UNIVERSITAS BERGENSIS

DET PSYKOLOGISKE FAKULTET

Ψ

An fMRI investigation into the multifunctional role of the STS

HOVEDOPPGAVE

profesjonsstudiet i psykologi

Philip U. Wigglesworth

Høst 2013

Veileder

Prof. dr. psychol. Karsten Specht

Forord til artikkelen/ hovedoppgaven

Studien som danner grunnlaget for denne artikkelen/ hovedoppgaven ble gjort i regi av forskningsgruppen Bergen fMRI Group, ledet av prof. Kenneth Hugdahl, og gjort under sub-forskningsgruppen ´Bergen Research Group on Auditory Perception´ (The BeRG-AP) ledet av prof. Karsten Specht. Selve testingen ble gjennomført på Haukeland Sykehus, på avdelingen for Radiologi. Det ble benyttet en funksjonell MR maskin for studien, som ble betjent av radiografer som jobber på avdelingen. U.t. bidro på aspekter av den designmessige utformingen av det eksperimentelle oppsettet, og det eksperimentelle oppsettet ble styrt av u.t. under gjennomføringen av testingen. Innledningsvis, i den eksperimentelle fasen, var også en forskningsassistent ved navn Marta Dyl deltakende i gjennomføringen av testingen av deltakere. Hun, sammen med u.t., var ansvarlig for rekrutteringen av deltakere til studien, samt med å sette sammen det eksperimentelle stimuli for testingen. fMRI rådataen ble bearbeidet av prof. Specht. Analyser av dataen ble gjort av u.t., men med veiledning av prof. Specht.

Hovedoppgaven ble skrevet som en artikkel (artikkelformat) klar for publisering i tidsskriftet *Neuroimage*. Artikkelen ble utformet i henhold til APA sine retningslinjer for utforming, og i henhold til de retningslinjer for utforming gitt av tidsskriftet. Retningslinjene gitt av tidsskriftet kan finnes på følgende nettside:

http://www.elsevier.com/journals/neuroimage/1053-8119/guide-for-authors,

En konvertert pdf-fil av tidsskriftets retningslinjer for forfattere kan også leses i *vedlegg 2.*, under seksjon 7.2 Tidsskriftet følger for det meste retningslinjer for utforming gitt av APA 6.utgave.

Abstract

The superior temporal sulcus (STS) has been implicated subserving speech perception, audiovisual integration, and theory of mind. Prior functional imaging studies have also reported that distinct neuronal patches within the STS region show overlapping activation in response to these three cognitive processes. This finding has led to a theory that the STS as whole, or at least parts of it, are crossmodal and multifunctional in nature, subserving multiple and different processing demands based on network connectivity. The multifunctional role of STS was investigated by applying an fMRI mixed block- and event-related design, in which 20 participants were tested on three paradigms; *speech perception*, *audiovisual integration,* and *theory of mind*. Data was analysed using one-way ANOVA. Individual analysis of each contrast showed activation within the STS region for all three paradigms, with speech perception and audiovisual integration activating a large bilateral posterior STS area, and theory of mind activating bilateral middle and anterior STS areas. Global conjunction analysis revealed conjunct activation in the bilateral posterior STS area, though greater in cluster size in the right hemisphere, and showed a second discrete left middle-posterior STS activated patch. The results are on the whole in line with previous research, and indicate that the posterior STS area subserves crossmodal integration and that distinct sub-structures of the STS might be multifunctional in their processing ability. This is briefly discussed in relation to the theory of network connectivity.

Sammendrag

Den superiore temporale sulcusen (STS) er blitt funnet til å betjene taleoppfattelse, audiovisuell integrering, og ´theory of mind´ prosessering. Tidligere funksjonelle avbildningsstudier har også rapportert at forskjellige nevronale substrukturer inni STS viser overlappende aktivering i respons til disse tre prosessene. Dette funnet har ledet flere innenfor feltet til å foreslå at STS som helhet, eller i hvert fall deler av den, er kryssmodal og multifunksjonell ved at den tilsynelatende betjener ulike prosesseringskrav på bakgrunn av mer omfattende nevronal nettverkstilkobling. Den multifunksjonelle rollen til STS ble undersøkt i dette studiet med fMRI metodikk. Designet av studien var et blandet blokk -og event-relatert design, og studien inkluderte 20 deltakere. Det eksperimentelle utformingen bestod av tre betingelser: *taleoppfattelse, audiovisuell integrering*, og *´theory of mind´*. Dataen ble analysert med enveis ANOVAs. Individuell analyse av de tre betingelsene viste aktivering innenfor STS regionen for alle tre paradigmer. Resultatet viste at taleoppfattelse og audiovisuelle integrering aktiverte et stort bilaterale posteriort STS område, mens ´theory of mind´ aktiverte mer begrensede bilaterale midtre og anteriore STS områder. En global kombinasjonsanalyse (´conjunction analysis´) av de tre betingelsene viste kombinert aktivering i det bilaterale posteriore STS området, med noe mer omfattende aktivering på venstre side, og noe begrenset aktivering i det venstre midtre-posteriore STS området. Resultatene fra studien er i tråd med tidligere forskning, og indikerer samlet sett at det posteriore STS området betjener kryssmodal integrering og at forskjellige substrukturer innenfor STS kan være multifunksjonelle i sin prosesseringsevne. Dette blir også diskutert i forhold til teorien om nevronal nettverkstilkobling.

An fMRI investigation into the multifunctional role of the STS

Keywords:

fMRI, STS, crossmodal, speech perception, audiovisual integration, theory of mind

1. Introduction

A growing number of research findings from neuroimaging studies and from human lesion studies have implicated the superior temporal sulcus (STS) in being a key cortical brain structure in an impressive array of perceptual and cognitive functions. Speech perception, Theory of Mind (ToM) and Audiovisual Integration (AV integration) are three functional processes which have in particular been found to be subserved by the STS cortical region. The STS is a large sulcus which divides the superior and middle temporal gyri (STG and MTG), extending from the foremost anterior to posterior part of the temporal lobe, running parallel and inferior to the lateral fissure. At its posterior point it transverses the angular gyrus at the intersection to the inferior parietal lobe.

Speech perception (SP)

A number of positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies have demonstrated the involvement of the superior temporal cortex in speech processing (Binder, Rao, Hammeke, Yetkin, Jesmanowicz et al., 1994; Dhankhar, Wexler, Fulbright, Halwes, Blamire et al., 1997; Howard, Patterson, Wise, Brown, Friston et al., 1992; Jäncke, Shah, Posse, Grosse-Ryuken, & Müller-Gärtner, 1998; Osnes, Hugdahl, & Specht, 2011[a]; Osnes, Hugdahl, Hjelmervik,

& Specht, 2011[b]; Petersen, Fox, Posner, Mintun, & Raichle, 1989; Price, Wise, Warburton, Moore, Howard et al., 1996; Rimol, Specht, Weis, Savoy, & Hugdahl, 2005; Specht & Reul, 2003; Specht, Rimol, Reul, & Hugdahl, 2005; Specht, Osnes, & Hugdahl, 2009; Wise, Chollet, Hadar, Friston, Hoffner et al., 1991). This is not surprising since the superior temporal cortex comprises part of the primary auditory cortex (PAC/AI) and much of the secondary auditory cortex (AII). Looking at more focal points of activation, functional imaging studies have demonstrated increased activation within the STS bilaterally in response to both speech vs. complex non-speech stimuli (auditory stimuli matched according to spectral and temporal features) (Binder, Frost, Hammeke, Bellgowan, Springer et al., 2000; Uppenkamp, Johnsrude, Norris, Marslen-Wilson, & Patterson, 2006; Specht & Reul, 2003; Specht et al., 2009; Zatorre, Evans, Meyer, & Gjedde, 1992) and speech vs. tone sequences (Binder, Frost, Hammeke, Rao, & Cox, 1996; Binder, Frost, Hammeke, Cox, Rao et al., 1997; Binder et al., 2000; Démonet, Price, Wise, & Frackowiak, 1992; Osnes et al., 2011a, 2011b; Rimol et al., 2005; Specht & Reul, 2003, Specht et al., 2009). Reviewing both their own research and other imaging studies, Hickok and Poeppel (2000) suggest that the posterior-superior temporal lobe area bilaterally constitutes the prime cortical substrate of speech perception (SP), with the left posterior STS (pSTP) and posterior-superior temporal gyrus (pSTG) being involved in speech production in addition, finding projections from pSTP/sSTG to frontal and parietal regions known to host auditory-motor interaction. A host of studies have also found lateralised findings within the STS region (e.g., Belin & Zatorre, 2000; Jäncke, Wüstenberg, Scheich, & Heinze, 2002; Mummery, Ashburner, Scott, & Wise, 1999; Scott, Blank, Rosen, & Wise, 2000; Wise, Scott, Blank, Mummery, Murphy et al., 2001). While some studies have found specific activation within the left middle STS (mSTS) in response to speech and speech-like sounds, others studies have reported specific activation within the left mSTS in response to phonological and prelexical processing (Jäncke et al., 2002; Price, Thierry, & Griffiths, 2005; Osnes et al., 2011b; Scott et al., 2000; Scott & Wise, 2004; Specht & Reul, 2003; Specht et al., 2005, 2009), lateralized activation within the left pSTS area in the context of word perception (eg. Mummery et al., 1999; Wise et al., 2001), and lateralized left anterior STS (aSTS) activation in relation to intelligible speech perception processing (Scott & Johnsrude, 2003; Scott et al., 2000). The common finding of lateralization of speech perception to the left STS is also supported by findings of higher temporal resolution in the left auditory cortex (Zatorre & Belin, 2001). Conversely, Zatorre and Belin (2001) found higher spectral resolution in the right auditory cortex. This finding, in line with studies showing that the processing of music and prosodic information is primarily mediated through known right temporal lobe auditory structures (Grimshaw, Kwasny, Covell, & Johnson, 2003; Tervaniemi, 2001; Tervaniemi and Hugdahl, 2003; Zatorre, Belin, & Penhune, 2002), and in line with studies reporting lateralisation to the right side in response to nonverbal stimuli (Engelien, Tüscher, Hermans, Isenberg, Eidelberg et al., 2006; Liebenthal, Binder, Spitzer, Possing, & Medler, 2005), suggests that there exists a functional lateralisation of speech perception to the left hemisphere and tone perception to the right hemisphere (Binder et al., 2000; Specht, Osnes & Hugdahl, 2009).

Lesion studies in humans and neuroanatomical studies from primates have also implicated the STS regions in speech perception. Lesion studies of human aphasics have shown that focal lesions contained within the left Wernicke´s area, overlapping the middle-posterior STS region, produce specific impairments in speech perception

(Hickok and Poeppel, 2000; Scott & Johnsrude, 2003). A study by Samson, Apperly, Chiavarino, and Humphreys (2004) found for instance that lesions to left pSTS, intersecting the parietal lobe, were strongly associated with deficits in speech comprehension. Neuroanatomical studies from primates have in contrary implicated the aSTS in auditory perception, identifying this region as a multimodal polysensory area, responsible for crossmodal perceptual integration (Hein & Knight, 2008; Scott & Johnsrude, 2003).

