What is the link between language and spatial images? Behavioral and neural findings in blind and sighted individuals

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A B S T R A C T

In order to find objects or places in the world, multiple sources of information, such as visual input, auditory input and asking for directions, can help you. These different sources of information can be converged into a spatial image, which represents configurational characteristics of the world. This paper discusses the findings on the nature of spatial images and the role of spatial language in generating these spatial images in both blind and sighted individuals. Congenitally blind individuals have never experienced visual input, yet they are able to perform several tasks traditionally associated with spatial imagery, such as mental scanning, mental pathway completions and mental clock time comparison, though perhaps not always in a similar manner as sighted. Therefore, they offer invaluable insights into the exact nature of spatial images. We will argue that spatial imagery exceeds the input from different input modalities to form an abstract mental representation while maintaining connections with the input modalities. This suggests that the nature of spatial images is supramodal, which can explain functional equivalent results from verbal and perceptual inputs for spatial situations and subtle to moderate behavioral differences between the blind and sighted.

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1. Introduction

Suppose you want to buy a pineapple. You need to go to the supermarket and you have to find the pineapples. In order to solve this task you may activate several information sources from memory: a visual image containing the shape and form of a pineapple; a sense of the tactile information of the texture one feels when grasping the fruit; olfactory information about its smell; a quasi motor program containing movement and directional information on how to walk towards the fruit stall. Yet, it is possible that you still do not have enough information to find the target location. In that case, an option is to ask for directions. Language can be used to communicate an abstract set of instructions allowing one to find the pineapples. Together all these information sources may be converged into a spatial image: a mental representation of the physical world which includes relations between objects and extensive information on location, orientation and distance (De Vega, Cocude, Denis, Rodrigo, & Zimmer, 2001).

There are two main types of information sources for spatial images. One involves imagery processes which are directly coupled to modality-specific sensory information, for example: visual, olfactory, gustatory and tactile representations. Motor imagery can be thought to be coupled in a top-down fashion to proprioceptive representations and efferent copies of the motor program. For these forms of imagery there is a clear overlap in neural circuitry between perception and imagery (Kosslyn, Ganis, & Thompson, 2001). Secondly, language can also function as a source of information. Whether or not language is modal has been an issue of debate in recent literature (e.g. Barsalou, 1999, 2008; Barsalou, Santos, Simmons, & Wilson, 2008; Chomsky, 2000; Jackendoff, 2002; Zwaan & Radvansky, 1998). According to Barsalou (1999) words can only have meaning if they are grounded, or are coupled to perceptual concepts. During perception relevant information is extracted as perceptual symbols. This information is gathered from any modality, resulting in multimodal perceptual symbols. These symbols can be combined into a perceptual concept, which can be reenacted through the process of simulation. According to this theory words are linguistic symbols which become associated to simulators for perceptual concepts. On the other hand, we can also consider language as a communication system which provides a set of processing instructions to generate a mental representation of a situation (Barsalou, 1999; Zwaan & Radvansky, 1998) and which does not incorporate meaning directly (Fauconnier, 1999).

Such a set of instructions, or propositions, can be considered abstract and amodal, since it does not involve a link to modal

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information specifically. There is, however, a strong relationship between words and modality-specific information, which is referred to by Barsalou and colleagues (2008) as the linguistic form. The linguistic form could be visual, tactile or auditory and can subsequently be used as pointers to conceptual information (Barsalou et al., 2008). These two theories are important, but the focus of this review is not on discussing how language is grounded. Therefore, we refer to language as words, which are in essence amodal, but can also be related to perceptual modal experience.

The different sources of information which can lead to a spatial image are organized along several levels. The lowest level corresponds to the input, which can either be perceptual bottom-up or be top-down retrieved from long-term memory (Cornoldi & De Beni, 2007; Cornoldi, De Beni, Giuberti, & Massironi, 1998), while the higher levels denote the resulting mental representations. There is a distinction between modality-based input channels on the one hand, yielding images coupled to sensory information, and language as an amodal input channel on the other hand, yielding a set of propositions. Together these different sources from both input levels can form a spatial image (Chatterjee, 2001).

The nature of spatial images has been the subject of many studies (e.g. Barsalou, 1999; Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Lambert, Sampaio, Mauss, & Scheiber, 2004; Noordzij, Neggers, Ramsey, & Postma, 2008; Noordzij, Van der Lubbe, & Postma, 2006a; Reichle, Carpenter, & Just, 2000); A central question has been to what extent spatial images can be considered amodal, multimodal or supramodal, however, no consensus has yet been reached. Multimodal representations are linked to the perceived modality and are established in the modality-specific brain areas. A supramodal representation exceeds the input from different modalities but maintains modality-specific information (Barsalou, 1999).

When discussing neural correlates it is important to consider evidence from multiple sources of information which should yield converging evidence. Behavioral experiments can determine whether direct physical input is analogous to mental representations and can generate similar behavioral results. In addition, neuroimaging researches, such as electroencephalogram (EEG) and functional magnetic resonance imaging (fMRI) can offer insight into the neural correlates of the overlap between perception and imagery. This neuroimaging evidence should be treated with some caution since it establishes correlations between task performance and neural activation. Therefore, the use of transcranial magnetic stimulation (TMS) and repetitive TMS (rTMS) study Kosslyn and colleagues (1999) have shown that visual perception and imagery of letters interact at an early stage over the visual cortex, suggesting that the mental images are represented visually. In a positron emission tomography (PET) and repetitive TMS (rTMS) study Kosslyn and colleagues (1999) have demonstrated that mental imagery of patterns of stripes recruits area 17 similar to visual perception (see Kosslyn et al., 2001), for a review). However, imagery does not require sensory processing. Visual imagery and perception are closely related and share similar mechanisms, but with unique characteristics. The idea of partially overlapping networks for visual imagery and perception has been further explored by Ganis and colleagues (2004). In an fMRI study where subjects visualized or saw faint drawings of objects, they also found a partially overlapping network. The overlap between imagery and perception was found predominantly in the frontal and parietal regions and less in the temporal and occipital regions. For an overview of a selection of literature on visual imagery see Table 1.

