viewer a qualitative feel of regions implicated and not intended to be precise locations. Act Pic: Refers to areas of greater activation of semantic judgment of action pictures over object pictures.[61] Act Words: Refers to areas of greater activation for semantic judgments of action words than object words.[61,85] Loc Rel: Refers to areas when damaged that are correlated with deficits in comprehending locative relations in sentence/picture-matching tasks.[102] Manner: Refers to areas of greater activation of manner than path of motion. MT/MST (medial temporal/medial superior temporal): Area involved in low-level motion perception.[61] Path: Refers to areas of greater activation of path than manner of motion.[60] Spatial Metaphor: Refers to areas of greater activation for comprehension of spatial metaphors than for literal motion sentences.[116] Thematic Role: Refers to areas when damaged that are correlated with deficits in comprehending thematic role assignments in sentence-picture matching tasks.

and the actions were different ("New Actor, New Action"). We also identified the following areas functionally in each subject: the pSTS, area MT/MST, the extrastriate body area (EBA), the lateral occipital cortex (LO), the fusiform face area (FFA), and the parahippocampal place area (PPA). The pSTS has been implicated in biological motion[55–58] and the EBA in processing visual images of human bodies.[74] These regions along with area MT/MST would be candidate regions for processing actions. Area LO is implicated in nonspecific static object perception,[75,76] the FFA in face perception,[77] and the PPA in place and building perception,[78] and our expectation was that these regions would not be involved in action processing. Compared with completely novel events, we found decreases in the fMRI signal for sequences in which the action was repeated, but not the person performing the action, in the pSTS, MT/MST complex, and EBA. Similar effects were not seen in LO, FFA, or PPA.[72] These results suggest that area MT/MST, EBA, and pSTS are part of a distributed network that is sensitive to actions even when different actors are performing them. These experiments are consistent with the general view that the posterolateral temporal cortex mediates action representations and also abstracts these representations from the actors themselves.

ACTION VERBS

The studies reviewed thus far confirm that the bilateral posterolateral temporal cortex mediates perception of manners of motion, semantic judgments of static action pictures, and abstracts action representations from the actors conducting these actions. How does this neural instantiation of action processing relate to its verbal counterpart? Neuropsychological studies recognize that deficits in naming actions, and possibly conceptualizing actions, can dissociate from naming objects[79–83] (although see[84]for a dissenting view). However, systematic analyses of the neural bases for these deficits are scant. In the study of action semantic judgments using picture triads referred to earlier, we also conducted an experiment using the comparable verb and noun triads.[61] We found that judgments of verbs compared with nouns activated an area just anterior and dorsal to the area activated by action pictures, and primarily in the left hemisphere. This area encompassed the pMTG and the posterior superior temporal sulcus (see Fig. 1). From this study we inferred that the lateral occipitotemporal lobe mediates different aspects of motion, with a gradient from the concrete apprehension of moving but meaningless stimuli in the inferior occipitotemporal junction (human MT/MST) to the motion implied by action verbs, closer to the peri-Sylvian cortex. This inference was predicated on the fact that words did not activate area MT/MST. To test this inference, we conducted a follow-up fMRI study using verb triads in which the association was based on manners of motion. For example, “hopping” would be matched to “skipping” rather than “running.” Importantly, in this study all of the choices referred to actions with translational motion.[85] We reasoned that making comparisons that focused on distinguishing manners of motion might provoke activation within area MT/MST. However, even with these more stringent stimuli, again we found that actions processed in the context of words did not activate area MT/MST. We replicated the previous findings of middle temporal gyrus as well as pSTS activations. Thus although these areas activated by action words were adjacent to areas specialized in processing visual motion, they were not identical to those areas. (Also see[61,62,86–88] for related observations). These findings support the idea that motion attributes are processed along the lateral temporal cortex with gradient in which concrete to abstract information is processed along a posterior to anterior (toward peri-Sylvian cortex) axis.

RELATIONAL KNOWLEDGE

As mentioned earlier, an important aspect of spatial language is its relational nature. For example, verbs in the context of sentences tell us who is doing what to whom, and prepositions tell us how one thing is related to another in space. Aphasic patients may have comprehension deficits at the level of an event, in which one participant is doing something to another.[80,89–95] They may also have difficulty comprehending locative sentences that describe spatial relationships between objects.[89,96–98] Again, the neural bases of these deficits have received scant attention. Based on our previous studies, we would expect a similar ventral/dorsal division. Lesions based more ventrally along the lateral temporal cortex would be more likely to result in thematic role assignment deficits and lesions based more dorsally to produce locative deficits. Landau and Jackendoff,[1] adapting the what/where visual processing distinction, speculated that locative prepositions might be processed within parietal cortices. One positron emission tomography study found that naming locative relations activated inferior parietal cortices,[99] and similar findings have been reported for sign language.[100] Kemmerer et al[101] found that lesions to the left parietal operculum and prefrontal cortices were more likely to produce deficits in knowledge of locative prepositions.

