NEW INSIGHTS INTO THE FUNCTIONS OF THE SUPERIOR TEMPORAL CORTEX

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One of the mysteries of the brain is the role of superior temporal cortex. Recent data have shed new light on the function of this area, supporting the idea that the rostral part of the superior temporal cortex acts as an interface between the dorsal and ventral streams of visual input processing to allow the exploration of both object-related and space-related information. The superior temporal cortex is also involved in processing species-specific vocalizations. It seems that, during evolution, the formerly bilateral functions of the superior temporal cortex have been segregated in the human brain between the left hemisphere, which subserves language, and the right hemisphere, which mediates spatial awareness and exploration.

SPATIAL NEGLECT
A lack of awareness of space and of object parts on the side contralateral to a brain injury.

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Although the superior temporal cortex in the left cerebral hemisphere of the human has long been known to subserve language processes, its function in the human right hemisphere has remained uncertain. It has been suggested[1,2] that lesions of the monkey superior temporal cortex induce behavioural abnormalities similar to those seen in humans with SPATIAL NEGLECT. However, since the early reports on patients with neglect, it has been believed that, in humans, the disorder is associated with lesions of the right inferior parietal lobule (FIG. 1a) and the junction area between the temporal, parietal and occipital lobes — the so-called 'TPO junction' (FIG. 1a). But in the monkey, ablation of the inferior parietal lobule (FIG. 1b) does not evoke the characteristic behaviour seen in human neglect. Instead, it causes misreaching for objects and inappropriate orientation of the hand. In view of this seeming discrepancy, my colleagues and I sought to determine whether previous reports on lesion location in human neglect might have been biased by the additional involvement of the optic radiation and neighbouring cortical areas in the posterior part of the right hemisphere[3]. In fact, this study led us to identify the crucial location for human spatial neglect in the right superior temporal cortex.

This surprising finding prompted the question: what are the functions of the intact right superior temporal cortex in monkey and human? Different experimental observations have led to divergent interpretations. Here I examine the neurophysiological and neuropsychological contributions to our understanding of the functions of the superior temporal cortex. I describe how these mechanisms might work together to create networked representations about the world, allowing us to interact successfully with our environment.

Spatial neglect in humans

A striking consequence of brain damage, particularly to the right hemisphere, can be the appearance of spatial neglect, in which patients no longer attend to the side contralateral to the lesion, and might even be unaware of that side of their own body. Patients with spatial neglect typically orient towards the ipsilesional side, and ignore contralesionally located people or objects. They might shave only one half of the face, dress just half of the body, or, when copying pictures, draw the details from only the ipsilateral side. When searching for targets in their surroundings, such patients show a characteristic bias in the centre of ocular and tactile exploratory movements towards the side of the lesion[4,5]
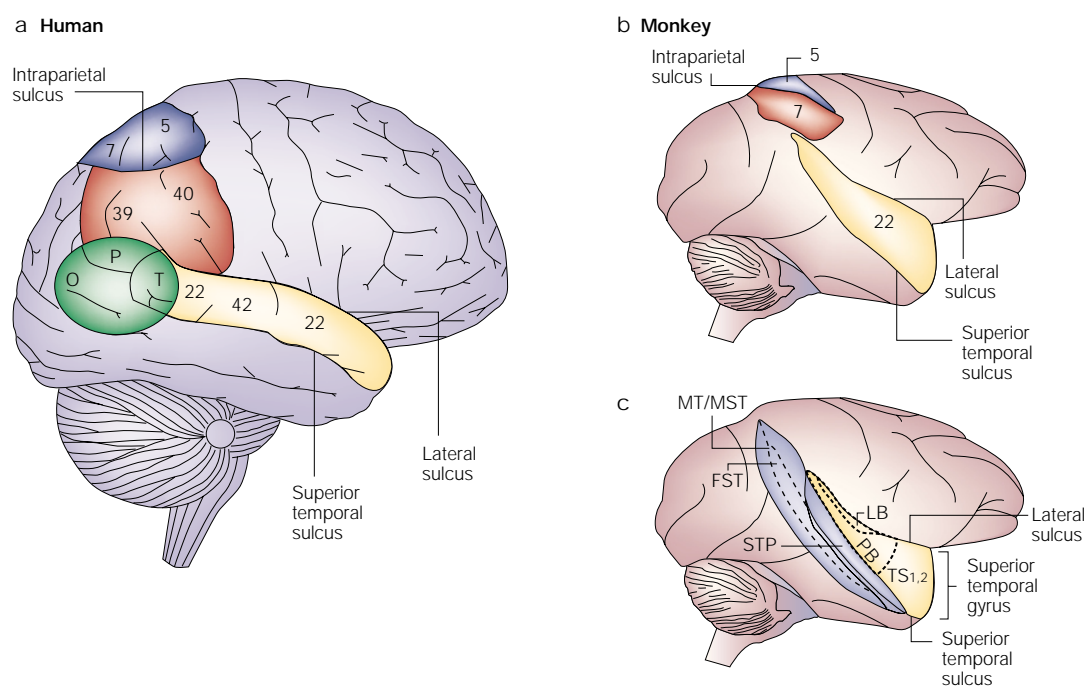
a Human