While less work has been done on tactile, auditory, olfactory, gustatory and motor imagery, partially overlapping networks for perception and imagery have also been reported here (for example Goyal, Hansen, and Blakemore (2006), Jeannerod (1995), Kobayashi et al. (2004), Kosslyn et al. (2001), Stevenson and Case (2005)). Yoo and colleagues (2003) observed in an fMRI study that the primary and secondary somatosensory areas are active during tactile imagery of gentle brushing of the hand and that there is a partial overlap with the activity found during actual tactile stimulation. However, there are also parts of the primary and secondary somatosensory areas which are only active during actual tactile stimulation. Moreover, tactile imagery activates the inferior parietal lobe, which seems to share commonalities across imagery modalities (Uhl et al., 1994; Yoo et al., 2003). Yoo and colleagues (2001) also investigated auditory imagery and its neural correlates. Again they found that imagery and perception have a partially overlapping network. Auditory imagery of a simple monotone can elicit bilateral activation in the primary and secondary auditory areas (Yoo et al., 2001). Although olfactory imagery is difficult to asses, it has been shown to activate similar brain areas compared to actual odor sensation, but once more to a lesser extent (Stevenson & Case, 2005). Stevenson and Case (2005) report converging evidence from behavioral findings, olfactory illusions in patients with Parkinson’s disease and Alzheimer’s disease, as well as EEG and fMRI findings.

In conclusion, modal perception and mental imagery seem highly alike. The overlap between perception and imagery agrees with the perceptual symbol systems theory proposed by Barsalou (1999). However, modality-specific inputs are not the only manner through which spatial representations can be achieved. Language provides an alternative elegant way to build a spatial image.

2. Imagery processes

For visual, haptic, olfactory, gustatory and auditory imagery the corresponding mental images are the contents of working memory, which have a quasi-perceptual and isomorphic nature and are derived either from sensory inputs or from memory traces of these inputs. Spatial imagery is different from sensory imagery in that it is not bound to a single input modality. In order to establish the format of spatial mental imagery, the role of the input from different modalities needs to be determined. The underlying processes that are involved in sensory imagery and spatial imagery could be different. By investigating the neural correlates of different types of imagery processes the underlying mechanisms can be compared.

Most research on imagery has concentrated on visual imagery (see Kaski (2002), for a review). The general consensus seems to be that visual imagery and visual perception are two distinct processes that partially share a neural network. In an event-related potential (ERP) study Farah and colleagues (1988) have shown that visual perception and imagery of letters interact at an early stage over the visual cortex, suggesting that the mental images are represented visually. In a positron emission tomography (PET) and repetitive TMS (rTMS) study Kosslyn and colleagues (1999) have demonstrated that mental imagery of patterns of stripes recruits area 17 similar to visual perception (see Kosslyn et al., 2001), for a review). However, imagery does not require sensory processing. Visual imagery and perception are closely related and share similar mechanisms, but with unique characteristics. The idea of partially overlapping networks for visual imagery and perception has been further explored by Ganis and colleagues (2004). In an fMRI study where subjects visualized or saw faint drawings of objects, they also found a partially overlapping network. The overlap between imagery and perception was found predominantly in the frontal and parietal regions and less in the temporal and occipital regions. For an overview of a selection of literature on visual imagery see Table 1.

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3. Spatial language

An intriguing question is whether a more indirect input, such as spatial language, goes beyond a mere propositional format and can provide information about the environment needed for navigation and other spatial actions such as distance comparison. There are
Table 1
A selection of important literature on imagery, blindness and spatial language comprehension.