In a series of individuals with aphasia, we examined their relational comprehension abilities in simple sentence picture-matching tasks that described thematic relations (who is doing what to whom) or described locative relations. Again, given our functional-anatomical hypotheses, we would expect that thematic role deficits would be associated more closely with posterolateral temporal lesions and locative relations with more dorsally located frontoparietal lesions. We tested 19 patients with focal left-hemisphere damage. These subjects matched sentences to one of four possible pictures. Five patients, all with very severe aphasia, performed at floor on all tasks, including our screening tasks (point to simple shapes) and were not included in further analyses. For the other 14 patients, performances across both thematic role and locative knowledge tasks correlated significantly ($r = 0.66$; $p < 0.05$). Seven patients performed outside the control subjects' range on the thematic role sentence picture-matching task. Six patients performed outside the control subjects' range on matching locative sentences to the appropriate pictures. Five patients had performances that fell outside the normal range on both tasks. However, two patients performed outside the normal range on the thematic role but not the locative task, and one patient performed outside the normal range on the locative but not the thematic role task, revealing double dissociations in these tasks.[102]

To determine brain–behavior correlations, we adapted voxel-based lesion symptom mapping (VLSM) techniques using permutation analyses. This method uses a technique in which the level of deficits across groups of subjects can be correlated with whether or not voxels within a standardized space are damaged. Thematic role knowledge deficits correlated with lesions to the middle and superior temporal gyrus. By contrast, locative knowledge deficits were correlated with posterior parietal, occipitoparietal junction, and inferior prefrontal damage (see Fig. 1). The locus for thematic role sentence picture matching is more anterior than our fMRI activation findings at the single-word level.[61,85] Again, these findings of relational knowledge confirmed our functional anatomical organizational prediction of a ventral dorsal division between action relational knowledge and locative relational knowledge.

SPATIAL METAPHORS

We have been suggesting that the lateral temporal cortex processes motion with increasing levels of abstraction as one moves anteriorly. What about the metaphoric use of spatial terms? Talmy[103] uses the terms "factive" and "fictive" to describe the distinction between literal and certain figurative uses of spatial terms. These terms are used to describe the quality of spatial representations, in contrast to terms like "factual" and "fictional," which describe the truth of things in the world. Factive expressions, like *the man runs to the store* map palpably to *actual movement* in the world. By contrast, fictive sentences like *the road runs along the river* might map onto a spatial aspect of the world but not palpably onto the concrete act of running. Fictive sentences further contrast with metaphoric sentences such as *the man runs for office* in which no spatial scene is being described. The nature of fictive or metaphoric extensions of spatial terms is not clear[104,105] but some hypothesize it to be derived from extensions of earlier acquired concrete meanings.[106–109]

Very little is known about how metaphoric extensions of spatial terms are mediated neurally. The right hemisphere may be engaged when processing metaphors (see[110] and abstract words[111,112] (but see[113–115] for alternate views). Thus a reasonable prediction would be that homologous regions in the right posterior temporal and parietal cortices would be engaged in metaphoric extensions of spatial events.

By contrast, if our hypothesis that the lateral temporal cortex processes motion in increasingly abstract ways, then the left hemisphere within the lateral temporal cortex might be expected to process these kinds of metaphors. Our reasoning was as follows. Action verbs have both concrete sensory attributes as well as conceptual attributes. Thus verbs used literally describe manners of motion and in the sentential context perhaps the paths or locations of these manners of motion. The conceptual attributes of verbs have to do with notions of source, goals, or changes of states. When verbs are used metaphorically, the sensory attributes are shed and only the conceptual attributes convey meaning. Thus "the man falling under a spell" does not describe physical motion, but it does describe arrival at a new state. On this analysis, and given our hypothesized organizational principle for the lateral temporal cortex, we would expect spatial metaphors to be processed more anteriorly within the lateral temporal cortex than sentences that convey literal motion.