In contrast to the classically held notion of functional lateralization to the language-dominant hemisphere, speech-responsive areas have been reported in both the left and right STS region. It seems, however, that the left STS (dominant hemisphere for most people) is nonetheless chiefly responsible for speech and speech-like analysis, whilst the right STS has been found to be particularly responsible for tone-speech differentiation. Functional imaging studies have spatially furthermore shown bilateral activation in the middle and posterior STS areas in relation to temporal feature-analysis, as well as anterior circumscribed STS activity in response to linguistic analysis processing (Binder et al., 1997, 2000; Scott & Johnsrude, 2003; Specht and Reul, 2003). The particular pattern of reported activation within the STS, the surrounding cortex, as well as throughout the brain, has furthermore led to a suggested model of speech perception in which there are two distinct neuronal pathways involved in speech perception, somewhat analogous to the ventral-dorsal distinction in visual perception. It is suggested that there is a somewhat left lateralised anterior-ventral pathway, which transverses the polymodal cortex of the anterior STS, thought to play a role in acoustic–phonetic analysis and thought to be a “what” pathway – subserving auditory object identification by relying on spectral dynamic analysis; and a posterior-dorsal pathway, extending over the polymodal cortex of the posterior STS, thought to be more involved in explicit sub-lexical speech processing and thought to be a “where” or “how” stream of processing analysing more temporal acoustic features (Binder et al., 1997, 2000; Hickok and Poeppel, 2000; Rimol et al., 2005; Scott & Johnsrude, 2003; Specht & Reul, 2003)

Audiovisual Integration (AVI)

As research has found activation within the STS region in response to unimodal auditory activation (e.g., speech perception), so have studies also found discrete activations within the STS region in response to certain unimodal visual stimuli. Some electrophysiological and imaging studies have for instance indicated that the STS region is involved in biological motion processing (Allison Puce, & McCarthy, 2000; Grossman & Blake, 2001, 2002; Puce & Perret, 2003). A number of imaging studies have found specific activation in the posterior STS (pSTS) in response to point-light stimuli portraying biological motion (Grossman and Blake, 2001, 2002), but also in response to facial stimuli (Haxby, Hoffman, & Gobbini, 2000; Hoffman and Haxby, 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998). The fact that activation has been demonstrated in the pSTS in response to both biological motion processing and facial-feature processing, has led some researchers (e.g., Grossman and Blake, 2002) to suggest that the STSp is crucial for complex kinetic motion processing, even at a very precise facial-feature level. Lesions findings have also shown STS region involvement in spatial awereness, with studies on patients with visual neglect showing damage in the right STG area (Karnath, 2001). Similarly, other studies have linked circumscribed lesions to the right STG with deficits in biological motion processing and visual neglect

(Akiyama, Kato, Muramatsu, Saito, Nakachi, et al., 2006; Akiyama, Kato, Muramatsu, Saito, Umeda, et al., 2006). These latter findings come in addition to the early findings from lesion and single-cell recording studies on primates, which have also implicated the STS in spatial-, facial-feature-, and biological motion processing deficits (Hein & Knight, 2008).

There is a recurrent finding from imaging studies that specific auditory and visual processes activate overlapping areas within the STS, with several studies specifically linking the pSTS with crossmodal binding of auditory and visual stimuli (Beauchamp, Argall, Bodurka, Duyn, & Martin, 2004; Beauchamp, Lee, Argall, & Martin, 2004; Beauchamp, Yasar, Frye, & Ro, 2008; Calvert, 2001; Calvert, Campbell, & Brammer, 2000; Calvert, Hansen, Iversen, & Brammer, 2001; Hein & Knight, 2008; van Attenveldt, Formisano, Goebel, & Blomert, 2004, 2007; Wright, Pelphrey, Allison, McKeown, & McCarthy, 2003). Evidence of a multimodal or crossmodal integrative neuronal patch within the STS region has also come from neuranatomical and electrophysiological studies on nonhuman primates, which have shown convergence of afferent sensory inputs along the fundus of the (primate) pSTS (Benevento, Fallon, Davies, & Rezak, 1977; Bruce, Desiome, & Gross, 1981; Seltzer & Pandya, 1978). This area in primates has been named the superior temporal polysensory (STP) area, as single units here activate in response to auditory, visual and somatosensory stimulation (Bruce et al., 1981). It believed that the STP is homologous to the human pSTS, which has been suggested to be the host region within the STS for audiovisual integration (AVI) (Beauchamp et al., 2004[b], 2008; Calvert 2001; Calvert et al., 2000, 2001). Human imaging studies have, however, yet to find clear evidence of a polysensory or multisensory are in the human STS, one which is responsive to all three modalities;

visual, auditory and somatosensory (Beauchamp et al., 2008). Findings though, from lesion studies, have still indicated multimodal processing within the STS. It has been reported that damage to the STS can produce deficits in aspects of both visual and auditory perception (Samson et al., 2004). Samson et al. (2004), however, found that these visual deficits also affected aspects of theory of mind (ToM), a result which would indicate a crossmodal integration process beyond that of simple audivisual integration. Considering specifically the pSTS as an multimodal integration patch, it is uncertain if it only subserves AVI or is part of a larger distributed set of regions involved in crossmodal integration, irrespective of whether the stimuli are audiovisual or unimodal auditory or unimodal visual (Hocking and Price, 2008).

Theory of Mind (ToM)

The superior temporal sulcus (STS) region has been consistently linked across different imaging techniques, and across multimodal and contrasting cognitive paradigms such as verbal and nonverbal tasks, with theory of mind processing. *Theory of mind* (ToM) refers the ability to attribute mental states to others, to assume the viewpoint of others, to imagine what they perceive. It thus concerns mentalising others' mental states and viewpoints. The typically approach to assess ToM ability is with short stories or animate cartoons, describing or showing events which affect the mental state of another person in contrast to emotionally neutral non-ToM stimuli (Hein & Knight, 2008). Early imaging studies using PET (Brunet, Sarfatti, Hardy-Baylé, Decety, 2000; Fletcher, Happé, Frith, Baker, & Dolan et al., 1995; Goel, Grafman, Sadato, & Hallet, 1995) have shown increased activation in the superior temporal area at large, including the STS, in response to ToM stimulation. Functional magnetic resonance imaging (fMRI) studies have shown multiple and more specific findings, demonstrating significant activation in the posterior STS (pSTS), the adjacent temporo-parietal junction (TPJ), the medial prefrontal cortex (mPFC), as well as the temporal poles, in response to ToM stimulation (Frith & Frith, 2003, 2006; Gallagher & Frith, 2003; Gallagher, Happe, Brunswick, Fletcher, Frith et al., 2000; Kobayashi, Glover, & Temple, 2007; Saxe & Kanwisher, 2003; Völlm, Taylor, Richardson, Corcoran, Stirling et al., 2006). Studies which have reported STS involvement have predominantly found specific activation in the right STS, and in more posterior areas (eg. Gallagher et al., 2000; Gallagher & Frith, 2003; Kobayashi et al., 2003; Saxe 2006; Saxe Carey & Kanwisher, 2004). These findings have associated the right STS with the ability to understand the meaning of human animate cartoons (Gallagher et al., 2000), with or without the requirement to mentalise (Gallagher & Frith, 2003), whilst other studies have found STS involvement in understanding the causality and intentionality of others' behaviours (Brunet et al., 2000), the interpretation of complex intentional movements (Castelli, Happé, Frith, & Frith, 2000), and in the ability to take self-perspective (Vogely, Bussfeld, Newen, Herrmann, Happé, et al., 2001). Though there is ample evidence which shows that frontal lobe lesions produce deficits in ToM ability (Stuss, Gallup, & Alexander, 2001), there are fewer findings that associate STS lesions with ToM. Samson et al. (2004) did, however, find that lesions in the upper bank of the left STS, intersecting the parietal lobe, led to difficulties in performing false belief tasks. They also, though, found that these lesions produced deficits in speech comprehension and biological motion processing, demonstrating that lesions in similar STS regions can cause different functional deficits. Such a finding argues against a strict functional subdivison of the STS (Hein & Knight, 2008). Within the ToM literature it is believed that the host brain regions or mediating cortical areas of ToM ability are the medial-frontal cortex and the paracingulate cortex. This is in accordance with Leslie's (1987) model of mentalising and theory of mind development, as well as the *anterior paracingulate decoupling mechanism hypothesis of ToM* (Frith & Frith, 2003, 2006; Gallagher & Frith, 2003). Within this framework, STS involvement is then thought to represent a support function, processing and analyse initial explicit social cues, such as the perception of intentionality and causality of others' behaviours, necessary for theory of mind ability (Allison et al., 2000; Brunet, et al., 2000; Frith & Frith, 2003, 2006; Gallagher & Frith, 2003). It can be reasoned that processing biological motion, gaze- and eye-movement, and processing facial-features are crucial and necessary components of theory of mind and mentalising ability. Accordingly, one could expect tasks tapping the aforementioned abilities to activate the same neuronal patches across the different modalities and cognitive paradigms, as well as overlap with ToM activated areas. Indeed, studies have found such co-activation and overlap between different paradigms. This has led researchers (e.g., Gallagher & Frith, 2003; Frith & Frith, 2006; Hein & Knight, 2008; Völlm et al., 2006; Saxe, 2006) to suppose that STS, particularly the right STS, is part of a network of social cognition cortical areas responsible for theory of mind processing.

Having shown to subserve speech perception, audiovisual integration and theory of mind, it is arguable to claim that the STS is a highly multifunctional cortical region. On the other hand, functional imaging findings have associated some discrete cortical areas within the STS to specific functional processes, indicating a somewhat still functional differentiation of the STS. In line with this supposition, and considering the aforementioned reviewed research, it is arguable that there is some anatomical subdivision and functional differentiation of the STS region into an anterior segment which primarily subserves intelligible speech perception, a middle section which subserves phonological and prelexical processing – and accordingly speech-like perception, and a posterior area which is responsible for theory of mind ability and audiovisual integration – having found coactivation in overlapping areas in response to both unimodal visual and auditory stimuli. And though evidence points to bilateral involvement of the STS region, data nonetheless indicates a somewhat left lateralised functional specialisation for speech perception, as well as a right lateralised functional specialisation for theory of mind ability. However, seeing that SP, AVI and ToM bilaterally recruits the pSTS region, it is defensible to posit that the STS is not wholly functionally subdivided. Crossmodal findings within the STS suggest accordingly that the STS, or at least certain cortical subdivisions of the STS – the pSTS, is multifunctional in nature – subserving different cognitive processes in response to specified cognitive demands. Indeed, in line with neuroanatomical findings showing bidirectional connections of the STS region with an array of other cortical structures, Hein and Knight (2008) suggest that the STS is not strictly functionally subdivided, but that the different functions of the STS regions are determined by the functional characteristics of coactivated higher-order brain regions. As such, the multifunctionality of the STS region might be based coactivations with other brain regions, such as frontal, parietal or temporal regions, with specific activation being determined by the nature of the network interactions.

The goal of this study is to further explore the multifunctionality of the STS region by applying an fMRI method to investigate and identify neuronal activation in the STS region in response to speech perception (SP), audiovisual integration (AVI) and theory of mind (ToM). The study applied a mixed event-related and block design to see whether the STS region responds to all three conditions separately, and to test whether there is any conjunct activation within any STS area across all three paradigms. The study does not include an investigation of any specific areas of interest, nor does it assume or explore activations to other and wider regions of activation outside of the STS region. It is hypothesised that all three cognitive processes (or paradigms); SP, AVI and ToM, will show independent activation within the STS, and that there will be STS areas showing conjunct activation across all three conditions.

2. Material and methods

2.1. Participants

The participants were 20, right handed, healthy male adults, recruited within the age range of between 20-30 years old. Participants were recruited from the student population at the University of Bergen and from the local hospital (Haukeland University hospital) staff population. Handedness was determined by a modified version of the Edinburgh Inventory (Annett, 1970). All participants gave written informed consent in accordance with the Declaration of Helsinki and institutional guidelines, and the regional ethics committee of the State Department of Health approved the study. All participants were screened by licensed radiographers working at the fMRI lab (Haukeland University Hospital) for neurological, cardiac and prosthetic issues or complications, which would exclude them from undergoing MR imaging and thus participation.

2.2. Activation paradigms and stimuli

The experimental testing included three conditions, one condition to test (capture activation) for each paradigm:

1. Speech perception
2. Audiovisual integration
3. Theory of mind

2.2.1. Speech Perception (SP)

In order to investigate and capture neuronal activation associated with SP, the study employed a speech perception stimulus design, based on the previously described ‘‘soundmorph” (SM) technique (Specht, Rimol, Reul, & Hugdahl, 2005; Specht et al., 2009), however slightly shortened. This soundmorph paradigm was chosen since it has proven to be an effective paradigm in capturing neuronal activation relating to speech perception, particularly in capturing activity within the STS region (Specht et al., 2005, 2009, 2011a, 2011). In this SM paradigm participants are presented with morphed and transitioned consonant-vowels (CV) /da/ and /ta/ as speech stimuli. The CVs were read by a male voice and lasted 420 ms. The SM condition also included two non-speech control sounds, a guitar sound (A3) and a piano chord (C major triad on a C3 root). Both speech stimuli and non-speech control stimuli were digitizing and matched in duration and mean intensity (Goldwave Software). Further, white noise was generated and inserted into the experimental setup. The white noise was also matched in duration and mean intensity to the speech and non-speech stimuli. The stimuli material was manipulated further by creating a transition from a non-speech sound into a speech sound. This transition was created by constructing seven separate sounds or group-based trials, in which the amount of white noise perturbation in the sounds was parametrically varied. Accordingly, this manipulation procedure gradually reveals the specific spectral and temporal characteristic of the speech (CV) sounds in a stepwise manner. The non-speech acoustic sounds were manipulated in the same manner. [An example of the stepwise “morphing” transition (procedure) of the speech stimulus can be viewed in fig.1]. The design differentiates only between speech and non-speech, i.e., not between the underlying stimuli themselves (e.g., between /da/ and /ta/ or between the piano and guitar sound). A more detailed description of the soundmorph technique can be gleaned from Specht et al. (2005, 2009, 2011b). In the present design each stimulus category and manipulation step had 14 repetitions. The SM condition included in total 182 regular events and 86 null events (e.g., trials with no stimuli), The order of the events/trials was pseudorandomised across manipulation steps and categories (speech/nonspeech) so that the morphing sequence was never presented in a consecutive order. This was done to avoid expectancy effects. In order to also preclude neuronal activation related to top–down processes (Dehaene-Lambertz, Pallier, Serniclaes, Sprenger-Charolles, Jobert et al., 2005; Dufor, Serniclaes, Sprenger-Charolles, & Démonte, 2007; Sabri, Binder, Desai, Medler, Leitl et al., 2008) and to keep attention relatively constant during fMRI data acquisition (Jäncke, Mirzazade, & Shah, 1999), the sound-morph condition included a speech-stimulus unrelated behavioural task. Participants were instructed to report, with a response button placed in dominant hand, whenever they heard a stimulus in one ear only. The design included 14 target trials which were randomly distributed, with an equal number of trials for the left and right ear, respectively. The total condition time for the SM paradigm was 18min:03s.