b Monkey

c

Figure 1 | **Organization of superior temporal and parietal cortex.** Superior temporal and parietal cortices are shown in the brains of **a** | the human and **b** | the macaque. The superior temporal gyrus (yellow) extends from the lateral sulcus to the superior temporal sulcus. The parietal lobe is divided by the intraparietal sulcus into a superior (dark blue) and an inferior (red) lobule. The green area in the human brain illustrates the junction area between the temporal (T), parietal (P) and occipital (O) lobes, termed the 'TPO junction'. Numerals designate cytoarchitectonic Brodmann areas. **c** | In the monkey cortex, the depth of the superior temporal suclus (light blue) has been opened up to reveal the location of the areas within it. FST, fundal superior temporal area; LB, lateral 'belt' area; MST, medial superior temporal area; MT, middle temporal area; PB, 'parabelt' region; STP, superior temporal polysensory area; $TS_{1,2}$, superior temporal areas TS1 and TS2.

SINGLE PHOTON EMISSION COMPUTED TOMOGRAPHY
A method in which images are generated by using radionuclides that emit single photons of a given energy. Images are captured at multiple positions by rotating the sensor around the subject; the three-dimensional distribution of radionuclides is then used to reconstruct the images. SPECT can be used to observe biochemical and physiological processes, as well as the size and volume of structures. Unlike positron emission tomography, SPECT requires the physical alignment of the photons for their detection, resulting in the loss of many available photons and the degradation of the image.

COLLATERAL TRIGONE
The ventricular region where the body, the posterior horn and the inferior horn of the lateral ventricle come together.

PARAFALCINE REGIONS
Cortical regions located adjacent to the falx cerebri, a sickle-shaped fold of the dura mater that dips sagittally from the skull between the cerebral hemispheres.

(FIG. 2). Patients might seem to be blind on the contralesional side, but perceive visual stimuli in that hemifield when explicitly instructed that such stimuli will appear there. This forced cueing is only transiently effective; patients do not adopt the compensatory shift to the contralesional side in the absence of forced requirements. So, although patients with neglect might see, feel and hear stimuli on the side opposite to the lesion, they do not react or respond to these stimuli spontaneously — they are not aware of this part of space.

Several imaging studies have investigated the neural correlate of spatial neglect in humans. An early analysis of computerized tomography (CT) scans of 10 patients with spatial neglect found that the inferior parietal lobule and the TPO junction (FIG. 1a) were crucial areas for spatial neglect[6]. More recent studies[7–11] have largely confirmed the observations of Heilman et al.[6], but have found additional pathology that leads to spatial neglect. Vallar and Perani[7] identified 14 neglect patients with lesions centred on either the inferior parietal lobule or the parieto-occipital junction, and 16 neglect patients in which the overlap area involved large parts of the frontal, temporal, parietal and occipital cortex. Leibovitch et al.[10,11] found a predominant involvement of the right parietal cortex with CT, and an involvement of the right TPO junction and anterior cingulate cortex using SINGLE PHOTON EMISSION COMPUTED TOMOGRAPHY (SPECT) in a large sample of more than

80 neglect patients. The CT scans also showed that the anterior, central and posterior white matter, as well as the primary motor and sensory cortices, were more involved in neglect patients than in brain-damaged control subjects without neglect. Samuelsson et al.[9] analysed the CT scans of 18 neglect patients, and found that the supramarginal gyrus and TPO junction were associated with neglect. Moreover, in 11 of the 15 patients with cortical damage, they found large lesions clustered in the posterior part of the middle temporal gyrus and/or the temporo-parietal paraventricular white matter at the level of the COLLATERAL TRIGONE.