In an event-related, functional MRI study, we contrasted spatial metaphors in sentences like *the man fell under her spell*, to literal motion sentences like *the child fell under the slide*. Consistent with our predictions, we found greater activation in the left inferior frontal cortex and left lateral temporal lobe for spatial metaphors as compared with literal sentences (see Fig. 1), and no differences in homologous areas of the right hemisphere.[116] Although considerable work remains to be done regarding predicate metaphors, such as the ones using spatial terms as we described here, our prediction was confirmed. These findings add further support for the idea that the temporal cortex processes aspects of motion in increasingly abstract ways within neural circuitry that is further removed from posterior perceptual networks.

In addition to the lateral temporal activations, we also found significant clusters of activation within the left inferior frontal gyrus (IFG). We interpret these activations as representing competition between meanings of spatial terms in the predicate metaphor condition, including at a minimum the literal and the metaphoric interpretations.[117–119] For instance, Bedny et al[120] provide evidence that activation in the left IFG represents top-down selection processes for word-level meanings in resolving competition when word meanings are ambiguous. On this account the left IFG performs executive functions on the representations, rather than encoding the representations themselves.

CONCLUDING COMMENTS

Our review of the findings presented here suggests that the following principle guides the neural organization of spatial perception, conception, and language. Depending on the conceptual domain, specific sensory and motor systems serve as "points of entry" for the semantics of verbs and prepositions. Increased levels of abstraction are instantiated in neural structures aligned with but not necessarily identical to these perceptual or motor cortices. That is, the distribution of these more abstract conceptual or linguistic networks is guided by the location of the relevant sensory and motor cortices. Thus motion processing appears to be important for representing actions. More specifically, the manner of motion is relevant for actions. Regions within pMTG close to area MT/MST mediate the linguistic representations of these actions. The sentential organization of thematic role knowledge is mediated still further anteriorly and centripetally within MTG and the superior temporal gyrus. Finally, spatial metaphors in a sentential context are also mediated along this axis within the left lateral temporal cortex. Analogously, for extrinsic information, such as path of motion, the posterior parietal cortex and frontal eye fields serve as points of entry. Studies examining static locative representations are currently under way in our laboratory. There is a paucity of such studies in cognitive neuroscience (see[121] for review). Networks closer to peri-Sylvian cortex, such as the angular gyrus and the inferior frontal gyrus, mediate linguistic mediation of locative information in sentences. This point of entry hypothesis falls within the family of sensory functional accounts of semantics (e.g.,[44,122,123] but differs slightly in the topographical claims based on gradients of abstraction.

The significance of this line of investigation is threefold. First, spatial thought for language has not received much scrutiny in cognitive neuroscience. Investigators tend to specialize in studying either language or spatial processing. Because of this propensity to specialize, there has been little systematic investigation of the interface of these two central cognitive domains. Of note, similar biases exist in other disciplines such as extensive work in developmental studies that focus on how infants perceive and conceptualize objects,[124–127] which have only recently been joined by studies of space for language.[128–136]

Second, spatial thought is fundamental to human cognition. It allows us to corral an ever-shifting world into stable concepts. Spatial thought provides the basis for complex cognitive abilities by delivering toolkits that enable flexibility in communication that would otherwise be confined to reference to static objects. Understanding these cognitive abilities that allow us to think relationally may be fundamental to understanding "why we're so smart."[43]

Finally, this research has important clinical implications. Understanding profound deficits of thought and language experienced by brain-damaged subjects is critical to designing targeted rehabilitation interventions. Ultimately, we need to know the nature of communication deficits experienced by aphasic individuals beyond simply their naming deficits. A greater focus on spatial language and its deficits will deepen our understanding of the communication problems aphasic individuals might experience that would not be evident when simply testing for object knowledge or even syntactic competence.

For some time it has been known that individuals with aphasia can have sentence-level deficits of comprehension.[89] Much of the research in this area has focused on syntactic structure and less on semantic understanding.[98] As we have shown, deficits at this level may persist chronically after stroke.[102] Even more subtly, our language in normal discourse is replete with the metaphorical use of spatial terms. We know little of the circumstances in which individuals with brain damage are no longer able to use these terms flexibly and what this does to their communicational abilities. Can they even think relationally or analogically? Although we have been emphasizing space, these actions occur in space *and time* to create events.[42] Do such individuals have abnormal representation of events, and how does this affect a sense of their own narratives? Do spatial deficits in children, either because of neonatal stroke or because of conditions such as William's syndrome,[137] impair their ability to understand relational concepts? Focusing on these issues exposes the richness of our conceptual systems that arise from the interface of perception and language and the subtle ways in which these systems break down. Understanding these systems is critical to directing treatment efforts or designing compensatory strategies for deficits that strike at the very core of human thought.

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