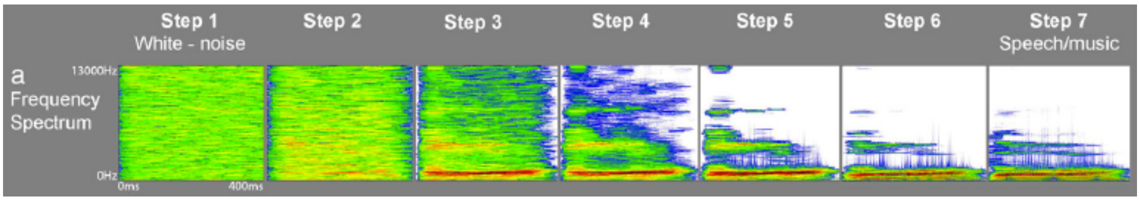


Fig. 1.

Example of a ‘‘sound-morphing transition, where the stimulus changes (is being “morphed”) from white noise (left) to a speech sound, to a “da” CV syllable (right). Fig. acquired with permission from Osnes et al. (2011[a])

2.2.2. Audiovisual Integration (AVI)

The AVI condition included three separate tasks: an audiovisual integration task, a control visual task, and a control auditory task. The premise her is that the two control tasks are used to cognitively subtract unimodal visual and auditory associated activity form the neuronal activity associated with the main experimental sub-task – audiovisual integration. The audiovisual integration task consisted of showing the participants a blank black screen in which a white asterix would appear, either synchronous or dis-synchronous with a simple short-pitched sine-wave tone (1000 Hz) being played into both ears. The key feature to this integration task was that the participants were instructed to indicate with a single response button (placed in dominant hand) whether the asterix and the tone appeared NOT synchronous. This task then forces the participants to have to perceive if an auditory and a visual stimulus appear together, a mental process which would require audiovisual integration. In the control visual task participants were only shown the blank black screen with appearing white or grey asterixes, and were instructed to indicate with the response button if an appearing asterix was grey. In the control auditory task participants were played a single short-pitched tone, on either both or one of their ears (left or right), and instructed to respond with the response button if they heard the tone only on one ear. The auditory control task was designed so that participants would hear interchangingly a tone on both ears during half the trials and a tone on either the left of right ear, in equal amounts, during the rest of the trials. During the control auditory task the visual stimuli-screen was left blank. The design of AVI condition was a block design, with 6 blocks for the integration task and three blocks each for the visual and auditory control tasks. Each block contained 15 trials, with each trial lasting on average 2.2 sec.. The three tasks were presented in a fixed intermittent sequence, and with instruction on how to respond before each block. The total time for the AVI condition was 10min:56s. (An example of each task in the AVI condition can viewed in fig. 2).

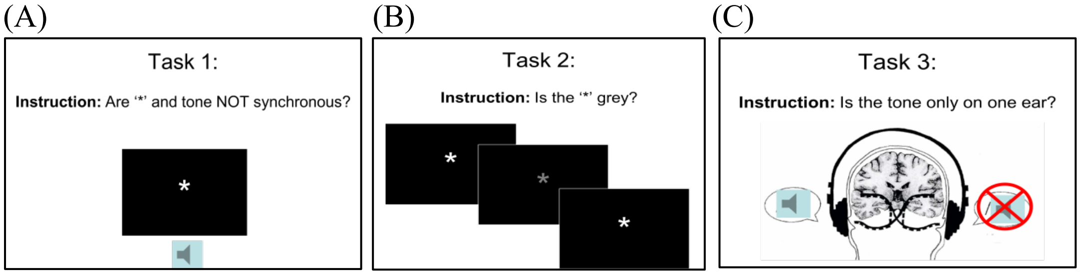


Figure 2.

Example of AVI experimental condition tasks. (A) AVI task, with instruction; press the button when /*/ and tone are NOT synchronous. (B) Visual control task, with instruction; press the button when you see grey /*/ (C) Auditory control task, with instruction; press the button when you hear the tone only on one ear.

2.2.3. Theory of Mind (ToM)

To assess theory of mind (ToM) processing and activation, the study used comic strip cartoons derived from Brunet, Sarfatti, Hardy-Baylé, and Decety (2000, 2003), and acquired from aforementioned first author. The design of the ToM condition included one experimental theory of mind task and one control task. The experimental setup of the applied comic strips is that they require either an attribution of intention of others (ToM cartoon – experimental task) or the use of knowledge about the physical properties of objects (control task) ("physical logic": Spelke, Vishton, & Von Hofsten, 1996, as cited in Brunet et al., 2000). The premise, as with the AVI condition, is that one can cognitively subtract the neuronal activity associated with the control task from the AVI task, and thus see which cortical areas which are solely involved in theory of mind or mentalising. The experimental setup of the ToM condition included twenty-eight ToM cartoon trials (stories), in which participants were tasked to select the correct best-fit answer to the story out of two possible responses, and twenty-eight control task trials, in which participants were presented three cartoon pictures, whereby two were copies (identical), and prompted to select out of two possible answers the cartoon picture which appeared twice (see fig. 4 below for examples of the two tasks). The design of the ToM condition was also a block design, comprising six blocks, with seven trials each. ToM and control cartoon trials were randomly arranged prior experimental testing and administered in a fixed sequence for every participant. Trials were randomised in order to avoid expectancy effects. Each response item, or cartoon slide, was presented for $4.^{1/2}$ seconds, with the total condition time set at 09min:08s. The participants were given two hand-held controls for this condition, one for each hand, with a button on each control to which to indicate response to each successive task: right hand button for right side response; left hand button for left side response. Participants were given instructions on screen and verbally by the test-technicians as to how to respond to the cartoon strips prior testing.

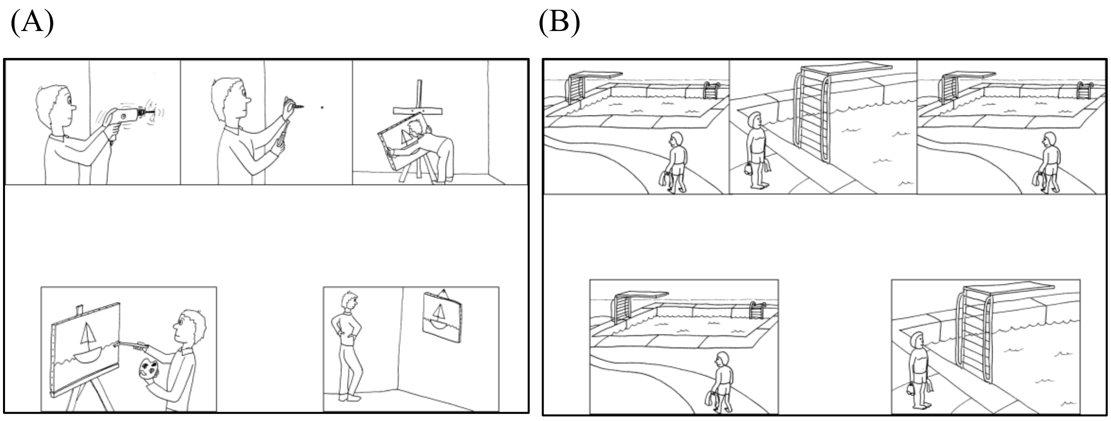


Figure 3.

Example of a story stimuli from Comic-Strip Task used to assess theory of mind (ToM): (A) ToM comic strip task, in which participants should choose between one of the two lower pictures as a response/answer (left picture correct answer here); (B) Control task, in which participants should see that of two of three upper cartoon pictures are identical, and should pick this picture out from the two option-pictures below (left picture correct answer here).

2.3. Experimental procedure

Auditory experimental stimuli were presented through MR compatible headphones with insulating materials that also compensated for the ambient scanner noise by 24 dB (NordicNeuroLab, www.nordicneurolab. no). Visual stimuli were presented through MR compatible goggles which were fastened to the participants' heads during the experimental paradigms which involved visual stimuli. The intensity of the stimuli was the same as described in Osnes et al. (2011a). Presentation of the visual and auditory stimuli, and recording of the behavioural responses, was controlled by the E-prime software (Psychology Software Tools Inc.) running on a PC placed outside of the MR chamber. The three paradigms were rotated in a fixed sequence across participants in the experimental setup, so that 1/3rd of participants went through the setup ToM-AVI-SM, a 1/3rd went through with AVI-SM-ToM, and a 1/3rd went through the setup SM-ToM-AVI.

2.4. Data acquisition

The fMRI study was performed on a 3-T GE Signa Exite scanner. To minimize the effect of scanner noise, a sparse sampling technique was used with 1.5 s of image acquisition and an additional silent gap of 2.3 s, where the stimuli were presented. Axial slices for the functional imaging were positioned parallel to the AC–PC line with reference to a high-resolution anatomical image of the entire brain volume and obtained using a T1-weighted gradient echo pulse sequence (MPRAGE). The functional images were acquired with an EPI sequence, which included: 285 EPI volumes for the SM paradigm, with an 1.5s image acquisition time and a 2.3s silent gap frame; 432 EPI volumes for the AVI paradigm, with an 1.5s image acquisition time and no silent gap; and 360 EPI volumes for the ToM paradigm, with 1.5s image acquisition time and no silent gap. Each EPI volume for the three paradigms contained 25 axial slices (64x64 matrix, 3x3x5.5 mm voxel size, TE 30 ms) that covered the cerebrum and most of cerebellum. The first three volumes for each paradigm were treated as dummy scans and removed prior to the subsequent processing. A short localizer procedure (4s) and a high resolution T1 structural imaging procedure (10min:43s), was conducted before the acquisition of the functional images. After the functional imaging of the three experimental paradigms was executed, participants were further subjected to a diffusion tensor imaging (DTI) procedure (8min:38s).

2.5. Data analysis

The BOLD-fMRI data were pre-processed and statistically analyzed with SPM8 (http://www.fil.ion.ucl.ac.uk/spm). The EPI images were first re-aligned to adjust for head movements during the image acquisition and the images were corrected for movement-induced distortions ("unwarping"). Data were subsequently inspected for residual movement artefacts. The realigned image series were then normalized to the stereotaxic Montreal Neurological Institute (MNI) reference space provided by the SPM8 software package and resampled with a voxel-size of 2x2x2 mm. The images were finally smoothed by using a Gaussian kernel of 8 mm. Results were analysed both on an individual paradigm level (1^{st}. level analysis) and on a group level (2^{nd}. level analysis), based on the General Linear Model (GLM). The group analysis was performed as an one-way ANOVA analysis, in which all three paradigms were entered. For the SM paradigm contrast, the linear increase in phonetic (speech) perception in response to the seven manipulation steps was plotted into the ANOVA to calculate significant brain activation, whilst for AVI and the ToM contrasts, the difference in activation between the experimental and control tasks was used to calculate significant brain activation for these paradigms. Group activations were examined by specifying contrast for each condition separately. In addition, a global conjunction analysis across all three paradigms was performed. In all analyses a family wise error corrected (FWE-corr.) threshold of $p>0.05$ was applied, together with a cluster threshold (Cl) of at least 10 voxels per cluster. Probability maps (PMs) of each paradigm were estimated by thresholding the individual 1^{st} level results at the $p<.0.05$, averaging them across the group. Results within PMs were explored across participants with a cut-off of 66% (2/3rds).