Frontal lobe lesions rarely cause neglect; of 114 neglect patients investigated in three different studies[3,7,9], only two had a lesion confined to the frontal lobe. The crucial area in patients with such lesions seems to be the right inferior frontal gyrus (Brodmann area 44)[9,12]. Likewise, lesions restricted to the parietal lobe are seldom associated with spatial neglect. In a group of 67 neglect patients examined in two studies[3,9], only three had a lesion restricted to the parietal lobe. The occurrence of spatial neglect after a lesion of the right cingulate cortex is even more rare; it has been reported in only two cases[13,14]. However, even in these cases, the lesions did not affect the cingulate cortex exclusively: the medial, PARAFALCINE REGIONS of the frontal and/or parietal lobes were also affected, calling into question the role of the cingulate cortex in representing spatial awareness.
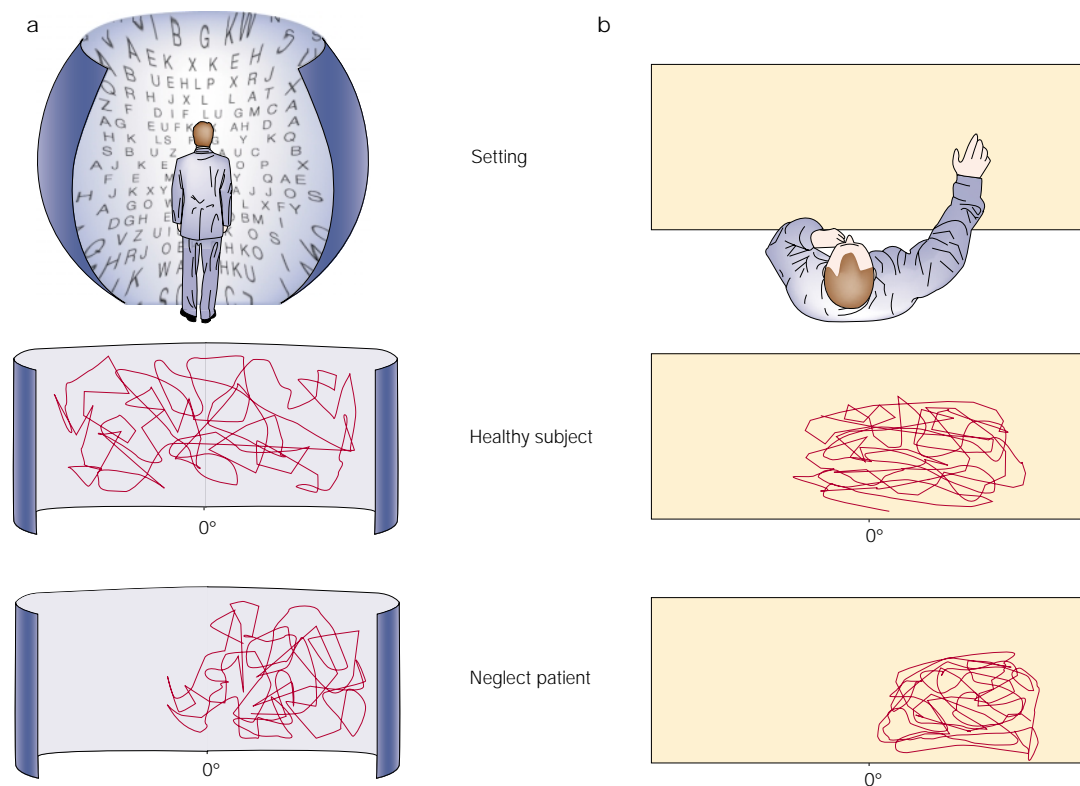
Figure 2 | **Scan paths during visual and tactile exploration of the surroundings.** The task consists of searching for a target **a** | in a visual scene with combined eye–head movements or **b** | on a table by tactile searching with the hand while the eyes are closed. Similar to a healthy subject, a neglect patient explores space with eye or hand movements that are symmetrically distributed around a preferred orientation in space. However, in the neglect patient, this centre of exploration is shifted to the right[4,5]. The average horizontal position of eye and hand movements lies right of the body's mid-sagittal plane. Information on the contralesional side is neglected.

Superior temporal cortex and neglect. Experimental lesions of the monkey posterior parietal cortex failed to elicit the complex behavioural abnormalities typically seen with spatial neglect in humans (for reviews, see REFS 15,16). This led to controversy about the anatomical and functional homology of human and monkey cortex. Whereas some investigators concluded that there is no homologue of the human inferior parietal lobule (Brodmann areas 39 and 40) in the monkey[17] (cf. FIG. 1a and b), others believed that the monkey homologue of human areas 39 and 40 is located outside the parietal cortex; for example, in the superior temporal sulcus (STS)[18,19] (FIG. 1).

In view of this debate, my group asked whether previous findings on lesion location in human neglect might have been complicated by the fact that these studies included a significant proportion of patients who suffered, not only from spatial neglect, but also from additional visual field defects[3]. If this were the case, lesion localization would have been biased towards regions associated with the latter defects; that is, towards posterior regions involving the optic radiation, and neighbouring cortical areas in the territory of the middle cerebral artery. In fact, if we excluded patients with additional visual field defects from our analysis, we found no involvement of the inferior parietal cortex (FIG. 1a) or the TPO

junction in neglect (FIG. 1a). Instead, the centre of lesion overlap covered the rostral portions of the right superior temporal gyrus (STG)[3].