<table>
<thead>
<tr>
<th>Author et al. (2001)</th>
<th>Auditory imagery</th>
<th>fMRI: imagery of a single tone</th>
<th>No perception condition was included</th>
<th>Medial, inferior and middle frontal, precuneus, superior temporal and anterior cingulate gyrus. Bilateral primary and secondary auditory areas</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jeannerod (1995)</td>
<td>Motor imagery</td>
<td>Review</td>
<td>Motor imagery and action execution share similar networks</td>
<td>Olfactory imagery can produce similar effects as experiencing an odor</td>
</tr>
<tr>
<td>Stevenson and Case (2005)</td>
<td>Olfactory imagery</td>
<td>Review</td>
<td>Olfactory imagery exists, but can be hard to measure</td>
<td>Olfactory imagery is linked to information processing during imagery, and can activate similar patterns</td>
</tr>
<tr>
<td>Carpenter et al. (1999)</td>
<td>Spatial imagery</td>
<td>fMRI: spatial sentence-picture verification</td>
<td>There is activation of linguistic and spatial networks during spatial sentence comprehension</td>
<td>Left posterior temporal gyrus: language comprehension, left and right parietal regions: visuo-spatial processing</td>
</tr>
<tr>
<td>Creem and Proffitt (2001)</td>
<td>Spatial imagery</td>
<td>Review</td>
<td>“Where” and “how” systems are structurally and functionally organized in the posterior parietal lobe</td>
<td>Posterior parietal cortex: spatial transformations</td>
</tr>
<tr>
<td>Galati et al. (2000)</td>
<td>Spatial imagery</td>
<td>fMRI: egocentric and allocentric judgment of horizontal lines</td>
<td>The allocentric task activates a subset of the areas involved</td>
<td>Common to both tasks: right SPL and right IPS</td>
</tr>
<tr>
<td>Greffkes et al. (2002)</td>
<td>Spatial imagery</td>
<td>fMRI: delayed match-to-sample task</td>
<td>Two objects had to be compared haptically or visually, or cross-modal</td>
<td>Cross-modal matching of visual and haptic object information: left IPS</td>
</tr>
<tr>
<td>Laeng (1994) Spatial imagery</td>
<td>Lesion study: categorical and coordinate judgments</td>
<td>3D shape matching</td>
<td>Lateralized</td>
<td>LH-patients: impaired on categorical judgments, RH-patients: impaired on coordinate judgments</td>
</tr>
<tr>
<td>Mellet et al. (2000)</td>
<td>Spatial imagery</td>
<td>fMRI: mental navigation and mental map task based on route and survey perspective</td>
<td>Both tasks activate a parieto-frontal network involved in spatial mental imagery</td>
<td>Spatial mental imagery: IPS, superior frontal sulcus, middle frontal gyrus and pre-supplementary motor area</td>
</tr>
<tr>
<td>Ricciardi et al. (2006)</td>
<td>Spatial imagery</td>
<td>fMRI: haptic and visual spatial one-back matrix task</td>
<td>Locations on two matrices had to be compared</td>
<td>Haptic and visual maintenance activates a fronto-parietal network including the bilateral precuneus and IPS</td>
</tr>
<tr>
<td>Saito et al. (2003) Spatial imagery</td>
<td>fMRI: haptic and visual cross-modal shape matching</td>
<td>2D shape matching</td>
<td></td>
<td>Shape information is integrated in the posterior IPS</td>
</tr>
<tr>
<td>Trojano et al. (2002)</td>
<td>Spatial imagery</td>
<td>fMRI: mental clock task with categorical and coordinate judgments</td>
<td>Categorical and coordinate spatial relations are lateralized</td>
<td>Categorical: left SPL and AG. Coordinate: right SPL and AG</td>
</tr>
<tr>
<td>Trojano et al. (2006)</td>
<td>Spatial imagery</td>
<td>rTMS: mental clock task with categorical and coordinate judgments</td>
<td>rTMS over the posterior parietal cortex</td>
<td>Categorical: impaired after left parietal stimulation. Coordinate: impaired after right parietal stimulation</td>
</tr>
<tr>
<td>Goyal et al. (2006) Tactile imagery</td>
<td>fMRI: tactile imagery and perception of a static or moving face/non-face</td>
<td>In late blind, but not in congenitally blind, extrastriate visual areas show cross-modal activation for visual and tactile processing</td>
<td></td>
<td>MT/5 and FFA are involved in imagery of moving patterns or faces in late blind and sighted. In late blind these areas were also active during tactile perception</td>
</tr>
<tr>
<td>Uhll et al. (1994) Tactile imagery</td>
<td>EEG: tactile imagery of texture</td>
<td>The blind also activate the primary visual cortex. The sighted also reported visual imagery, which could account for their occipital lobe activation</td>
<td></td>
<td>Parietal sensory association cortex: tactile imagery in the blind and sighted</td>
</tr>
<tr>
<td>Yoo et al. (2003) Tactile imagery</td>
<td>fMRI: Tactile stimulation versus tactile imagery</td>
<td>Specific areas in the somatosensory areas were involved in tactile perception only. Left parietal lobe was only active during imagery</td>
<td></td>
<td>Contralateral primary and secondary somatosensory areas, precentral gyrus and left parietal lobe</td>
</tr>
<tr>
<td>Kosslyn et al. (2001) Visual and auditory imagery</td>
<td>Review</td>
<td>Mental imagery recruits similar neural networks as actual perception, but imagery does not require sensory processing. This is also true for auditory processing and imagery</td>
<td></td>
<td>Primary visual cortex active during perception and imagery. Primary auditory cortex active during perception only</td>
</tr>
<tr>
<td>Farah (1989) Visual imagery</td>
<td>Image generation and rotation</td>
<td>ERP's showed lateralization for different tasks. There is also evidence for a 'what' and 'where' distinction in imagery</td>
<td></td>
<td>Occipital cortex and higher order visual areas in the parietal and temporal lobes are involved in perception and imagery</td>
</tr>
<tr>
<td>Ganis et al. (2004) Visual imagery</td>
<td>fMRI: visualization or perception of faint drawing with judging specific aspects</td>
<td>Visual imagery and visual perception recruit very similar networks. The overlap is largest in the frontal and parietal regions and less in the temporal and occipital regions</td>
<td></td>
<td>Occipital cortex and higher order visual areas in the parietal and temporal lobes are involved in perception and imagery</td>
</tr>
<tr>
<td>Kaski (2002) Visual imagery</td>
<td>Review</td>
<td>Mental scanning task</td>
<td></td>
<td>Occipital cortex and higher order visual areas in the parietal and temporal lobes are involved in perception and imagery</td>
</tr>
<tr>
<td>Kosslyn et al. (1978) Visual imagery</td>
<td>Four tasks: image generation, image maintenance, image scanning and image rotation</td>
<td>Perception and visual imagery are closely related and have common mechanisms with unique characteristics</td>
<td></td>
<td>Occipital cortex and higher order visual areas in the parietal and temporal lobes are involved in perception and imagery</td>
</tr>
<tr>
<td>Kosslyn et al. (1990) Visual imagery</td>
<td>PET and rTMS: visualization of stripe patterns</td>
<td>Early visual cortex is involved in the visualization of stimuli and the activation is linked to information processing</td>
<td></td>
<td>Occipital cortex and higher order visual areas in the parietal and temporal lobes are involved in perception and imagery</td>
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<tr>
<td>Kosslyn et al. (1999) Visual imagery</td>
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<tr>
<td>Author</td>
<td>Modality</td>
<td>Task</td>
<td>Comments</td>
<td>Brain Areas</td>
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<tr>
<td>Mazard, Laou, Joliot, and Mellet (2005)</td>
<td>Visual imagery</td>
<td>fMRI: mental inspection and perception of object and non-object drawings</td>
<td>Imagery resulted in stronger left inferior frontal and inferior temporal gyrus activation than perception of objects. This could reflect verbal retrieval of the object.</td>
<td>The left occipito-temporal-frontal network is strongly activated when imagining objects versus non-objects. Figurative imagery could involve V1.</td>
</tr>
<tr>
<td>Almen et al. (2001)</td>
<td>Imagery and blindness</td>
<td>Odd-one-out and spatial imagery task with spatial interference</td>
<td>Blind were able to perform the spatial and pictorial imagery tasks, but made more errors than sighted subjects.</td>
<td>In blind and visually impaired the visual cortices reorganize.</td>
</tr>
<tr>
<td>Cattaneo et al. (2008)</td>
<td>Imagery and blindness</td>
<td>Review</td>
<td>Blind and sighted perform similar on spatial tasks, but subtle differences exist which could be due to sequential processing instead of parallel processing in the blind.</td>
<td></td>
</tr>
<tr>
<td>Cornoldi et al. (2009)</td>
<td>Imagery and blindness</td>
<td>2D mental pathway task</td>
<td>Blind and sighted perform the same when using a verbal strategy. When using a spatial strategy blind perform poorer than sighted.</td>
<td></td>
</tr>
<tr>
<td>De Reni and Cornoldi (1988)</td>
<td>Imagery and blindness</td>
<td>Memorization of single nouns, pairs or triplets</td>
<td>When memory load was high blind subjects were impaired. Blind process spatial images similar to sighted, but require slightly more time. Metric spatial information is preserved.</td>
<td></td>
</tr>
<tr>
<td>Kerr (1983)</td>
<td>Imagery and blindness</td>
<td>Mental scanning, scanning objects with different sizes, cued-recall test</td>
<td>Blind were able to perform the spatial and pictorial imagery tasks, but made more errors than sighted subjects.</td>
<td></td>
</tr>
<tr>
<td>Klatzky and Golledge (1995)</td>
<td>Imagery and blindness</td>
<td>A battery of ‘tabletop’ and spatial locomotor tasks</td>
<td>Performance of early blind, late blind and sighted was highly comparable. However, a linear discriminant analysis could distinguish three groups.</td>
<td></td>
</tr>
<tr>
<td>Knauff and May (2006)</td>
<td>Imagery and blindness</td>
<td>Deductive reasoning</td>
<td>Congenitally blind perform less accurately and slower than sighted subjects. But, sighted subjects suffer from the visual impedance effect, congenitally blind do not.</td>
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</tr>
<tr>
<td>Lambert et al. (2004)</td>
<td>Imagery and blindness</td>
<td>fMRI: mental imagery from animal names vs. listening to abstract words</td>
<td>Mental imagery of animals activates V1 in blind subjects. The ventral pathway processes figurative features while the dorsal pathway processes dimensional and spatial features. Blind subjects generate mental images in the dorsal pathway and they rely on haptic sensitivity.</td>
<td>V1 active during imagery. Visual for sighted, haptic for blind.</td>
</tr>
<tr>
<td>Noordzij et al. (2006b)</td>
<td>Imagery and blindness</td>
<td>Route and survey descriptions of an environment: three spatial tasks</td>
<td>Early and late blind can build up a spatial mental model from a verbal description, but more efficiently from route descriptions. Visual experience is not essential for the development of spatial representations.</td>
<td></td>
</tr>
<tr>
<td>Noordzij et al. (2007)</td>
<td>Imagery and blindness</td>
<td>Visual, spatial, auditory imagery tasks</td>
<td>There were no differences between blind and sighted subjects on the auditory imagery task. However, for the spatial imagery task there was a benefit from visual experience.</td>
<td></td>
</tr>
<tr>
<td>Postma et al. (2007)</td>
<td>Imagery and blindness</td>
<td>Haptic matching shapes to a cut-out board and giving verbal labels to the locations</td>
<td>Early and late blind were faster than blindfolded sighted. Blind used more object-references in the verbal labels, while sighted referred more to the surrounding frame.</td>
<td></td>
</tr>
<tr>
<td>Postma et al. (2008)</td>
<td>Imagery and blindness</td>
<td>Haptic parallel-setting task</td>
<td>In a direct setting condition early blind, late blind and sighted performed similar. With a delay, late blind and sighted improved due to the use of visual imagery. Early blind did not improve performance the same for blind and sighted.</td>
<td></td>
</tr>
<tr>
<td>Vanlierde et al. (2003)</td>
<td>Imagery and blindness</td>
<td>PET: 2D pattern symmetry recognition task</td>
<td>Verbal memory control task</td>
<td>Visuo-spatial imagery activates precuneus, SPL and occipital gyri in both blind and sighted.</td>
</tr>
<tr>
<td>Vanlierde and Wanet-Defalque (2004)</td>
<td>Imagery and blindness</td>
<td>2D pattern symmetry recognition task</td>
<td>Performance was the same for blind and sighted, but with different strategies. Sighted and late blind use a visuo-spatial strategy. Early blind a coordinate (X,Y) strategy.</td>
<td></td>
</tr>
<tr>
<td>Vecchi (2001)</td>
<td>Imagery and blindness</td>
<td>3D matrix spatial task</td>
<td>Visuo-spatial working memory is involved in spatial mental imagery. However, it is differently organized in blind subjects due to serial processing. Congenitally blind and sighted performed the same on single matrices. Blind were better at integrating two matrices than at remembering both. In sighted the pattern was reversed.</td>
<td></td>
</tr>
<tr>
<td>Vecchi et al. (2004)</td>
<td>Imagery and blindness</td>
<td>2D matrix spatial task</td>
<td>Visuo-spatial imagery activates precuneus, SPL and occipital gyri in both blind and sighted.</td>
<td></td>
</tr>
<tr>
<td>Baciu et al. (1999)</td>
<td>Spatial language comprehension</td>
<td>fMRI: dot-bar categorical/coordinate task</td>
<td>There is hemispheric specialization for spatial relations. During practice the activity in the right angular gyrus decreases, while the activity in the left homologue increases. This could be due to the formation of new categories.</td>
<td>Left AG: categorical spatial relations. Right AG: coordinate relations</td>
</tr>
<tr>
<td>Damasio et al. (2001)</td>
<td>Spatial language comprehension</td>
<td>PET: naming actions and spatial relations</td>
<td>The left SMC is perhaps related to retrieving spatial prepositions. The right SMC is associated with the conceptual part of processing spatial relations</td>
<td>Left SMC: processing spatial relations. Right SMC: naming spatial relations from abstract shapes (continued on next page)</td>
</tr>
</tbody>
</table>
two ways in which a spatial sentence can be interpreted in working memory. It is processed either by a verbal strategy, or by a pictorial strategy (MacLeod, Hunt, & Mathews, 1978). When spatial language is processed by means of a verbal strategy the propositional information of the sentence is analyzed and maintained in working memory. However, when a pictorial strategy is used the spatial description is parsed and then transformed into a spatial image (Reichle et al., 2000). This dichotomy is similar to the Dual Coding theory proposed by Paivio (1971) which states that information can be represented in verbal and image codes. Noordzij and colleagues (2005) have shown that visual-spatial strategy activates parietal areas.