3. Results

An initial one-way ANOVA analysis (FWE-corr. $p<0.05$, Cl>10 voxels) of each paradigm (condition); soundmorph (SM), audiovisual integration (AVI) and theory of mind (ToM), revealed foci of significant brain activity in the STS region in response to all three paradigms. As shown in table 1 and can be viewed in fig.4, both SM and AVI activated a substantial and circumscribed cluster in both the right and left pSTS region, in Brodmann areas 22 and 48 respectively. The analysis revealed that ToM activated multiple large and distributed clusters across the occipital lobe, the lateral posterior frontal lobe, and across parts of the parietal and temporal lobe, (see fig. 4). Looking specifically at the STS region, it was found that ToM activated small cortical patches in the left aSTS and mSTS/MTG aresa (Brodmann areas 38 and 21 - respectively), and a small cortical patch in the right aMTS area (Brodmann 20). Fig. 4 shows that the left mSTS/MTG patch stretches towards the pSTS region. The local peak voxels for these three patches are reported in table 1.

Table 1

Foci of significant brain activations associated with SM, AVI and ToM stimuli, only for STS region **

Paradigm	cluster-level		peak-level			MNI, mmm			Brodmann
	$P_{FWE\text{-}corr}$	k_E	$P_{FWE\text{-}corr}$	T	Z	x	y	z	(area)
SM	0.000	635	0.000	8.51	6.69	64	12	0	22 (pSTS/STG)
	0.000	695	0.000	8.27	6.55	-60	-14	-2	22 (pSTS)
AVI	0.000	540	0.000	8.23	6.54	52	-18	0	48 (pSTS)
	0.000	556	0.000	7.11	5.90	-48	-18	-4	48 (pSTS)
ToM		*	0.001	5.62	4.94	-44	18	-26	38 (aSTS)
	0.004	10	0.002	5.49	4.84	-54	-6	-22	21 (mSTS/MTG)
	0.004	11	0.000	5.73	5.01	48	8	-36	20 (aMTS)

Note. Parametric analysis using one-way ANOVA of each individual contrast, with FWE-corrected threshold of $\mathbf{p}<0.05$ and a cluster threshold of 10 voxels. The table describes the activations in terms of cluster size (voxel size 2x2x2 mm) (k_E), significance value (t), effect size (z), and localization (MNI space and Brodmann). Peak-level voxel for main cluster is also shown. [x coordinates with a negative value are located in the left hemisphere].

* This local (maxima) activation was found as an extension of a larger activated posterior frontal lobe cluster, located at (MNI, mmm) -48,18,-14 (peak voxel of cluster), cluster size (k_E) = 1263, p(FEW-corr)<.000, t=10.76. (*see* **)

** For SM and AVI the table shows global maxims, which were located in STS region. For ToM, local peak maxims within STS region had to be specifically explored. A complete table of global ToM activated clusters can be viewed in *Appendix 1*, under the *table 3*.

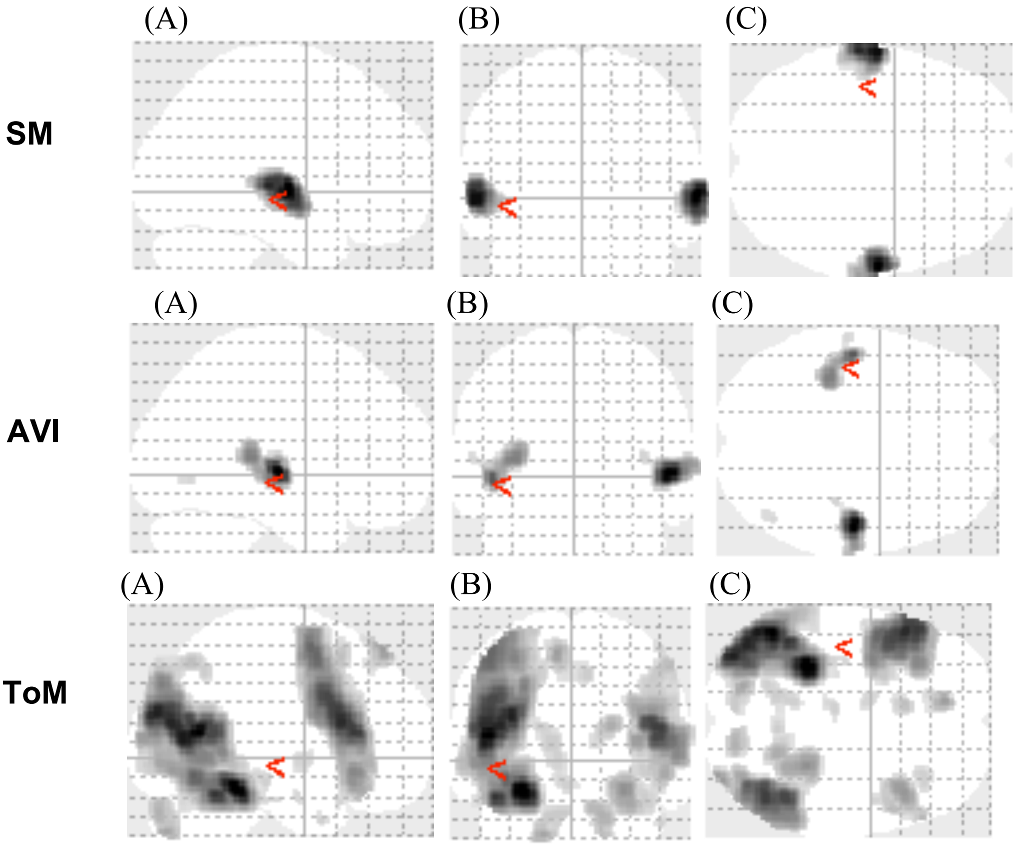


Fig. 4. Significant areas of activation in the individual analysis for the three contrasts: SM, AVI and ToM, [p<0.05 (FWE), Cl.>10]. (A) Sagittal view. (B) Coronal view. (C) Transverse view.

A global conjunction one-way ANOVA analysis (FWE-corr., $p<0.05$, Cl>10 voxels) of SM, AVI and ToM revealed three significant cortical clusters of activation. As table 2 and fig. 5 shows, there are two closely distributed activated clusters in the left STS region; a small cluster located in the far pSTS region and an even smaller cluster in the middle-posterior STS region, and a moderate sized cluster in the right pSTS region. As seen in fig.6, the activated clusters are located in the posterior and upper bank region in both the left and right STS region. As can be discerned from table 2 and viewed in fig.3, there is a greater – total – activated patch or cluster in the right STS region.

Table 2

Global conjunction analysis of significant brain activations associated with SM, AVI and ToM stimuli

cluster-level		peak-level			MNI, mmm			Brodmann
$P_{FWE\text{-}corr}$	k_E	$P_{FWE\text{-}corr}$	*T*	*Z*	x	y	z	(area)
0.002	26	0.001	2.97	5.58	-52	-40	2	21 (pSTS/MTG)
0.000	100	0.002	2.87	5.44	50	-38	2	21 (pSTS/MTG)
0.010	10	0.006	2.67	5.15	-50	-22	-10	20 (pSTS/STG)

Note: Parametric conjunction analysis using one-way ANOVA of all three contrasts, with FWE-corrected threshold of $p<0.05$ and a cluster threshold of 10 voxels. The table describes the activations in terms of cluster size (voxel size 2x2x2 mm) (k_E), significance value (*t*), effect size (*z*), and localization (MNI space and Brodmann). Peak-level voxel for main cluster is also shown. [-*x* coordinates denote left hemisphere]

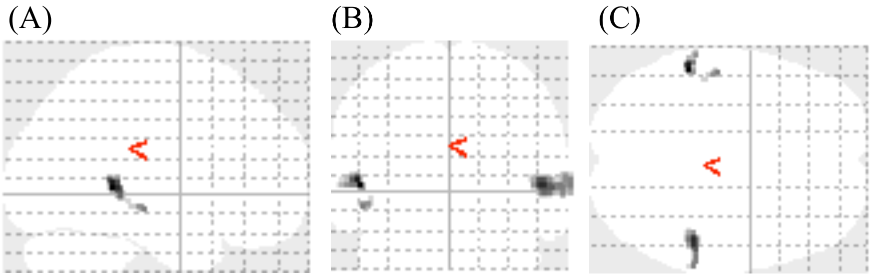


Fig. 5. Significant activation foci for global conjunction analysis of SM, AVI, and ToM, [p<0.05 (FWE), Cl.>10]. (A) Sagittal view. (B) Coronal view. (C) Transverse view.

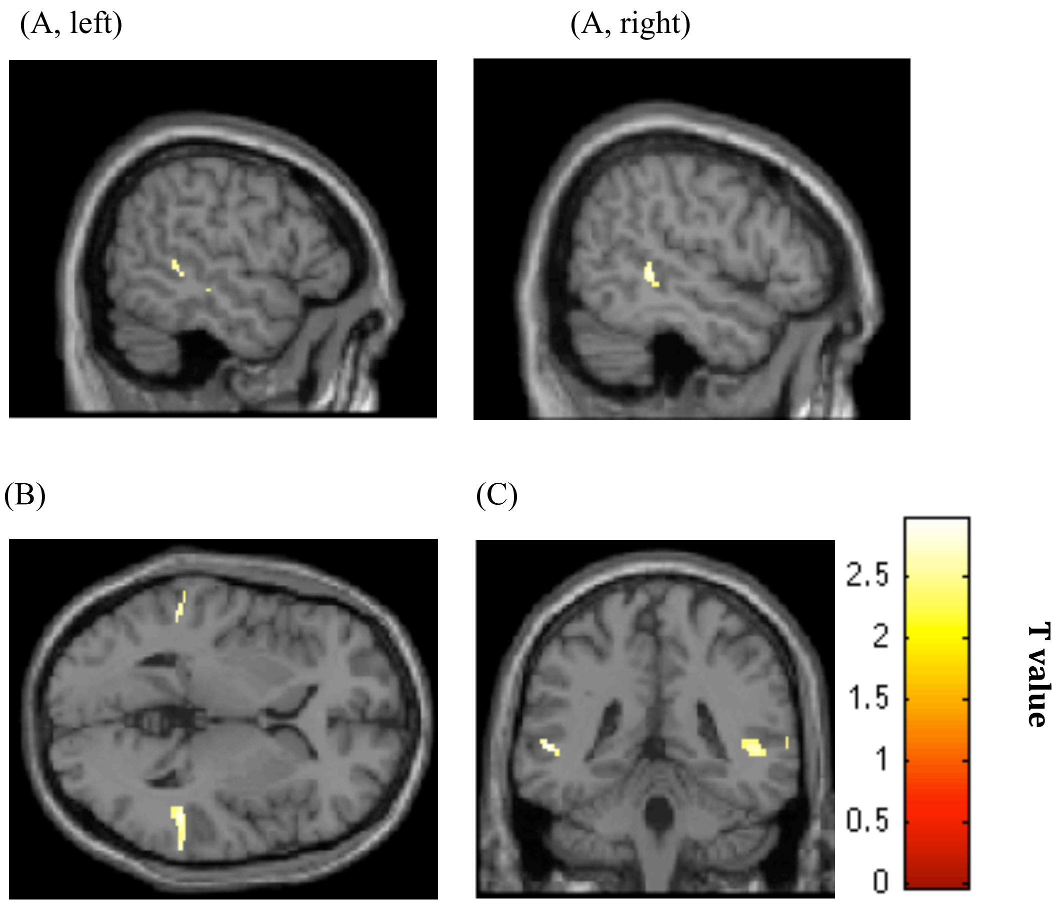


Fig.6. Significant activation foci for global conjunction analysis of SM, AVI, and ToM, [p<0.05 (FWE), Cl.>10]. (A left) Sagittal view of left hemisphere. (A right) Sagittal view of right hemisphere. (B) Transverse view. (C) Coronal view.