This result is compatible with observations made in monkeys with lesions of the superior temporal cortex. Reduced orienting to contralaterally presented visual stimuli has been found in two monkeys after unilateral left- or right-sided lesions of the dorsal bank and depth of the STS[1] (FIG. 1b and c). Watson *et al.*[2] compared the effects of ablating the inferior parietal lobule (Brodmann area 7) or portions of the superior temporal cortex in monkeys by using a 'clinical' rating scale for various behavioural abnormalities that are seen in humans with spatial neglect. The authors recorded whether the monkeys ran into obstacles on the side opposite to their lesion, failed to move towards that side when it was appropriate, or explored the environment only ipsilateral to their lesion. They also evaluated whether the animals failed to orient with head, eye or hand movements to stimuli from the contralesional side, failed to orient to auditory stimuli on the contralesional side, or did not react to contralesional tactile stimuli. Watson *et al.* found that spatial neglect was observed with lesions of the superior temporal cortex that included both banks of the STS and extended well into the STG[2] (FIG. 1b and c). By contrast, no neglect was found after ablation of the inferior parietal lobule.

Unfortunately, only two of these five monkeys received a lesion at one location only. In all other animals in which Watson *et al.*[2] made STS lesions, ablation was added to pre-existing brain lesions (of inferior parietal cortex in two cases, and of frontal cortex and corpus callosum in the third). One of these monkeys (the one with frontal and corpus callosum defects) was categorized as having severe neglect, whereas neglect behaviour in the two other cases was rated as mild to moderate. In the only case in which an STS lesion was added to a contralateral inferior parietal lesion, no neglect was apparent. So, the results of this study have to be regarded with some caution. The work needs to be complemented by lesion or inactivation studies that focus selectively on the superior temporal cortex, without prior lesioning in other cortical areas.

Subcortical neglect. Over the past 40 years, various studies have documented that lesions restricted to the basal ganglia or the thalamus can also induce contralesional neglect. By using a LESION SUBTRACTION TECHNIQUE, my colleagues and I recently identified the structures within these subcortical nuclei that are crucial for spatial neglect[20]. In the right basal ganglia, the putamen and (to a much smaller degree) the caudate nucleus were found to be associated with neglect. Within the right thalamus, lesions of the pulvinar were, predominantly, found to be crucial for spatial neglect, complementing neurophysiological studies in monkeys and functional imaging studies in humans, which have supported a role for this thalamic region in attentional processes. For example, sectorial inactivation using microinjections of muscimol (a GABA (γ-aminobutyric acid) receptor agonist) within the pulvinar of the rhesus monkey revealed a slowing of attention shift in the direction contralateral to the injection site[21].

Cortico–subcortical network for spatial awareness
The importance of the STG, putamen, caudate nucleus and pulvinar in spatial neglect prompts the question of whether these structures are isolated loci that contribute to the representation of spatial awareness, or whether there are close anatomical connections between them. The association areas of the STG have direct connections with the putamen and the caudate nucleus[22]. The rostral and middle parts of the STG are connected to the rostroventral and caudoventral portions of the putamen, whereas the caudal portion of the STG projects more dorsally to the caudal putamen. In addition, the rostral and middle parts of the STG are connected with ventral portions of the caudate nucleus, whereas the caudal portion of the STG projects more dorsally, within caudate head and body[22]. So, the two structures within the basal ganglia that are relevant for spatial neglect[20] show dense anatomical connectivity with the entire area of lesion overlap that is found in patients with spatial neglect after cortical damage[3].

The thalamic pulvinar is subdivided into medial, lateral, inferior and anterior nuclei[23]. The inferior and later-
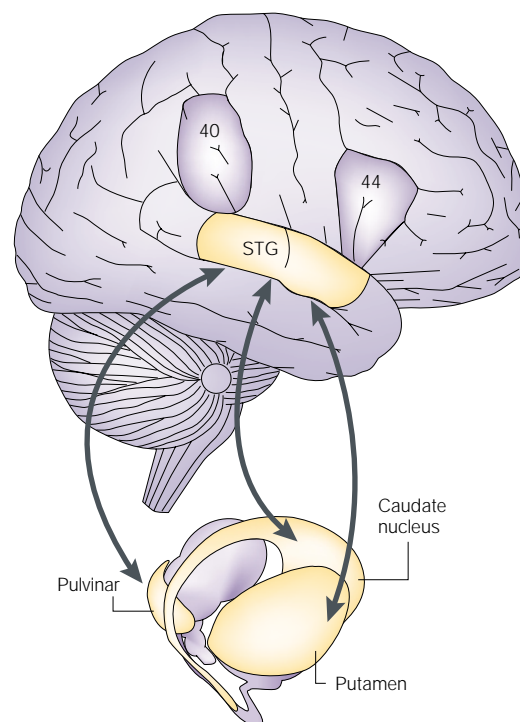
Figure 3 | **The cortico–subcortical network that underlies spatial neglect.** The putamen, caudate nucleus and pulvinar are the subcortical nuclei that are associated with neglect behaviour[20]. They are known to have direct anatomical connections with the superior temporal cortex. The superior temporal gyrus (STG) is the area that is typically involved in patients with neglect after cortical damage[3]. Lesions confined to either the parietal or the frontal lobe (Brodmann areas 40 or 44) are rarely associated with spatial neglect (parietal lobe[3,9], 4–5%; frontal lobe[3,7,9], ~2%).