The finding by Noordzij and colleagues (2005) stresses an important issue. In their task the subjects only generated a spatial image when a picture was expected. Perhaps the generation of a spatial image depends on the task and the instructions. In an experiment with more complex descriptions of an environment subjects performed a priming task (Noordzij & Postma, 2005). There were three priming conditions: close in text/close in space, far in text/close in space, and far in text/far in space. The results showed that a spatial priming effect occurred only for metric distances and not for text distances. Subjects responded faster to targets close in space to a prime than to targets far in space to a prime. This effect was not found for textual distance. This finding indicates that when the memory load increases people adopt a pictorial strategy. The level of automatic generation of a spatial image from spatial language can also be influenced by the specific task instructions. Avraamides and colleagues (2004) demonstrated that in remembering the orientation and distances of multiple targets spontaneous processing results in less variability in the responses for visual perception than for spatial language. However, after forced spatial updating, by letting the subject walk backwards after learning, the results for visual perception and spatial language were similar. These results confirm that visual and verbal inputs can generate spatial images that support functionally equivalent behavior.

4. Spatial Imagery

The general pattern of overlap between sensory processing and corresponding mental imagery cannot be transferred easily to spatial imagery since there is no such thing as direct spatial sensory perception. Instead spatial images are actively constructed from multiple targets.