Using Mricron (http://www.mccauslandcenter.sc.edu/mricro/mricron/), a statistical and rendering tool for functional MRI data, to analyse the percentage of participants who showed activation in the STS region in relation to SM, AVI and ToM, we found that at least 2/3 of participants showed activation within STS across all three contrasts. Fig. 7 shows that the greatest activation across participants was found for ToM, showing large patches of activation bilaterally in the middle-posterior lateral frontal lobe, large patches of activation in the lateral occipital lobe transversing the middle posterior temporal lobe, and some small bilateral activation in the anterior and posterior STS region. AVI shows less distributed activation, with some bilateral activation to medial-lateral posterior occipital lobe, and fairly circumscribed bilateral activation in the posterior STS region. SM shows the least distributed activation, with only very circumscribed activation showing bilaterally in the posterior STS region, as well an activated patch in the right middle STS region. Fig. 7 also shows that SM and AVI activate in close proximity to each other in the bilateral pSTS area, whilst ToM shows only some very discrete activation inferior and posterior to SM and AVI, in the bilateral mSTS/MTG area.

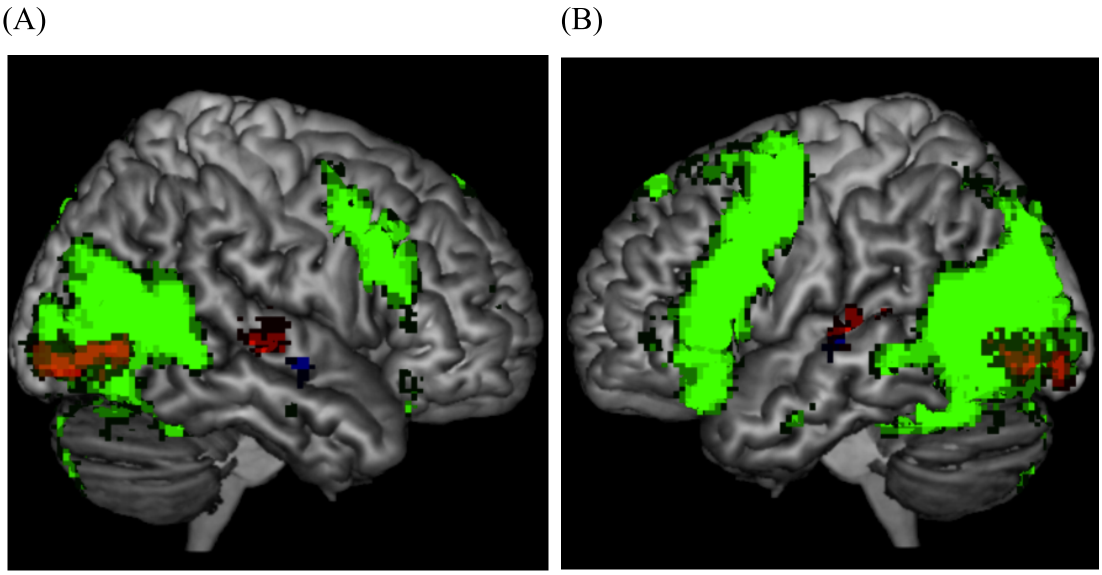


Fig. 7. Probability maps (PMs) ($p<0.05$) of activation across all three paradigms (contrasts); ToM [green], AVI [red], SM [blue]), and across participants with a cut-off of 66% (2/3rds of participants). (A) Right hemisphere. (B) Left hemisphere.

4. Discussion

The aim of this study was to investigate and identify neuronal activation in the STS region in response to speech perception (SP[SM]), audiovisual integration (AVI), and theory of mind (ToM) using an fMRI method. It was firstly hypothesised that all three paradigms (or cognitive processes) would show individual activation within the STS region. The results confirmed this hypothesis, demonstrating STS region activation in response to individually the SP, AVI, and TOM paradigm. Of interest, the SP and AVI paradigms showed both substantial bilateral activation in the pSTS and mSTS areas, and the ToM paradigm showed some discrete activation in the left STS/MTG area, stretching somewhat posterior. It was secondly hypothesised that the STS region would show conjunct activation in relation to all three paradigms. A global conjunction analysis of SP, AVI and ToM did indeed show joint activation within the STS region at three focal spots: bilateral activation in the pSTS area and some discrete activation in the left m-pSTS area.

There are several aspects of the results worth noting. Firstly, it is worth pointing out that the left STS showed conjunct activation in two places, in the pSTS and the mSTS area, whereas the right STS only showed activation in the pSTS. It is likely that the left mSTS activation seen in the conjunction analysis can be accounted for (is mainly driven) by the substantial activation seen by SP and AVI in the left mSTS area. Secondly, the conjunction analysis used in the current study was a global conjunction analysis, and as such, it cannot say if all three paradigms showed coactivation in the three stated patches. A global conjunction analysis tests whether two or more paradigms (contrasts) are not NOT significant compared to each other, i.e., it says that is at least one paradigm significantly activated a given neuronal patch and that the other paradigms were definitively not not-significant as well. A *pure conjunction* analysis, on the other hand, shows whether all three paradigms significantly activate the given patch. The present results therefore demonstrate that all three paradigms showed activation bilaterally in the pSTS area and in the right mSTS area, although not that all three showed significant activation, which would be the case in a ”pure” conjunction. Considering that the global conjunction analysis did not show any conjunct activity between SP and AVI, which both activated large but discrete areas in the pSTS area, and ToM which showed activation across much of the frontal and parietal lobe, reinforces the supposition that ToM – to a certain degree – also activated the bilateral pSTS area. A third interesting point, is that looking at the PMs one sees that SP and AVI seemingly activate very close but mostly distinct sub-structures within the pSTS, and that ToM activates quite few clusters and more inferiorly in the mSTS/MTG. This could indicate that there is mostly close but not overlapping activation in the pSTS region. The PMs, however, are not spatially precise or statistically relevant in delineating conjunct activation.

Considering previous research, we see that the current findings only partially fit. The study’s finding that speech perception and audiovisual integration activates posterior regions of the STS is in line with previous functional imaging studies (e.g., Binder et al., 2000; Specht & Reul, 2003; Specht et al., 2009; Uppenkamp et al., 2006). Though the present study did not find activation in the anterior region of the STS, as some previous studies have found (Scott & Johnsrude, 2003; Scott et al., 2000), some activation was nonetheless observed in the middle to posterior portion of the STS area, supporting previous finding that have shown mSTS activation in response to perception of speech-like sounds, and to phonological and prelexical processing (e.g., Jäncke et al., 2002; Price et al., 2005; Scott & Wise, 2004; Specht & Reul, 2003; Specht et al., 2005). These previous findings have also specifically linked the left mSTS and pSTS areas to speech perception. In the present study, the conjunction analysis did indeed indicate a somewhat modest left lateralised m-pSTS finding, which as stated, is probably due to strong SP activation in the dominant (left) pSTS.

Likewise to speech perception, previous studies have in particular associated audiovisual integration to the pSTS region (e.g., Beauchamp et al., 2004a,b, 2008; Calvert et at., 2000, 2001; van Attenveldt et al., 2004, 2007). In line with this research the current study also found pSTS activation in response to audiovisual integration processing, both in terms of individual paradigm activation and considering the conjunct activation in the pSTS area.

Whereas previous research has shown recurrent middle and posterior STS activation in response to ToM (e.g., Frith & Frith, 2006; Gallagher & Frith, 2003; Gallagher et al., 2000; Völlm et al., 2006), and in particular right pSTS activation ToM (eg., Kobayashi et al., 2003; Saxe 2006; Saxe et al., 2004) the closet activation found here individually for ToM was in the mSTS/MTG area. It is furthermore contrasting that the present study found greater left than right STS activation. Previous findings have typically linked the right pSTS area to ToM (eg., Kobayashi et al., 2003; Saxe 2006; Saxe et al., 2004). The current finding that more anterior areas, and to a larger extent the left STS, were activated could be a consequence of participants verbalising ToM stimuli, thus activating more speech associated left and anterior STS areas. It is still worth noting, however, that the conjunction analysis does indicate that there might also be some pSTS activity in response to ToM. This however, as mentioned, cannot though be significantly stated since a global conjunction analysis was used.

The results from the present study showed that speech perception, audiovisual integration, and theory of mind, activated distinct neuronal structures within the STS. Of most interest, it was revealed that all three processes showed bilateral activation within the posterior STS area. This finding is thus in line with previous research which has implicated this area of the STS in crossmodal processing. The present results indicate that SP, AVI and ToM activate close and to some extent overlapping substructures within the pSTS area. It is however, not possible to discern the precise extent of the overlapping activation, or coactivation within the STS, using the present method. As mentioned, previous research has indicated that sections of the STS are not wholly functionally subdivided. This has led many in the field to suggest that areas of the STS which show overlapping activation to multiple mental processes, as the pSTS has shown in relation to SP, AVI and ToM, are multifunctional in nature. It is proposed that these multifunctional cortical structures subserve a host of mental processes by way of network coactivation. That is, the multifunctionality of the pSTS might be based on coactivations with other brain regions, with specific activation being determined by the nature of the network interactions and the specific processing demands. In the present case – speech perception, audiovisual integration, and theory of mind processing demands. This supposition is further substantiated by neuroanatomical findings showing bidirectional connections of the STS region with an array of other cortical structures and by studies reporting temporally associated activity between the STS area and other brain regions (Hein & Knigh, 2008). Recent advances in fMRI analysis method, which have made explicit testing of the network assumption possible, have also reinforced the network coactivation hypothesis. One such approach, Dynamic Causal Models (DCMs), permit analysis of activity within the STS region as part of an integrated neural network.

It does so by exploring changes in neural activity in different brain regions as a function of external input and not within a restricted anatomical model (Friston, Harrison, & Penny, 2003). A few recent studies which have applied such DCM models (e.g., Noppeney, Josephs, Hocking, Price, & Friston, 2007; Sukhbinder, Stephan, Warren, Friston, & Griffiths, 2007) have shown strong connections between the STS and early auditory regions. In the case of the current study, such an analysis could reveal preceding neural activations elsewhere to the STS activation, making it clearer how the different sub-structures of the STS activate. It could consequently reveal in greater nuance to which level the different sub-structures within the pSTS are overlapping in activation and could be multifunctional.

Continued research into the processing role of the STS should extend the use of a design that includes testing multiple paradigms in relation to STS activation, as well as employ DCM modelling to further investigate the functional connectivity of the STS region to other cortical areas, in order to better uncover the basis of STS activity and potential multifunctionality.

5. Acknowledgments

I am grateful to the radiographers at the Haukeland UniversityHospital for their assistance and technical expertise, to Marta Dyl who helped to assemble the experimental stimuli and helped to conduct the experimentation, and lastly and most importantly, to my supervisor Prof. Dr. Specht who gave me guidance and help through the project.

6. References

Akiyama, T., Kato, M., Muramatsu, T., Saito, F., Nakachi, R., & Kashima, H. (2006). A deficit in discriminating gaze direction in a case with right superior temporal gyrus lesion. *Neuropsychologia, 44* (2), 161–170. doi:10.1016/j.neuropsychologia.2005.05.018

Akiyama, T., Kato, M., Muramatsu, T., Saito, F., Umeda, S., & Kashima, H. (2006). Gaze but not arrows: A dissociative impairment after right superior temporal gyrus damage. *Neuropsychologia, 44* (10), 1804–1810. doi:10.1016/j.neuropsychologia.2006.03.007

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences, 4,* 267–278. doi:10.1016/S1364-6613(00)01501-1

Annett, M., 1970. A classification of hand preference by association analysis. *British Journal of Psychology, 61* (3), 303–321. doi:10.1111/j.2044-8295.1970.tb01248.x

Beauchamp, M., Argall, B. D., Bodurka, J., Duyn, J. H., & Martin, A. (2004^{a}). Unravelling multisensory integration: patchy organization within the human multisensory cortex. *Nature Neuroscience 7* (11), 1190-1192. doi:10.1038/nn1333

Beauchamp, M., Lee, K. E., Argall, B. D., & Martin, A. (2004[b]). Integration of auditory and visual information about objects in superior temporal sulcus. *Neuron, 41* (4), 809–823. doi:10.1016/S0896-6273(04)00070-4

Beauchamp, M., Yasar, N. E., Frye, R. E., & Ro, T., (2008). Touch, sound and vision in human superior temporal sulcus. *Neuroimage 41* (3), 1011–1020. doi:10.1016/j.neuroimage.2008.03.015

Belin, P., & Zatorre, R. J. (2000). 'What', 'where' and 'how' in auditory cortex. *Nature Neuroscience, 3*, 965–966. doi:10.1038/nn904

Benevento, L. A., Fallon, J., Davis, B. J., & Rezak, M. (1977). Auditory-visual interaction in single cells in the cortex of the superior temporal sulcus and the orbital frontal cortex of the macaque monkey. *Experimental Neurology, 57* (3), 849–872. doi:10.1016/0014-4886(77)90112-1

Binder, J. R., Frost, J. A., Hammeke, T. A., Bellgowan, P. S. F., Springer, J. A., Kaufman, J. N., & Possing, E. T. (2000). Human temporal lobe activation by speech and nonspeech sounds. *Cerebral Cortex, 10*, 512–528. doi:10.1093/cercor/10.5.512

Binder, J. R., Frost, J. A., Hammeke, T. A., Rao, S. M., & Cox, R. W. (1996). Function of the left planum temporale in auditory and linguistic processing. *Brain 119* (4), 1239–1247. doi:10.1093/brain/119.4.1239

Binder, J. R., Frost, J. A., Hammeke, T. A., Cox, R. W., Rao, S. M., & Prieto, T. (1997). Human brain language areas identified by functional MRI. *Journal of Neuroscience, 17* (1), 353–362.