al nuclei receive projections from the superior colliculus, pretectum, and striate and extrastriate visual cortex. By contrast, connections of other parts of the pulvinar complex are less obviously visual. The anterior pulvinar nucleus is connected to parts of areas 5 and 7, adjacent to the primary sensory cortex. With respect to the cortical correlate of spatial neglect[3], it is interesting that the thalamocortical axons that arise in the medial pulvinar nucleus of the monkey project to the entire STG[23–25]. The cortical projections of the medial pulvinar stretch from the temporal pole to the exposed surface of the STG through the anterior bank of the STS. So, these thalamic projections also encompass the entire area of lesion overlap found in neglect patients with cortical damage[3].

Therefore, the right putamen, caudate nucleus, pulvinar and STG form a coherent cortico–subcortical network for representing spatial awareness. FIGURE 3 illustrates this network, taking into account the empirical findings on lesion location in the parietal and frontal cortices[3,7,9].

Functions of intact superior temporal cortex
On the basis of the traditional belief that neglect in humans is predominantly induced by lesions of the posterior parietal lobe, Watson *et al.*[2] interpreted their observations with STS lesions as indicating that the

monkey superior temporal region is homologous to the human inferior parietal lobule (Brodmann areas 39 and 40). By contrast, Milner and Goodale[19] proposed that "mechanisms have evolved in the inferior parietal or parietotemporal region of humans for dealing with abstract spatial processing that are simply not available for this purpose in monkeys". However, in line with the interpretation of Watson *et al.*, Milner and Goodale stated that "this recently evolved system may have as its non-human antecedent such polysensory areas as STP [the superior temporal polysensory area; cf. FIG. 1c], which lies in the depths of the STS of the monkey". In the light of recent anatomical findings in humans with neglect[3], there is no further need to claim an 'evolutionary shift' of this function from the temporal to the parietal lobe[2,19]. Rather, the few data available at present indicate that such a shift might have taken place within the superior temporal cortex — from the monkey STS[1,2] to a more dorsal location on the human STG[3].

But what exactly is the role of the intact superior temporal cortex? In the caudal part of superior temporal cortex, Chakraborty and Thier[26] identified the visual posterior sylvian area (VPS), which is located in the depth of the lateral sulcus, as a structure that is crucial for the monkeys' subjective sense of spatial stability. More rostrally, but closely connected with the VPS, is the parieto-insular vestibular cortex (PIVC)[27,28]. This area integrates vestibular, somatosensory and visual cues to generate a multi-modal neuronal representation of subject motion and orientation in space. The little we do know of the VPS indicates that it receives visual input from the motion areas located in the caudal part of the STS. This latter region of caudal superior temporal cortex encompasses areas such as the medial superior temporal area (MST), the middle temporal area (MT) and the fundal superior temporal area (FST) (FIG. 1c). These areas are part of the dorsal stream of visual information processing, and are primarily involved in motion analysis.

The more rostral parts of the STS and STG cannot be assigned to either the dorsal or the ventral stream of visual processing — they are located at the transition between the two pathways. Traditionally, the ventral pathway from V1 to the inferior temporal cortex was thought to process form, or 'what' an object is, whereas the dorsal stream projecting to the posterior parietal cortex provides information about 'where' an object is[29,30]. Milner and Goodale[19] redefined the two systems. They asserted that the dorsal stream transforms the information about objects, mainly in egocentric coordinates, to control visually guided action. By contrast, the ventral stream embodies the enduring characteristics of objects in both egocentric and allocentric frameworks, promoting a conscious awareness of the world.

The STG receives polysensory inputs from both streams, therefore representing a site for multimodal sensory convergence[18,31–34]. The superior temporal cortex receives afferent inputs from the inferior temporal cortex, as well as from the inferior parietal lobule and intraparietal sulcus[32,33]. When different tracers were injected into the posterior parietal and inferotemporal cortex of the same hemisphere, overlapping labelling was found near the fundus of the STS[35,36], supporting the idea that this area receives converging inputs from the dorsal and ventral streams.