For example, Denis and Zimmer (1992) reported on a series of experiments to test whether verbal descriptions could be adequately converted into a spatial image. The results showed that subjects took longer to scan longer distances and were later asked to mentally scan from one location to the other. In one of their experiments subjects had to study a map with locations and were later asked to mentally scan from one location to the other location. The results show that subjects took longer to scan longer distances. This indicates that the metric properties of the map are preserved during imagery, and that functional proximity on the image is similar to the physical proximity on the map (Reisberg, 1997).

Notably, the analogy between the physical world and the spatial image is also found when the image is derived from a verbal description (De Vega et al., 2001; Denis, Pazzaglia, Cornoldi, & Bertolo, 1999; Loomis, Klitzky, Avraamides, Lippa, & Gollledge, 2007; Noordzij & Postma, 2005) and the relevant spatial information can be retrieved from both types of inputs. For example, Denis and Zimmer (1992) reported on a series of experiments to test whether verbal descriptions could be adequately converted into a spatial image.
mental representation. They conducted a spatial priming, distance comparison and mental scanning task. Their findings suggest that verbal descriptions can be used to generate a mental representation similar to visual experience. Additionally, both mental representations also show reliable metric properties. This finding was replicated by Denis (2008) in a distance comparison task based on verbal descriptions. In addition to this task subjects were tested on the Minnesota Paper Form Board, which measures visuo-spatial imagery capabilities. Denis found that high visuo-spatial imagers outperformed low visuo-spatial imagers in the difficult trials. Although the spatial images based on spatial language and perception seem to be highly alike on a behavioral level, the question remains whether they also share a similar neural representation. The functional equivalence of spatial images from verbal and perceptual inputs could be due to similar, but distinct processes that combine modal representations, or because both inputs feed into an abstract amodal representation.

Modal information can be combined in either a multimodal or a supramodal representation. As stated in the introduction multimodal representations are established in modality-specific brain areas (Barsalou, 1999). In his theory on perceptual symbol systems Barsalou (1999) argues that spatial concepts are also grounded and are simulators of schematic perceptual symbol information and, therefore, are multimodal. If spatial images are indeed multimodal then only modality-specific brain areas will be activated when evaluating the image, for example through simulation. There will be no specific brain areas that represent a spatial image, but are not linked to a sensory input modality. An example of a multimodal representation is shown in panel A of Fig. 1. The mental images of different input sources are combined into a multimodal spatial image. Since the modality-specific input is maintained, this model can explain subtle to moderate behavioral differences on spatial tasks with different input modalities. For example, there was functional equivalence from visual perception and verbal descriptions of a spatial layout. However, without forced spatial updating subjects performed slightly better on distance judgments after visual perception than after verbal descriptions of a spatial layout (Avraamides et al., 2004). On the other hand, supramodal representations exceed the input from different modalities but maintain modality-specific information (Barsalou, 1999). Therefore, if the imagery mechanism involves a supramodal process we can expect both a supramodal representation in a distinct area, and an overlap with the associated modalities. For example, when spatial images are generated from spatial language we could expect language areas to be active as well as a supramodal area. When spatial imagery is a supramodal process the input modality will be reflected in the activation pattern. If the input for spatial images is visual, then a trace of the input should remain when the spatial image is activated. This is portrayed in panel B of Fig. 1. The bi-directional arrows between the spatial image and the input represent the trace of overlap with the associated modality. This model could also account for the subtle to moderate behavioral differences as mentioned above, since a link with the input modality is preserved. However, if spatial imagery is a more abstract process and considered amodal, then there should be no reference to the original input modality. Amodal processes are independent from input modality and are not necessarily constructed from multiple input sources. Regardless of the input modality that contributed to the spatial image, the same pattern of activation in a specific area is to be expected. This model has some similarities to the model described by Bryant (1997). He describes a spatial representation system (SRS) framework in which the SRS receives input from different modalities, as well as linguistic information. The relevant spatial information is extracted and combined with general knowledge into a spatial mental model. This final step, the spatial mental model, could be our amodal representation, although we do not specify a SRS as Bryant does. Panel C of Fig. 1 demonstrates such an abstract representation. The arrows from the input levels to the spatial image only go in one direction. Once the spatial image is formed, the modality-specific input can no longer be reactivated. In order to account for the behavioral differences between verbal descriptions and visual perception we need to make the assumption that both inputs generate a highly similar spatial image, but the quality differs slightly. As a result behavior is equivalent on a functional level, but might differ at the level of availability of information.

Moreover, different input channels can have different relative contributions to the spatial image, as tentatively displayed in Fig. 1. The emphasis on visual input stresses the strong dependence on visual information, which might account for the initially slightly better performance after visual perception in the study by Avraamides and colleagues (2004). Language and motor input are the next most important sources of information which contribute to

![Fig. 1. Three different models of how different sources of information can contribute to the generation of a spatial image. The line width represents a schematic weighting of the contribution of the different sources. Panel A is a multimodal representation established in modality-specific brain areas. Together these form the multimodal representation. Panel B is a supramodal representation, which exceeds modality-specific input to generate a spatial image, but maintains a bi-directional link with modality-specific input. Panel C is an amodal representation in which a spatial image is extracted from the input and no backward connections remain.](image-url)
spatial images (Cattaneo et al., 2008; Knauff & May, 2006). The presence of bi-directional arrows also enables switching between modalities during imagery. For example, in a tactile task sighted subjects might also retrieve visual information, especially if a delay is induced in the task (Zuidhoek, Kappers, Van der Lubbe, & Postma, 2003). The combination of modalities can strengthen the mental image. Whether this process works with direct input or through mental imagery will not be discussed. Transfer between modalities was also found by Cattaneo and Vecchi (2008). In a 2D mental gesture task subjects had to explore a matrix visually or haptically and were tested on a modality congruent or incongruent matrix. The results show that there were modality-specific effects: a general advantage for visual exploration and similar results for matrices explored in the same modality (irrespective of the testing modality). However, the fact that there was no significant difference between congruent or unimodal and incongruent or cross-modal conditions indicates that there was also a supramodal representation. Further research is needed in order to disentangle the relative contributions of different sources of inputs and the associated spatial images.

5. Neural correlates of spatial imagery

The first systematic studies of the neural correlates of visuo-spatial mental imagery date back three decades. The research on visuo-spatial mental imagery started out with the determination of the different components of imagery. Farah (1989) and Kosslyn and colleagues (1990) revealed several independent components of visuo-spatial mental imagery. These components are image generation, image maintenance, image scanning and image rotation. In an ERP study Farah (1989) found that image generation and image rotation are lateralized. Image generation depends on activation in the left posterior areas while mental rotation depends on activation in the right posterior areas.