Binder, J. R., Rao, S. M., Hammeke, T. A., Yetkin, Y. Z., Jesmanowicz, A., Bandettini, P. A., Wong, E. C., Estkowski, L. D., Goldstein, M. D., Haughton, V. M., & Hyde, J. S. (1994). Functional magnetic resonance imaging of human auditory cortex. *Annals of Neurology, 35* (6), 662–672. doi:10.1002/ana.410350606

Bruce, C., Desimone, R., & Gross, C. G. (1981). Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *Journal of Neurophysiology, 46*, 369–384.

Brunet, E., Sarfatti, Y., Hardy-Baylé, M. C., & Decety, J. (2000). A PET investigation of the attribution of intentions with a nonverbal task. *Neuroimage, 11*, 157–166. doi:10.1006/nimg.1999.0525

Brunet, E., Sarfatti, Y., Hardy-Baylé, M. C., & Decety, J. (2003). Abnormalities of brain function during a nonverbal theory of mind task in schizophrenia. *Neuropsychologia, 41* (12), 1574-1582. doi:10.1016/S0028-3932(03)00119-2

Calvert, G. A. (2001). Crossmodal processing in the human brain: Insights from functional neuroimaging studies. *Cerebral Cortex 11*, 1110–1123.

doi:10.1093/cercor/11.12.1110

Calvert, G. A., Campbell, R., & Brammer, M. J. (2000). Evidence from functional magnetic resonance imaging of crossmodal binding in the human heteromodal cortex. *Current Biology,10* (11), 649–657. doi:10.1016/S0960-9822(00)00513-3

Calvert, G. A., Hansen, P. C., Iversen, S. D., & Brammer, M. J. (2001). Detection of audio-visual integration sites in humans by application of electrophysiological criteria to the BOLD effect. *Neuroimage, 14*, 427–438. doi:10.1006/nimg.2001.0812

Castelli, F., Happé, F., Frith, U., & Frith C. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage, 12*, 314–25. doi:10.1006/nimg.2000.0612

Dehaene-Lambertz, G., Pallier, C., Serniclaes, W., Sprenger-Charolles, L., Jobert, A., & Dehaene, S. (2005). Neural correlates of switching from auditory to speech perception. *Neuroimage, 24* (1), 21–33. doi:10.1016/j.neuroimage.2004.09.039

Démonet, J.-F., Price, C., Wise, R., & Frackowiak, R. S. J. (1994). Differential activation of right and left posterior sylvian regions by semantic and phonological tasks: A positron emission tomography study in normal human subjects. *Neuroscience Letters, 182* (1)*,* 25–28. doi:10.1016/0304-3940(94)90196-1

Dhankhar, A., Wexler, B. E., Fulbright, R. K., Halwes, T., Blamire, A. M., & Shulman, R. G. (1997). Functional magnetic resonance imaging assessment of the human brain auditory cortex response to increasing word presentation rates. *Journal of Neurophysiology, 77* (1), 476–483.

Dufor, O., Serniclaes, W., Sprenger-Charolles, L., & Demonet, J.-F. (2007). Top-down processes during auditory phoneme categorization in dyslexia: A PET study. *Neuroimage, 34*, 1692–1707.

Engelien, A., Tüscher, O., Hermans, W., Isenberg, N., Eidelberg, D., Frith, C., Stern, E., & Silbersweig, D. (2006). Functional neuroanatomy of non-verbal semantic sound processing in humans. *Journal of Neural Transmission, 113*, 599–608. doi:10.1007/s00702-005-0342-0

Fletcher, P.C., Happé, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S. J., & Frith, C. D. (1995). Other minds in the brain: A functional imaging study of 'theory of mind' in story comprehension. *Cognition 57* (2), 109–128. doi:10.1016/0010-0277(95)00692-R

Friston, K. J., Zarahn, E., Josephs, O., Henson, R. N., & Dale, A. M. (1999). Stochastic designs in event-related fMRI. *Neuroimage, 10* (5), 607–619. doi:10.1006/nimg.1999.0498

Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society of London, Series B (Biological Sciences)*, *358*, 459–473. doi:10.1098/rstb.2002.1218

Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron, 50*, 531–534. doi:10.1016/j.neuron.2006.05.001

Friston, K. J., Harrison, J. B., & Penny, W. (2003). *Dynamic causal modeling. Neuroimage, 19* (4), 1273–1302. doi:10.1016/S1053-8119(03)00202-7

Gallagher, H. L., Happe, F., Brunswick, N., Fletcher, P. C., Frith, U., & Frith, C. D. (2000). Reading the mind in cartoons and stories: An FMRI study of ''theory of mind'' in verbal and nonverbal tasks. *Neuropsychologia, 38*, 11–21. doi:10.1016/S0028-3932(99)00053-6

Galllagher, H. L., & Frith, C. D (2003). Functional imaging of ′theory of mind′. *Trends in Cognitive Neuroscience, 7* (2), 77–83. doi:10.1016/S1364-6613(02)00025-6

Goel, V., Grafman, J., Sadato, N., & Hallet, M. (1995). Modelling other minds. *Neuroreport 6*, 1741–1746.

Griffiths, T. D., Rees, G., Rees, A., Green, G. G. R., Witton, C., Rowe, D., Büchel, C., Turner, R., & Frackowiak, R. S. J. (1998). Right parietal cortex is involved in the perception of sound movement in humans. *Nature Neuroscience, 1*, 74–79.

doi:10.1038/276

Grimshaw, G. M., Kwasny, K. M., Covell, E., & Johnson, R. A. (2003). The dynamic nature of language lateralization: Effects of lexical and prosodic factors. *Neuropsychologia 41*,1008–1019. doi:10.1016/S0028-3932(02)00315-9

Grossman, E. D., & Blake, R. (2001). Brain activity evoked by inverted and imagined biological motion. *Vision Research, 41* (10-11), 1475–1482. doi:10.1016/S0042-6989(00)00317-5

Grossman, E. D., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron, 35*, 1167–1175. doi:10.1016/S0896-6273(02)00897-8

Haxby, J., Hoffman, E., & Gobbini, I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Neuroscience, 4* (6), 223–233. doi:10.1016/S1364-6613(00)01482-0

Hein, G., Knight, R. T. (2008). Superior temporal sulcus – it's my area: or is it? *Journal of Cognitive Neuroscience, 20* (12), 2125–2136. doi:10.1162/jocn.2008.20148

Hickok, G., & Poeppel, D. (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Neuroscience, 4* (4), 131–138. doi:10.1016/S1364-6613(00)01463-7

Hocking, J., & Price, C. J. (2008). The role of the posterior superior temporal sulcus in audiovisual processing. *Cerebral Cortex, 18*, 2439–2449. doi:10.1093/cercor/bhn007

Hoffman, E., & Haxby, J. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience, 2* (1), 574–580. doi:10.1038/71152

Howard, D., Patterson, K., Wise, R., Brown, W. D., Friston, K., Weiller, C., & Frackowiak, R. S. J. (1992). The cortical localization of the lexicons. *Brain, 115,* 1769–1782. doi:10.1093/brain/115.6.1769

Jäncke, L., Shah, N. J., Posse, S., Grosse-Ryuken, M., & Müller-Gärtner, H.-W. (1998). Intensity coding of auditory stimuli: An fMRI study. *Neuropsychologia 36* (9), 875–883. doi:10.1016/S0028-3932(98)00019-0

Jäncke, L., Wüstenberg, T., Scheich, H., & Heinze, H.-J. (2002). Phonetic perception and the temporal cortex. *Neuroimage, 15,* 733–746. doi:10.1006/nimg.2001.1027

Jäncke, L., Mirzazade, S., & Shah, N. J. (1999). Attention modulates activity in the primary and the secondary auditory cortex: A functional magnetic resonance imaging study in human subjects. *Neuroscience Letters, 266* (2), 125–128. doi:10.1016/S0304-3940(99)00288-8

Karnath, H. (2001). New insights into the functions of the superior temporal cortex. *Nature Reviews Neuroscience, 2*, 568–576. doi:10.1038/35086057

Kobayashi, C., Glover, G. H., & Temple, E. (2007). Children's and adults' neural bases of verbal and nonverbal ''theory of mind''. *Neuropsychologia, 45*, 1522–1532. doi:10.1016/j.neuropsychologia.2006.11.017

Leslie, A. M. (1987). Pretense and representation in infancy: The origins of 'theory of mind'. *Psychological Review, 94* (4), 412–426. doi:10.1037/0033-295X.94.4.412

Liebenthal, E., Binder, J. R., Spitzer, S. M., Possing, E. T., & Medler, D. A. (2005). Neural substrates of phonemic perception. *Cerebral Cortex, 15* (10), 1621–1631. doi:10.1093/cercor/bhi040

Mummery, C. J., Ashburner, J., Scott, S. K., & Wise, R.J. (1999). Functional neuroimaging of speech perception in six normal and two aphasic subjects. *Journal of the Acoustical Society of America, 106*, 449–457.

Noppeney, U., Josephs, O., Hocking, J., Price, C. J., & Friston, K. J. (2008). The effect of prior visual information on recognition of speech and sounds. *Cerebral Cortex, 18* (3), 598–609. doi:10.1093/cercor/bhm091

Osnes, B., Hugdahl, K., & Specht, K. (2011^{a}). Effective connectivity analysis demonstrates involvement of premotor cortex during speech perception. *Neuroimage 54*, 2437-2445. doi:10.1016/j.neuroimage.2010.09.078

Osnes, B., Hugdahl, K., Hjelmervik, H., & Specht, K. (2011^{b}). Increased activation in superior temporal gyri as a function of increment in phonetic features. *Brain & Language, 116*, 97–101. doi:10.1016/j.bandl.2010-10.001

Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., & Raichle, M. E. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature, 331*, 585–589. doi:10.1038/331585a0

Price, C. J., (2000). The anatomy of language: Contributions from functional neuroimaging. *Journal of Anatomy, 197* (3), 335–359. doi:10.1046/j.1469-7580.2000.19730335.x

Price, C. J., Wise, R. J. S., Warburton, E. A., Moore, C. J., Howard, D., Patterson, K., Frackowiak, R. S. J., & Friston, K. J. (1996). Hearing and saying. The functional neuro-anatomy of auditory word processing. *Brain, 119*, 919–931. doi: 10.1093/brain/119.3.919

Price, C., Thierry, G., & Griffiths, T. (2005). Speech-specific auditory processing: where is it? *Trends in Cognitive Neuroscience, 9* (6), 271–276. doi:10.1016/j.tics.2005.03.009

Puce, A., Allison, T., Bentin, S., Gore, J.C., & McCarthy, G. (1998). Temporal cortex activations in viewing eye and mouth movements. *The Journal of Neuroscience, 18* (6), 2188–2199.