The properties of neurons in the rostral parts of the STS, namely those within a large portion of the upper bank and fundus of the rostral STS — the STP area (FIG. 1c) — comprise large RECEPTIVE FIELDS, which always include the centre of gaze and usually extend well into both visual hemifields[31,37]. These neurons typically show sensitivity to movement, have polymodal responsiveness to visual, somatosensory and/or auditory input, and are insensitive to stimulus form[31,37]. Evidence for involvement of the STP in visuospatial processes derives from ablation studies. Removal of area STP in monkey leads to an increase in SACCADE latency for contralesional targets, whereas saccades directed to targets in the ipsilesional hemifield are not impaired[38]. More extensive lesions that include, not only STP, but other parts of the STS (and even of the STG) as well, also produced defects in visuospatial orientation in monkeys. Luh *et al.*[1] observed reduced orientation to unilaterally presented visual stimuli on the side contralateral to the lesion, and Watson *et al.*[2] reported a variety of further behavioural abnormalities that occur with spatial neglect in humans.

Although the initial studies found that most STP neurons were insensitive to stimulus form[31], cells in area STP and other portions of the rostral STS have been observed to have categorical specificity (for example, for faces), and might even be selective for certain aspects of faces, such as head or eye orientation[31,39–41]. Consistent with these findings, large STS lesions impair the ability of monkeys to discriminate the direction of eye gaze in photographs of faces[42,43]. Eacott *et al.*[43] suggested a more general impairment in visual discrimination learning after lesion of the monkey STS, rather than a simple interpretation of this area as a 'face area' that is concerned only with the perception and significance of parts of the body and their movements.

The various observations have led to diverging ideas about the function of the rostral superior temporal cortex, and about the STP in particular. Bruce *et al.*[31] considered its function to be primarily concerned with visuospatial analyses — namely, orienting to novel stimuli — but others assumed that it was involved in complex visual object recognition[39–41], and the interpretation of biologically significant objects and signals[44]. The functional heterogeneity of this brain region could be due to the fact that it receives input from both the dorsal and the ventral visual streams[32,33,35,36,45] for possible integration[19]. So, the different interpretations of its function might not be antagonistic; rather, they might reflect the fact that this portion of superior temporal cortex is involved in processes that deal with analyses of both object

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RECEPTIVE FIELD
The area of the sensory space in which stimulus presentation leads to the response of a particular sensory neuron.

SACCADE
A rapid eye movement that brings the point of maximal visual acuity — the fovea — to the image of interest.

Box 1 | **Monkey and human parietal lobes: functionally homologous?**

In both humans and monkeys, the parietal cortex is separated by the intraparietal sulcus into a superior and an inferior lobule (FIG. 1a and b). The entire monkey inferior parietal lobule (IPL) has been designated as Brodmann area 7; however, area 7 is the superior parietal lobule (SPL) in the human brain (see FIG. 1a and b). The IPL in the human is distinguished as areas 39 and 40 according to Brodmann, but Brodmann's map of the monkey brain contains no regions designated as 39 or 40. So, it has been questioned whether these areas in humans might represent the functional homologue of area 7 in the monkey[51,70].

Several studies have indicated that Brodmann areas 7 in monkey and human are functionally homologous. In monkeys, lesions of this area cause inaccuracy in reaching for objects with the contralesional hand, as well as inappropriate orientation of the hand with respect to the target, but does not evoke the complex pattern of behavioural abnormalities typical of human spatial neglect[2,71–75]. As in monkeys, lesions of human area 7 on the left or right produce misreaching for targets under visual guidance, termed 'optic ataxia'[8]. Such patients might also show inappropriate hand posture when grasping[76]. In contrast to these defects in the immediate control of reaching and grasping, delayed reaching for targets seems to be less disturbed in optic ataxia[64].

As Brodmann areas 39 and 40 do not seem to be crucial in representing spatial awareness and exploration[3], what is the function of these 'evolutionally new' Brodmann areas in the parietal cortex of the human brain? Mattingley *et al.*[77] found that patients with right IPL lesions have an impairment in initiating leftward movements towards targets in the left hemispace. Darling *et al.*[62] investigated pre-movement programming of goal-directed reaches to targets in peripersonal space in patients with brain lesions. Some of their subjects had lesions confined to the right or left IPL. In line with previous observations in large patient samples[3,9], the prominent disturbance of these patients was not spatial neglect. Rather, they showed direction errors when reaching, without vision, for remembered targets[62]. Recent functional imaging work in healthy subjects revealed that the right and left supramarginal gyri are activated when pointing with the right hand to remembered targets[63].