The parietal lobe has also been associated with spatial updating (see Creem and Proffitt (2001) for a review) and coding different elements of space, see Table 1 for an overview of relevant papers. For example, Galati and colleagues (2000) reported activation of the right superior parietal lobule (SPL) and right intraparietal sulcus (IPS), common to egocentric and allocentric judgments of horizontal lines in an fMRI task. The IPS was also reported by Mellet and colleagues (2000). In their fMRI experiment this area was associated with spatial updating. The combination of modalities can strengthen the evidence of lateralization of categorical and coordinate tasks.


6. Blindness and spatial imagery

By investigating the process of spatial imagery in individuals who have been blind since they were born it is possible to disentangle whether or not spatial imagery is bound to a modality, with

metric relations. Trojano and colleagues (2002) tested the mental clock task, based on Paivio (1978), in an fMRI paradigm. They found that the categorical task activated the left SPL and left angular gyrus (AG), while the coordinate task activated the right SPL and right AG. The activation of the AG was replicated in a dot-bar task, which also involved categorical and coordinate judgments (Baciu et al., 1999). As mentioned before, neuroimaging techniques such as EEG and fMRI establish correlations between neuroanatomy and function. The lateralization for categorical and coordinate spatial processing was confirmed by rTMS (Trojano, Conson, Maffei, & Grossi, 2006) as well as by the evidence from stroke patients. Laeng (1994) tested 30 patients with left hemisphere damage and 30 patients with right hemisphere damage on a perceptual categorical/coordinate task. The findings from these patients also strengthen the evidence of lateralization of categorical and coordinate processing (see Jager and Postma (2003), for a review on a wide variety of researches on hemispheric lateralization).

Categorical spatial relations are closely related to spatial language, which is also demonstrated by the left hemispheric involvement. These categorical spatial relations are often used in spatial imagery instructions and spatial language in general.

Damasio and colleagues (2001) have shown, in a PET study, that in sighted subjects areas in the left parietal lobe are involved in processing spatial relations. In particular, the left supramarginal gyrus (SMG) was activated while naming spatial relations between objects. In an fMRI study Carpenter and colleagues (1999) asked subjects to read spatial sentences that had to be compared to a picture. This task activated the right posterior temporal gyrus, which is considered a language comprehension area. Furthermore, bilateral parietal areas were associated with spatial processing. These areas included the SPL, the posterior SMG and the AG. Both the left SMG and the left AG are involved in processing spatial relations and could be the interfaces for converting spatial language into spatial representations. The activity found in the left AG and SMG has been associated with processing spatial relations and locative prepositions in particular (for reviews see Chatterjee (2008), Kemmerer (2006)).

Tranel and Kemmerer (2004) conducted a lesion study and found that the highest region of lesion overlap in patients, who were impaired on processing locative prepositions, was found in the left frontal operculum and left SMG. Subsequently, it has been shown with fMRI that the left SMG is activated when people process a spatial sentence in a verbal or a visuo-spatial context (Noordzij et al., 2008). In this experiment subjects had to verify a spatial sentence to either another sentence (verbal context), or a picture (visuo-spatial context). Noordzij and colleagues (2008) concluded that the function of the left SMG is to generate an amodal representation of locative prepositions which can be flexibly compared to verbal or visuo-spatial information.

Based on our current definitions of amodal, multimodal and supramodal representations we wish to conclude that the left SMG might be a neural correlate of a supramodal representation instead of an amodal representation. It seems unlikely that this representation is multimodal, since it is found in the same area in both verbal and visuo-spatial contexts. However, it could be that the left SMG supports a supramodal representation while other areas support the modality-specific activation. The current neuroimaging evidence does not provide enough information to dissociate between amodal and supramodal spatial imagery.
particular emphasis upon the visual modality. Studying the results from experiments with blind and sighted can provide evidence for the modality specificity of spatial images. Suppose that spatial imagery is a multimodal representation of spatial configurations, then the visual representations will be absent in the blind. This will provide an opportunity to evaluate the development of the system in the absence of input from the visual channel. However, other modal and amodal representations will still be present. The absence of visual spatial representations in blind might lead to behavioral differences with sighted. If we assume that spatial imagery is a supramodal process it will use both forward and backward connections with the modal areas. In congenitally blind subjects the modal connection to the visual cortex for visual mental images will be absent. As a result the distribution of the inputs from different input channels shown in Fig. 1 might change, which could result in behavioral differences between the blind and sighted. However, if spatial imagery is amodal, then one would not expect any differences in the performance between blind and sighted since the spatial representations need not necessarily be constructed from the same input. The results from behavioral and neuroimaging studies can indicate whether or not spatial imagery is functionally and neuro-anatomically equivalent in blind and sighted subjects.

The distribution of the forward and backward connections in supramodal processing might change in the absence of vision. There might be little or no compensation as evidenced by equal weight distributions to all input channels, irrespective of the presence of visual input (see Fig. 2 panel A for a schematic distribution in sighted subjects and panel B for a comparison with blind subjects). However, another plausible situation might be the complete compensation for the visual input channel by higher weight distributions to the other channels (see Fig. 2 panel C). The second option seems plausible considering the plasticity of the visual cortex of blind people. People who are born blind lack any visual stimulation of the visual cortex. Instead of losing the functionality of the occipital cortex, reorganization occurs (e.g. Noppeney, 2007; Noppeney, Friston, Ashburner, Frackowiak, & Price, 2005). The visual cortex has become associated with non-visual functions such as tactile processing, Braille reading and other language functions (e.g. Amedi, Floel, Knecht, Zohary, & Cohen, 2004; Burton & McLauren, 2006; Cohen et al., 1997; Ofan & Zohary, 2007; Pascual-Leone, Amedi, Fregni, & Merabet, 2005). Moreover, the proportion of brain area involved in for example tactile processing increases. Therefore, the relative weights of the non-visual sources of information which can contribute to spatial images can change to compensate for the absence of vision.