Puce, A., & Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society of London, Series B (Biological Sciences)*, *358*, 435–445. doi:10.1098/rstb.2002.1221

Rimol, L. M., Specht, K., Weis, S., Savoy, R., & Hugdahl, K. (2005). Processing of sub-syllabic speech units in the posterior temporal lobe: An fMRI study. *Neuroimage, 26*,1059–1067. doi:10.1016/j.neuroimage.2005.03.028

Sabri, M., Binder, J. R., Desai, R., Medler, D. A., Leitl, M. D., & Liebenthal, E. (2008). Attentional and linguistic interactions in speech perception. *Neuroimage, 39* (3), 1444–1456. doi:10.1016/j.neuroimage.2007.09.052

Samson, D., Apperly, I. A., Chiavarino, C., & Humphreys, G. W. (2004). Left tempoparietal junction is necessary for representing someone else's belief. *Nature Neuroscience, 7*, 499–500. doi:10.1038/nn1223

Saxe, R. (2006). Uniquely human social cognition. *Current Opinion in Neurobiology, 16* (2), 235–239. doi:10.1016/j.conb.2006.03.001

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people: The role of the temporo-parietal junction in “theory of mind”. *Neuroimage, 19*, 1835–1842. doi:10.1016/S1053-8119(03)00230-1

Saxe, R., Carey, S., & Kanwisher, N. (2004). Understanding other minds: linking developmental psychology and functional neuroimaging. *Annual Review of Psychology, 55*, 87–124. doi:10.1146/annurev.psych.55.090902.142044

Scott, S. K., & Johnsrude, I. S. (2003). The neuroanatomical and functional organization of speech perception. *Trends in Neuroscience, 26* (2), 100–107. doi:10.1016/S0166-2236(02)00037-1

Scott, S. K., & Wise, R. J. (2004). The functional neuroanatomy of prelexical processing in speech perception. *Cognition, 92* (1–2), 13–45. doi:10.1016/j.cognition.2002.12.002

Scott, S. K., Blank, C. C., Rosen, S., Wise, R. J. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain, 123* (12), 2400–2406. doi: 10.1093/brain/123.12.2400

Seltzer, B., & Pandya, D. N. (1978). Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the rhesus monkey. *Brain Research, 23* (1), 1–24. doi:10.1016/0006-8993(78)90584-X

Specht, K., Rimol, L. M., Reul, J., & Hugdahl, K. (2005). ‘‘Soundmorphing”: A new approach to studying speech perception in humans. *Neuroscience Letters, 384* (1–2), 60–65. doi:10.1016/j.neulet.2005.04.057

Specht, K., Osnes, B., & Hugdahl, K. (2009). Detection of differential speech-specific processes in the temporal lobe using fMRI and a dynamic **“**sound morphing**”** technique. *Human Brain Mapping, 30* (10), 3436–3444. doi:10.1002/hbm.20768

Specht, K., & Reul, J. (2003). Functional segregation of the temporal lobes into highly differentiated subsystems for auditory perception: An auditory rapid event-related fMRI-task. *Neuroimage, 20*, 1944–1954. doi:10.1016/j.neuroimage.2003.07.034

Stuss, D. T., Gallup, G. G., & Alexander, M. P. (2001). The frontal lobes are necessary for `theory of mind′. *Brain, 124*, 279–286. doi:10.1093/brain/124.2.279

Sukhbinder, K., Stephan, K. E., Warren, J. D., Friston, K. J., & Griffiths, T. D. (2007). Hierarchical processing of auditory objects in humans. *PLoS Computational Biology, 3* (6), 0977–0985. doi:10.1371/journal.pcbi.0030100

Tervaniemi, M. (2001). Musical sound processing in the human brain: Evidence from electric and magnetic recordings. *Annals of the New York Academy of Sciences, 930*, 259–272. doi:10.1111/j.1749-6632.2001.tb05737.x

Tervaniemi, M., & Hugdahl, K. (2003). Lateralization of auditory-cortex functions.

Brain Research Reviews, 43:231–246. doi:10.1016/j.brainresrev.2003.08.004

Uppenkamp, S., Johnsrude, I. S., Norris, D., Marslen-Wilson, W., & Patterson, R. D. (2006). Locating the initial stages of speech–sound processing in human temporal cortex. *Neuroimage, 31*, 1284–1296. doi:10.1016/j.neuroimage.2006.01.004

van Atteveldt, N. M., Formisano, E., Goebel, R., & Blomert, L. (2004). Integration of letters and speech sounds in the human brain. *Neuron, 43*, 271–282. doi:10.1016/j.neuron.2004.06.025

van Atteveldt N.M., Formisano, E., Goebel, R., & Blomert, L. (2007). Top-down task effects overrule automatic multisensory responses to letter-sound pairs in auditory association cortex. *Neuroimage, 36* (4), 1345–1360. doi:10.1016/j.neuroimage.2007.03.065

Vogeley K, Bussfeld P, Newen A, Herrmann S, Happé F, Falkai, P., Maier, W., Shah, N. J. Fink, G. R., & Zilles, K. (2001). Mind reading: Neural mechanisms of theory of mind and self-perspective. *Neuroimage*, *14* (1), 170–181. doi:10.1006/nimg.2001.0789

Völlm, B. A., Taylor, A. N. W., Richardson, P., Corcoran, R., Stirling, J., McKie, S., Deakin, J. F. W., & Elliot, R. (2006). Neuronal correlates of theory of mind and empathy: A functional magnetic resonance imaging study in a nonverbal task. *Neuroimage, 29* (1), 90–98. doi:10.1016/j.neuroimage.2005.07.022

Warren, J. D., Zielinski, B. A., Green, G. G. R., Rauschecker, J. P., & Griffiths, T. D. (2002). Perception of sound-source motion by the human brain. *Neuron 34* (1), 139–148. doi:10.1016/S0896-6273(02)00637-2

Wise, R., Chollet, F., Hadar, U., Friston, K., Hoffner, E., & Frackowiak R. S. J. (1991). Distribution of cortical neural networks involved in word comprehension and word retrieval. *Brain 114* (4)*,* 1803–1817. doi:10.1093/brain/114.4.1803

Wise, R., Scott, S. K., Blank, C., Mummery, C. J., Murphy, K., & Warburton, E. A. (2001). Separate neural subsystems within 'Wernicke's area'. *Brain, 124* (1), 83–95. doi:10.1093/brain/124.1.83

Wright, T. M., Pelphrey, K. A., Allison, T., McKeown, M. J., & McCarthy, G. (2003). Polysensory interactions along lateral temporal regions evoked by audiovisual speech. *Cerebral Cortex, 13* (10), 1034–1043. doi:10.1093/cercor/13.10.1034

Zatorre, R. J., & Belin, P. (2001). Spectral and temporal processing in human auditory cortex. *Cerebral Cortex, 11* (10), 946–953. doi:10.1093/cercor/11.10.946

Zatorre, R. J., Evans, A. C., Meyer, E., & Gjedde, A. (1992). Lateralization of phonetic and pitch discrimination in speech processing. *Science, 256*, 846–849. doi:10.1126/science.256.5058.846

Zatorre, R. J., Belin, P., & Penhune, V. B. (2002). Structure and function of auditory cortex: Music and speech. *Trends Cognitive Sciences, 6*, 37–46. doi:10.1016/S1364-6613(00)01816-7

Zatorre, R. J., Bouffard, M., Ahad, P., & Belin, P. (2002). Where is 'where' in the human auditory cortex? *Nature Neuroscience, 5*, 905–909. doi:10.1038/nn904

7. Appendices

7.1. Appendix 1

Table 3

Foci of significant brain activations associated with ToM, global analysis, $p<0.05$ (FWE), Cl.>10.

set level		cluster level		peak level			area
P	c	$P_{FWE\text{-}corr}$	k_E	$P_{FWE\text{-}corr}$	*T*	*Z*	MNI, mmm
0.000	17	0.000	8314	0.000	12.47	Inf	-30 -42 -18
				0.000	12.3	Inf	-48 -62 12
				0.000	11.77	Inf	-50 -70 8
		0.000	5931	0.000	11.31	Inf	-50 18 18
				0.000	10.89	7.78	-52 26 12
				0.000	10.52	7.64	-46 10 30
		0.000	3577	0.000	10.67	7.69	48 -66 16
				0.000	10.54	7.64	48 -52 12
				0.000	9.72	7.28	40 -76 18
		0.000	846	0.000	8.09	6.46	28 -40 -18
				0.002	5.99	5.19	40 -52 -22
		0.000	1164	0.000	7.97	6.39	44 18 24
				0.000	6.7	5.65	58 28 14
				0.000	6.62	5.6	54 12 50
		0.000	159	0.000	7.49	6.12	-10 42 56
		0.000	263	0.000	7.43	6.09	-18 -80 -42
				0.002	6.12	5.28	-6 -84 -30
				0.002	6.05	5.23	-14 -78 -32
		0.000	233	0.000	7.17	5.94	22 -58 18
		0.000	247	0.000	6.9	5.78	16 -84 -32
				0.001	6.49	5.52	16 -82 -42
		0.000	163	0.000	6.52	5.53	-8 18 52
		0.000	119	0.003	5.89	5.12	32 28 -12
		0.002	63	0.004	5.87	5.11	-4 -24 -14
		0.003	54	0.004	5.87	5.11	6 -58 44
		0.019	11	0.006	5.73	5.01	48 8 -36
		0.002	69	0.006	5.72	5.01	-10 -4 -4
		0.020	10	0.012	5.49	4.84	-54 -6 -22
		0.011	22	0.015	5.41	4.78	-30 20 60

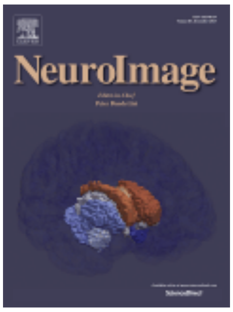
7.2. *Appendix 2. Neuroimage* guidelines for authors

NEUROIMAGE

ELSEVIER

AUTHOR INFORMATION PACK

TABLE OF CONTENTS



ISSN: 1053-8119

DESCRIPTION

NeuroImage, a Journal of **Brain Function** provides a vehicle for communicating important advances in acquiring, analyzing, and modelling **neuroimaging** data and in applying these techniques to the study of structure-function and brain-behavior relationships. Though the emphasis is on the macroscopic level of **human brain organization**, meso-and microscopic neuroimaging across all species will be considered if informative for understanding the aforementioned relationships.

The main criterion on which papers are judged for *NeuroImage* is to what extent the scientific contribution advances our understanding of brain function, organization, and structure. *NeuroImage* also welcomes papers that explicitly address these questions in animal models or clinical populations. Papers that include reference to advancing the understanding of pathology, abnormal development, use of biomarkers or other questions of clinical utility should be referred to NeuroImage: Clinical.

The journal publishes original research articles, papers on methods or modelling, theory and position papers that describe the use of imaging approaches to studying the brain. The journal strives to incorporate theoretical and technological innovations as part of its publishing remit and is committed to publishing the highest quality papers in both print and electronic media. The administration of the journal is integrative, reflecting the fact that **imaging neuroscience** is a multi-disciplinary science.

Submitted papers will generally be considered under five sections. These comprise Methods and Modelling, Anatomy and Physiology, Systems Neuroscience, Cognitive Neuroscience, and Social Neuroscience.

AUDIENCE

Imaging Neuroscientists, Computational Neuroscientists, Neuroanatomists, Neurophysiologists, Cognitive Neuroscientists, Experimental Psychologists, System Neuroscientists, Biostatisticians, Academic Neurologists and Psychiatrists.

IMPACT FACTOR

2012: 6.252 © Thomson Reuters Journal Citation Reports 2013

ABSTRACTING AND INDEXING

Scopus

EDITORIAL BOARD

Editor-in-Chief

Peter Bandettini, Bethesda, MD, USA

Anatomy and Physiology Section Editor :

Marc Tittgemeyer, Köln, Germany

Handling Editors:

Andrew Alexander, Madison, WI, USA **Paul Cumming,** Erlangen, Germany **Simon Eickhoff,** Jülich, Germany
Heidi Johansen-Berg, Oxford, England, UK
Jason Lerch, Toronto, ON, Canada
Bruce Pike, Montreal, QC, Canada

Methods and Modelling Section Editor:

Michael Breakspear, Brisbane, QLD, Australia

Handling Editors:

Tom Eichele, Bergen, Norway
Tom Liu, La Jolla, CA, USA
Stephen Smith, Oxford, England, UK
Klaas Stephan, Zurich, Switzerland

Systems Neuroscience Section Editor:

Andreas Kleinschmidt, Gif-sur-Yvette, France

Handling Editors:

Vincent Clark, Albuquerque, NM, USA
Hartwig Siebner, Hvidovre, Denmark

Cognitive Neuroscience Section Editor:

Sonja Kotz, Leipzig, Germany
Cindy Lustig, Ann Arbor, MI, USA

Handling Editors:

Michael Chee, Singapore, Singapore **Emrah Duzel,** London, England, UK **Gregory Hickok,** Irvine, CA, USA
Thomas Münte, Lübeck, Germany

Social Neuroscience Section Editor:

Aina Puce, Bloomington, IN, USA

Handling Editors:

Joan Chiao, Northwestern University, Evanston, IL, USA

Editorial Board :