Together, the observations allow us to assume that the SPL and intraparietal sulcus in humans are dedicated to the immediate guidance of our actions in space. Furthermore, we may cautiously assume that areas 39 and 40 — the human IPL — are involved in the longer-term coding of spatial relationships[19,64] for processes such as delayed reaching for targets[62,64]. However, it is still too early to draw firm conclusions on the role of the IPL in humans — research in this area has only just begun.

The superior temporal cortex does not seem to have a decisive role in the direct coding of space for action. Patients with spatial neglect (in which lesion typically overlaps in the superior temporal gyrus[3]) show largely undisturbed reaching for objects in peripersonal space. Even with severe spatial neglect in the acute stage of the disease, patients show no deficit in terminal accuracy of pointing, with or without visual feedback about actual hand position[78]. Furthermore, this study did not find any characteristic difference between neglect and control groups when finger position during pointing was compared[78]. A more recent investigation found that movements during pointing were more curved in two patients with right brain damage and neglect (as was the case in the only control patient without neglect in that study)[79]. The trajectories had more rightward curvature in one neglect patient, but not in the other. However, as in the preceding study[78], all three patients showed no misreaching, landing precisely on target[79].

properties and their location in space. Oram and Perret[46] have reported evidence that both types of information from the two pathways converge in the rostral superior temporal cortex. They found that STP cells integrate form and motion, providing a conjoint representation of object identity and direction of motion. The idea that the superior temporal cortex is involved in the perception of biological motion was supported by lesion data in humans; these data showed that patients with damage including rostral temporal areas can have impaired motion perception in both visual hemifields[47].

Milner and Goodale[19] assumed that the human homologue of the monkey STP might be able to transform visual information into representations of objects as well as their spatial distribution. Lesions of the rostral part of superior temporal cortex[3] might, therefore, be expected to lead to disturbances related to object properties, as well as their egocentric locations. In fact, the characteristic failure of neglect patients to explore the contralesional side has been found to occur, not only with respect to egocentric reference frames, but also relative to object-centred coordinates (for reviews, see REFS 48,49). Both aspects probably constitute different manifestations of the same (disturbed) system, acting in different situations. The same physical stimulus at the same location in a scene might be attended or neglected, depending on the behavioural goal of the subject (H.-O.K. and M. Niemeier, unpublished observations). This idea led to a model of space representation that integrates both egocentric and object-centred reference systems[50]. The idea behind this integrated space–object map (ISO map) model is that visual input is represented in two modes simultaneously: in veridical egocentric coordinates and in normalized, within-object coordinates.

The idea that the brain organizes and reorganizes the same physical input in different reference frames according to changing task requirements favours the idea that object- and space-related information is processed by the same or closely related brain structure(s). The superior temporal cortex is a good candidate for such an area. It receives space-based and object-based information from both the dorsal and the ventral visual streams. Moreover, patients with lesions located predominantly in the superior temporal cortex show neglect of information in both space-based and object-centred reference systems.

Auditory functions of the STG. I have mentioned the relative homology of superior temporal cortex function in monkey and human. However, there is also a conspicuous difference between the two species. Whereas ablation and single-unit recording studies showed no functional differences between corresponding structures in the monkey's left and right hemispheres, the lateralization of functions in humans is obvious, especially in the superior temporal cortex. Manifest spatial neglect in humans is rarely found after lesions of the left hemisphere; they occur predominantly with lesions of the right[51]. These lesions overlap in Brodmann areas 22 and 42 (REF. 3). The same Brodmann areas in the human left hemisphere are involved in speech processing[52,53]. Strokes in this region, or 'functional lesions' elicited by electrical stimulation during surgery, induce comprehension disorders[54,55].

In monkeys, the rostral portions of the superior temporal cortex also seem to be involved in the processing of species-specific vocalizations. Neurons on the dorsal aspect of the STG surface, the so-called lateral 'belt' area[56] (FIG. 1c), show a preference for vocalizations

from the monkey's own repertoire[57,58]. The cortical auditory system of monkeys seems to be divided into at least two processing streams. A 'spatial' stream originates in the caudal part of the STG and projects to the posterior parietal and dorsolateral prefrontal cortex, whereas a 'pattern analysing' stream originates in the more anterior portions of the STG and projects to the ventral and orbital prefrontal cortex[59–61]. It was proposed that the first system determines the spatial location of acoustic stimuli, whereas the second is involved in decoding speech-like stimuli[58,61]. Information from the two auditory streams converges within the rostral superior temporal cortex. Signals used for auditory communication that originate in the anterior STG are relayed, not only to the prefrontal cortex, but also to the caudal STG, where they are combined at the single-unit level with information about the locations of sounds in space. Tian *et al.*[58] speculated that such neurons could participate in the identification of speakers on the basis of spatial cues.