Lambert and colleagues (2004) investigated the functionality of the visual cortex in blind and sighted with fMRI. Their subjects were instructed to form mental images from animal names and to listen to abstract words. They suggested that during mental imagery apart from the regular circuit (superior occipital, inferior and superior parietal areas, premotor area and visual association area) blind individuals also activate somatosensory areas and the temporal and fusiform gyrus. In blind subjects the dorsal pathway is activated when generating mental images from verbal instructions, which now relies on haptic sensitivity instead of on visual sensitivity. They conclude that the occipital cortex is active in blind individuals for haptic information and in sighted individuals for visual information. Research on plasticity in the blind has not only focused on tactile tasks, but also focused on auditory tasks (Amedi, Raz, Pianka, Malach, & Zohary, 2003; Burton, Snyder, Diamond, & Raichle, 2002; Noppeney, Friston, & Price, 2003; Röder, Stock, Bien, Neville, & Rösler, 2002; Sadato, Okada, Honda, & Yonekura, 2002). All the results indicate occipital cortex activity in early blind subjects. Interestingly, in all these experiments the task involved language processing, but in different modalities. This led Burton and colleagues (2002) to believe that the occipital cortex in blind individuals is involved in dealing with linguistic aspects. Indeed, their results support the notion that linguistic processes activate the occipital cortex in blind individuals. They postulate that blindness results in new mechanisms in especially the left occipital cortex. These mechanisms reach across multiple visual areas, the degree to which depends on the age of onset of the blindness. Burton and colleagues (2002) only found evidence of reorganization in blind individuals in the occipital cortex. During a verb generation task both early and late blind and the sighted control group showed similar activity in the language areas: the left inferior frontal gyrus, left dorsolateral prefrontal gyrus and left posterior superior temporal gyrus. Since general language processing seems to be preserved in the general language areas, with additional striate activation in the blind (for a review see Noppeney, 2007), it would be interesting to try and tease apart the involvement of the visual cortex in spatial imagery and its link to spatial language.

Although blind people lack visual information about their environment they are able to navigate. Apparently, the information they obtain from their other senses provides enough knowledge about the environment to find their way. Evidently, and as argued above, space can be represented by more than just visual information. There seems to be a common compound that is extracted from different sources of information. A reasonable candidate for such a common compound could be a spatial image, as shown in Fig. 1, panels B and C.

Thinus-Blanc and Gaunet (1997) give an elegant review of behavioral differences between blind and sighted subjects. They discuss literature on a variety of experiments measuring spatial ability. According to the authors, the inconsistencies in the experiments performed at that time made it hard to draw general conclusions. On the one hand, the trend in most experiments, discussed in their review, seemed that spatial memory is not affected by the age of onset of blindness (e.g. Loomis et al., 1993; Rieser, Guth, & Hill, 1986). On the other hand, inferential abilities to generate spatial relationships from information, which is not actu-
ally experienced at that moment, did appear to be affected by the age of onset (e.g. Byrne & Salter, 1983; Dodds, Howarth, & Carter, 1982; Rieser et al., 1986). The latter abilities are essential when you need to make a detour or a shortcut.

Thinus-Blanc and Gaunet (1997) describe a two-level model of spatial processing. In this model they make a distinction between schemata, which are abstract representations from specific maps, and simple rules of encoding, which can be deduced from specific spatial memories. The schemata are independent from the position of a person and are encoded with an exocentered reference frame. Simple encoding rules and specific spatial memories are encoded with an egocentered reference frame. These two different levels of encoding can yield a similar representation and give the same behavioral results on how spatial information is acquired and how this spatial knowledge is used. A logical assumption is that blind people rely more, or perhaps only, on the egocentered organized spatial information. All their spatial information is experienced from a body-centered perspective. This assumption is supported by Noordzij and colleagues (2006b), who found that blind subjects showed a preference for route descriptions (with a body-centered perspective), while sighted subjects preferred a survey description (with an environment-centered description). In a task where subjects had to haptically match shapes to the cutouts in a board and subsequently give a verbal description of the location, blind subjects referred more to other objects on the board, while the blindfolded sighted referred more to the surrounding frame (Postma, Zuidhoek, Noordzij, & Kappers, 2007). This finding is in line with the route and survey preference, respectively, in the study from Noordzij and colleagues (2006b).

Research on spatial processing abilities of the blind has revealed that blind individuals are able to generate spatial mental maps (e.g. Aleman, Van Lee, Mantione, Verkoijen, & De Haan, 2001; Kerr, 1983; Klitzky & Colledge, 1995). They can use descriptions to generate a spatial image in which spatial properties such as distance and location are preserved (see Table 1 for a selection of literature relevant to this discussion). Kerr (1983) showed that metric properties of objects and locations were preserved in blind and sighted, although the blind were slightly slower than the sighted. Blind subjects are also able to generate a mental representation of a clock and compare clock times (Noordzij et al., 2007). All subjects, early blind, late blind and sighted, showed the classical symbolic distance effect (Moyer & Bayer, 1976). This suggests that each group used spatial imagery to solve the task. Nevertheless, the early blind made more errors than the sighted and the late blind seemed to perform slightly better, which suggests a small advantage for visual experience.

In a recent review Cattaneo and colleagues (2008) discuss papers on the growing evidence that blind can rely on sensory input, such as auditory or haptic, and verbal input to overcome their visual deprivation. Vanlierde and colleagues provide evidence that blind subjects can rely on non-visual sensory input (Vanlierde, De Volder, Wanet-Defalque, & Veraart, 2003; Vanlierde & Wanet-Defalque, 2004). They describe similar performance for early blind, late blind and sighted on a pattern symmetry task about mental representations of verbal 2D patterns in a grid. While the accuracy was the same for blind and sighted, both groups used a different strategy. The sighted adopted a visuo-spatial strategy, while the blind adopted a “coordinate XY” strategy. Performance on several tasks appeared highly similar for blind and sighted, however, subtle to moderate differences were also found. For example Knauff and May (2006) showed that blind subjects are not susceptible to the “visual-impedance-effect” in deductive reasoning. Subjects had to make a decision about a situation and when the visual relations in the situation were easily imagined the sighted subjects were hindered. Although blind subjects were not hindered in this particular case, compared to the sighted, they were overall slower and less accurate. The seminal work by De Beni and Cornoldi (1988) has shown that similarities between blind and sighted can also rely on task properties. They conducted a memorization experiment where single nouns, pairs or triplets had to be remembered in connection with a cue. They found that blind subjects were impaired when the memory load increased (with noun pairs and triplets), but when the memory load was small the blind were able to create interactive images. A similar pattern was found by Vecchi and colleagues (2004). Blind subjects and sighted subjects performed on a par when a series of locations had to be remembered on a single matrix. However, blind subjects performed worse when the locations from two matrices had to be remembered than when the locations of the two matrices had to be integrated. This pattern was reversed for the sighted subjects. During visual perception it is common to handle multiple inputs, for haptic perception this is quite impossible.

These results indicate that when the memory load increased by the sequential memorization of two matrices the performance of the blind subjects decreased. Cattaneo and colleagues (2008) suggested that although performance of blind and blindfolded sighted subjects can be highly similar this could be due to the employment of different strategies, non-visual versus visual, respectively, as was also suggested by Thinus-Blanc and Gaunet (1997) and Vanlierde and Wanet-Defalque (2004). Cornoldi and colleagues (2009) systematically examined strategy effects in blind and sighted on a 2D mental pathway task. Three different strategies were found in both blind and sighted. Their strategies could be spatial, verbal or mixed. The results showed that when the entire pathway had to be remembered both groups performed the same when using a verbal strategy. However, when using a spatial strategy the blind performed worse than the sighted. This finding is in line with their previous work (De Beni & Cornoldi, 1988) in that this task with a high memory load is more difficult for the blind when using a spatial strategy.

Nevertheless, even in the absence of vision, congenitally blind people are able to generate a proper spatial image and use this information for a wide variety of spatial tasks and navigation. Given the subtle to moderate behavioral differences between blind and sighted, spatial imagery cannot be amodal, which would have resulted in identical behavioral performance for blind and sighted. Moreover, an amodal representation would not be sensitive to time manipulations. In a haptic parallel-setting task early blind and blindfolded sighted performed similarly in the direct setting condition (Postma, Zuidhoek, Noordzij, & Kappers, 2008). When a delay between feeling the reference bar and rotating the test bar was induced performance increased for late blind and blindfolded sighted participants, but did not change for early blind participants. According to the authors a delay induces visual mental imagery, which increases accuracy. The early blind are not able to use visual mental imagery, therefore, their performance remains the same as in the direct condition. Given an amodal representation it would not be possible to retrieve a visual mental representation to improve performance. Alternatively, spatial imagery could be multimodal or supramodal. In his perceptual symbol systems theory Barsalou (1999) initially referred to simulators of spatial relations as multimodal symbols. Moreover, through the process of conceptual combination simulations might easily lead to simulations of related concepts (Wu & Barsalou, 2009). This might also work during mental imagery and explain the possibility to take advantage from visual mental imagery in addition to spatial mental imagery in the haptic parallel-setting task, as mentioned above. According to our model (see panel A of Fig. 1) neuroimaging results should identify brain areas that are associated with the input modality. However, this would mean that in the sentence–sentence and sentence–picture verification tasks by Noordzij and colleagues (2008) the context manipulation should have revealed activation...
in different areas for each context, verbal and visual. Rather, they found activation in the left SMG that supported both contexts. This would suggest a supramodal representation with the left SMG as a possible neural correlate. In a response to the perceptual symbol systems theory Freksa and colleagues (1999) suggested that space can have a twofold role. It can either be a single perceptual symbol representing a specific location. This role would suggest a multimodal perceptual symbol similar to regular perceptual symbols of, for example, objects. Alternatively, space can organize perceptual symbols in providing structural constraints. Such spatial symbols combine a shared structure for different perceptual modalities. The latter role of spatial symbols supports our supramodal representation of spatial images, as shown in panel B of Fig. 1. Different perceptual inputs can feed into a shared spatial image, which represents the spatial organization in this specific example. In a reaction to the response by Freksa and colleagues (1999), Barsalou (1999) reasons that spatial symbols may depend on modality-specific systems, but also on modality-general systems. The findings discussed here, for example the functionally equivalent spatial images from verbal descriptions and perceptual input, suggest that these modality-general systems might indeed exist. The possible employment of different strategies for blind and sighted (Cattaneo et al., 2008; Cornoldi et al., 2009; Vanliere & Vanet-Defalque, 2004) could be a result of the recruitment of different neural networks. However, using completely different neural networks would probably yield large behavioral differences between the blind and sighted. Given the only subtle to moderate behavioral differences between blind and sighted, a certain degree of overlap in the underlying neural networks seems more plausible and would support the idea that spatial representations are supramodal. Further neuroimaging evidence on research with blind is needed to answer these questions.

7. Conclusions

Spatial images allow a mental representation preserving configurational layout of the outside world. Importantly, spatial images can be derived from different sources of information: e.g. visual inputs, somatosensory inputs, and spatial language. The main question addressed in this review was to what extent spatial images are intrinsically linked to modality-specific sources or whether they appear at a superordinate level. For sensory imagery, such as visual imagery, there is a high degree of overlap in the neural networks between perception and imagery. For spatial imagery several sources of information can be used for construction. Perceptual and verbal inputs can generate functionally equivalent spatial images and the relevant information can be addressed from both types of inputs. This supports the idea that spatial images are not modality-specific, but seem to appear at a superordinate level. According to the perceptual symbols system from Barsalou (1999) spatial images should be considered multimodal. However, this cannot explain the finding by Noordzij and colleagues (2008) that the left SMG is activated regardless of the context (verbal or visuo-spatial). Noordzij and colleagues (2008) have argued that their finding supports an amodal representation, however, according to our definitions this finding could also support a supramodal representation. Given that spatial images seem to appear at a superordinate level and can produce functionally relevant information, research with blind people has provided insight into the link between input and spatial images. Spatial language has proven to be a very elegant tool to generate spatial images, especially in the blind. Although behavior on numerous spatial tasks has shown a high degree of similarity between blind and sighted subjects, there are subtle to moderate differences. This supports a supramodal representation of spatial information, since an amodal representation would result in behaviorally identical results. As such, spatial imagery exceeds different input modalities, while forward and backward connections with the input modalities are preserved and multiple sources of information can be used to construct spatial images. The absent or functionally different connections in the occipital cortex of blind subjects could account for the behavioral differences. Based on our definition of supramodal we would like to suggest that the left SMG is involved in supramodal spatial imagery. The idea of a supramodal organization of the brain is supported by Cattaneo and colleagues (2008) who reported on supramodal organization for tactile perception in two other areas, namely the lateral occipital tactile-visual area and an area in the dorsal visual pathway involved in visual motor perception. Both areas were active not only during visual perception, but also during tactile perception. These findings could be an extension of the perceptual symbol systems proposed by Barsalou (1999). Besides multimodal perceptual representations that reside in modality-specific areas, spatial images can be considered supramodal with neural correlates that respond to different sources of inputs.

References