Homologies between human and monkey brain

Neurophysiological and neuropsychological findings indicate that the rostral superior temporal cortex might act as an interface between the dorsal and the ventral streams of input processing to allow exploration of both object- and space-related information. The superior temporal cortex is also involved in the processing of species-specific vocalizations. The evidence indicates that these functions are, in principle, homologous in the monkey and human superior temporal cortex, but (and this is merely speculative) that the evolutionary development from monkey to human brain led to the lateralization of these formerly bilateral functions in the left and right hemispheres. Whereas the left superior temporal cortex specialized for language processes, the right superior temporal cortex became functionally dominant, serving as a multimodal matrix for the exploration of object- and space-related information in the surroundings. The basis for this speculation is the clinical finding that the disturbance of language functions and the occurrence of spatial neglect in humans are associated with lesions of only one of the two hemispheres. Functional imaging has revealed that both the left and right hemispheres are involved in language processes in humans, indicating that the bilateral processing of species-specific vocalizations seen in monkeys[57,58] still seems to exist in humans. However, the clear dissociation of disturbed behaviour following unilateral lesions of the two hemisperes shows that, in humans, the neural tissue on the affected side must be the decisive carrier of the respective function; that is, of language on the left, and of spatial awareness and exploration on the right.

Recent observations allow us, cautiously, to assume that parietal lobe function, including the superior and the inferior parietal lobule[62,63], might, in principle, be homologous in human and monkey, contributing to different processes in visuomotor behaviour (BOX 1). In contrast to patients with parietal lesions, those with spatial neglect (in which lesion overlap occurs in the superior temporal cortex[3]) show no misreaching for objects that are located in peripersonal space. This dissociation indicates that different functions are represented in the parietal and the superior temporal cortex. The domain of the parietal lobe seems to be the organization and control of visuomotor acts for processes such as reaching in space, grasping of objects, performing saccadic and pursuit eye movements, and whole body locomotion[19,62,64–66]. By contrast, patients with lesions of the superior temporal cortex in the right hemispere show a severe disturbance in orienting towards and exploring the contralesional part of space or objects (FIG. 2), whereas patients with lesions of this structure in the left hemisphere typically develop comprehension disorders[54,55].

Perspectives for future research

The contribution of lesion studies in the monkey to our current understanding of the functions of superior temporal cortex is still very limited. Previous experiments carried out in the superior temporal cortex focused mainly on areas in the STS[1,2,38,42,43]. So, we still do not know how a monkey behaves when the STG, or parts of this structure, are selectively inactivated. Reversible inactivation by muscimol injection or by cooling techniques are attractive tools for such studies.

These experiments would be particularly helpful if they were carried out in combination with electrophysiological studies. So far, single-unit recordings have neglected large parts of the STG. Although we know a considerable amount about the polysensory character of area STP at the upper bank and fundus of the rostral STS, only a small part of the STG surface has been investigated with microelectrodes. These studies, carried out largely in the belt area, did not test for polysensory responsiveness in a systematic way; rather, they focused on the auditory modality[57,58]. Ventral to the belt area, in the so-called 'parabelt' region[56] of the STG (FIG. 1c), systematic recordings with microelectrodes have not been attempted at all.

A further issue that needs to be clarified is whether structures identified in the depth of the lateral sulcus — areas VPS[26] and PIVC[27,28] — are involved in spatial awareness and exploration. Preliminary evidence seems to indicate such a role. Both areas are located at the transition between the superior temporal and parietal lobes. The properties of the neurons in the VPS indicate that this area is a key element that contributes to the monkey's subjective sense of spatial stability. We know that PIVC neurons, which are located more rostrally in the lateral sulcus, integrate vestibular, neck-proprioceptive and visual input to generate a multimodal neuronal representation of orientation in space[27,28]. In accordance with these findings, neuropsychological studies have shown that asymmetric vestibular[67], optokinetic[68] and neck-proprioceptive[69] stimulation have compensatory effects on spatial neglect in humans. So, it is possible that damage to regions in the depth of the lateral sulcus might contribute to the asymmetric exploration behaviour that is characteristic of spatial neglect[4,5] (FIG. 2).

Finally, it would be interesting to clarify the role of the right inferior parietal and the right inferior prefrontal cortex in spatial neglect. Although lesions confined to these regions only rarely lead to spatial neglect[3,7,9] (see FIG. 3), their functional contribution is still unclear. As the superior temporal cortex receives afferent inputs from the inferior parietal lobule[32,33], and projects to the ventral prefrontal cortex[59–61], one plausible explanation is that lesions in the inferior

parietal and prefrontal cortex might induce to disconnection from superior temporal cortex function.

Links

MIT ENCYCLOPEDIA OF COGNITIVE SCIENCES
Hemispheric specialization | Object recognition, animal studies | Object recognition, human neuropsychology | Spatial perception | Visual neglect | Visual processing streams

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