C. Beaulieu, Edmonton, AB, Canada
C. Beckman,
P. Bentley, London, England, UK
G. Berns,
M. Boly, Liège, Belgium
M. Brookes, Nottingham, UK
V. Calhoun, Albuquerque, NM, USA
K. Cheng, Wako, Japan
M.X. Cohen, Amsterdam, Netherlands
A. Daffertshofer, Amsterdam, Netherlands
J. Daunizeau, Paris, France
C. Davatzikos, Philadelphia, PA, USA
S. Debener, Oldenburg, Germany

A. Duarte, Atlanta, GA, USA
D. Eidelberg, Manhasset, NY, USA
R. Elliott, Manchester, England, UK
T. Ethofer, Tuebingen, Germany
A. Gazzaley, San Francisco, CA, USA
J.C. Gee, Philadelphia, PA, USA
N. George, Paris, France
P. Greenwood, Fairfax, VA, USA
D. Grieve,
J. Gross, Glasgow, UK
G. Gründer, Aachen, Germany
D.S.F. Hyder, New Haven, CT, USA
S. Jbabdi, Headington, Oxford, UK
R. Kakigi, Okazaki, Japan
S.M. LaConte, Roanoke, VA, USA
R. Lanzenberger, Vienna, Austria
H. Laufs, Frankfurt,
J. Lerch, Toronto, ON, Canada **C.-S.R. Li,** New Haven, CT, USA **F.-H. Lin,** Taipei, Taiwan
M. Lowe, Cleveland, OH, USA
K. Mathiak, Aachen, Germany
W.P. Medendorp, Nijmege, Netherlands
V. Menon, Stanford, CA, USA
K. L. Miller, Oxford, England, UK
J. Mourao-Miranda, London, England, UK
K. Murphy,
S. Nagarajan, San Francisco, CA, USA
T. Nichols, Coventry, UK
U. Noppeney, Tübingen, Germany
D. Norris, Nijmegen, Netherlands
L. O'Donnell, Boston, MA, USA
S. Ortigue, Syracuse, NY, USA
S. Posse, Albuquerque, Mexico
P. Ritter, Berlin, Germany
A. Roebroeck, Maastricht, Netherlands
S.A. Rombouts, Leiden, Netherlands
D. Salat, Charlestown, MA, USA
S. Schwartz, Genève 4, Switzerland
B. Seymour,
A. Silva,
O. Sporns, Bloomington, IN, USA
K. Uludag, Maastricht, Netherlands
S. Whitfield-Gabrieli, Cambridge, MA, USA
G. Wig, St Louis, MO, USA
M. Woolrich,
E. Yacoub, Minneapolis, MN, USA

Editors Emeriti:

R. Frackowiak, London, UK

GUIDE FOR AUTHORS

Your Paper Your Way
ypyw-gfa-banner.gifyour paper your way

BEFORE YOU BEGIN

Ethics in publishing

For information on Ethics in publishing and Ethical guidelines for journal publication see http://www.elsevier.com/publishingethics and http://www.elsevier.com/journal-authors/ethics.

Policy and ethics

Submitted papers will generally be considered under five sections. These comprise Methods and Modelling, Anatomy and Physiology, Systems Neuroscience, Cognitive Neuroscience and Social Neuroscience. On occasion, the Editors may reassign a submission from the authors original choice. These five sections reflect fields of specialisation in neuroimaging and implicitly define the area in which a paper may have its greatest impact. If it is not clear under which Section a paper should be handled, then we welcome pre-submission enquiries.

Elsevier facilitates author response to the NIH voluntary posting request (referred to as the NIH "Public Access Policy"; see http://www.nih.gov/about/publicaccess/index.htm) by posting the peer-reviewed author's manuscript directly to PubMed Central on request from the author, 12 months after formal publication. Upon notification from Elsevier of acceptance, we will ask you to confirm via e-mail (by e-mailing us atNIHauthorrequest@elsevier.com) that your work has received NIH funding and that you intend to respond to the NIH policy request, along with your NIH award number to facilitate processing.

Upon such confirmation, Elsevier will submit to PubMed Central on your behalf a version of your manuscript that will include peer-review comments, for posting 12 months after formal publication. This will ensure that you will have responded fully to the NIH request policy. There will be no need for you to post your manuscript directly with PubMed Central, and any such posting is prohibited.

Exceptions: It is the policy of Elsevier that authors need not obtain permission in the following cases only: (1) to use their original figures or tables in their future works; (2) to make copies of their papers for use in their classroom teaching; and (3) to include their papers as part of their dissertations.

The Neuroscience Peer Review Consortium

NeuroImage is a member of the Neuroscience Peer Review Consortium (NPRC). The NPRC has been formed to reduce the time expended and, in particular, the duplication of effort by, and associated burden on reviewers involved in the peer review of original neuroscience research papers.

It is an alliance of neuroscience journals that have agreed to accept manuscript reviews from other Consortium journals. By reducing the number of times that a manuscript is reviewed, the Consortium will reduce the load on reviewers and Editors, and speed the publication of research results. If a manuscript has been rejected by another journal in the Consortium, authors can submit the manuscript to *NeuroImage* and indicate that the referees' reports from the first journal be made available to the Editors of *NeuroImage*. (N.B. Only manuscripts which were first submitted to another journal after the 1st January 2008 are eligible for the NPRC scheme.)

It is the authors' decision as to whether or not to indicate that a set of referee's reports should be forwarded from the first journal to *NeuroImage*. If an author does not wish for this to happen, the manuscript can be submitted to *NeuroImage* without reference to the previous submission. No information will be exchanged between journals except at the request of authors. However, if the original referees' reports suggested that the paper is of high quality, but not suitable for the first journal, then it will often be to an author's advantage to indicate that referees' reports should be made available.Authors should revise the original submission in accordance with the first journal's set of referee reports, reformat the paper to *NeuroImage* specification and submit the paper to *NeuroImage*with a covering letter describing the changes that have been made, and informing the Editors that they are happy for referees' reports to be forwarded from the first Consortium journal. Authors will be asked upon submission to *NeuroImage* the title of the first journal submitted to and the manuscript ID that was given by that journal. The editorial office of NeuroImage will request the referees' reports from the first journal. The Editors of*NeuroImage* will use forwarded referees' reports at their discretion. The Editors may use the reports directly to make a decision, or they may request further reviews if they feel such are necessary.

Visit http://nprc.incf.org for a list of Consortium journals, as well as further information on the scheme.

Conflict of interest

All authors are requested to disclose any actual or potential conflict of interest including any financial, personal or other relationships with other people or organizations within three years of beginning the submitted work that could inappropriately influence, or be perceived to influence, their work. See also http://www.elsevier.com/conflictsofinterest. Further information and an example of a Conflict of Interest form can be found at: http://help.elsevier.com/app/answers/detail/a_id/286/p/7923.

Submission declaration and verification

Submission of an article implies that the work described has not been published previously (except in the form of an abstract or as part of a published lecture or academic thesis or as an electronic preprint, see http://www.elsevier.com/postingpolicy), that it is not under consideration for publication elsewhere, that its publication is approved by all authors and tacitly or explicitly by the responsible authorities where the work was carried out, and that, if accepted, it will not be published elsewhere in the same form, in English or in any other language, including electronically without the written consent of the copyright-holder. To verify originality, your article may be checked by the originality detection service CrossCheck http://www.elsevier.com/editors/plagdetect.

Changes to authorship

This policy concerns the addition, deletion, or rearrangement of author names in the authorship of accepted manuscripts:
Before the accepted manuscript is published in an online issue: Requests to add or remove an author, or to rearrange the author names, must be sent to the Journal Manager from the corresponding author of the accepted manuscript and must include: (a) the reason the name should be added or removed, or the author names rearranged and (b) written confirmation (e-mail, fax, letter) from all authors that they agree with the addition, removal or rearrangement. In the case of addition or removal of authors, this includes confirmation from the author being added or removed. Requests that are not sent by the corresponding author will be forwarded by the Journal Manager to the corresponding author, who must follow the procedure as described above. Note that: (1) Journal Managers will inform the Journal Editors of any such requests and (2) publication of the accepted manuscript in an online issue is suspended until authorship has been agreed.
After the accepted manuscript is published in an online issue: Any requests to add, delete, or rearrange author names in an article published in an online issue will follow the same policies as noted above and result in a corrigendum.

Copyright

This journal offers authors a choice in publishing their research: Open Access and Subscription.

For Subscription articles
Upon acceptance of an article, authors will be asked to complete a 'Journal Publishing Agreement' (for more information on this and copyright, see http://www.elsevier.com/copyright). An e-mail will be sent to the corresponding author confirming receipt of the manuscript together with a 'Journal Publishing Agreement' form or a link to the online version of this agreement.
Subscribers may reproduce tables of contents or prepare lists of articles including abstracts for internal circulation within their institutions. Permission of the Publisher is required for resale or distribution outside the institution and for all other derivative works, including compilations and translations (please consult http://www.elsevier.com/permissions). If excerpts from other copyrighted works are included, the author(s) must obtain written permission from the copyright owners and credit the source(s) in the article. Elsevier has preprinted forms for use by authors in these cases: please consult http://www.elsevier.com/permissions.

For Open Access articles
Upon acceptance of an article, authors will be asked to complete an 'Exclusive License Agreement' (for more information see http://www.elsevier.com/OAauthoragreement). Permitted reuse of open access articles is determined by the author's choice of user license (see http://www.elsevier.com/openaccesslicenses).

Retained author rights

As an author you (or your employer or institution) retain certain rights. For more information on author rights for:
Subscription articles please see http://www.elsevier.com/journal-authors/author-rights-and-responsibilities.
Open access articles please see http://www.elsevier.com/OAauthoragreement.

Role of the funding source

You are requested to identify who provided financial support for the conduct of the research and/or preparation of the article and to briefly describe the role of the sponsor(s), if any, in study design; in the collection, analysis and interpretation of data; in the writing of the report; and in the decision to submit the article for publication. If the funding source(s) had no such involvement then this should be stated. Please see http://www.elsevier.com/funding.

Funding body agreements and policies

Elsevier has established agreements and developed policies to allow authors whose articles appear in journals published by Elsevier, to comply with potential manuscript archiving requirements as specified as conditions of their grant awards. To learn more about existing agreements and policies please visit http://www.elsevier.com/fundingbodies.

Open access

This journal offers authors a choice in publishing their research:

Open Access

- Articles are freely available to both subscribers and the wider public with permitted reuse
- An Open Access publication fee is payable by authors or their research funder

Subscription

- Articles are made available to subscribers as well as developing countries and patient groups through our access programs (http://www.elsevier.com/access)
- No Open Access publication fee

All articles published Open Access will be immediately and permanently free for everyone to read and download. Permitted reuse is defined by your choice of one of the following Creative Commons user licenses:
Creative Commons Attribution (CC BY): lets others distribute and copy the article, to create extracts, abstracts, and other revised versions, adaptations or derivative works of or from an article (such as a translation), to include in a collective work (such as an anthology), to text or data mine the article, even for commercial purposes, as long as they credit the author(s), do not represent the author as endorsing their adaptation of the article, and do not modify the article in such a way as to damage the author's honor or reputation.
Creative Commons Attribution-NonCommercial-ShareAlike (CC BY-NC-SA): for non-commercial purposes, lets others distribute and copy the article, to create extracts, abstracts and other revised versions, adaptations or derivative works of or from an article (such as a translation), to include in a collective work (such as an anthology), to text and data mine the article, as long as they credit the author(s), do not represent the author as endorsing their adaptation of the article, do not modify the article in such a way as to damage the author's honor or reputation, and license their new adaptations or creations under identical terms (CC BY-NC-SA).
Creative Commons Attribution-NonCommercial-NoDerivs (CC BY-NC-ND): for non-commercial purposes, lets others distribute and copy the article, and to include in a collective work (such as an anthology), as long as they credit the author(s) and provided they do not alter or modify the article.

To provide Open Access, this journal has a publication fee which needs to be met by the authors or their research funders for each article published Open Access.
Your publication choice will have no effect on the peer review process or acceptance of submitted articles.

The publication fee for Open Access in this journal is **$2,200**, excluding taxes. Learn more about Elsevier's pricing policy: http://www.elsevier.com/openaccesspricing.

Language (usage and editing services)

Please write your text in good English (American or British usage is accepted, but not a mixture of these). Authors who feel their English language manuscript may require editing to eliminate possible grammatical or spelling errors and to conform to correct scientific English may wish to use the English Language Editing service available from Elsevier's WebShop (http://webshop.elsevier.com/languageediting/) or visit our customer support site (http://support.elsevier.com) for more information.

Submission

Submission to this journal proceeds totally online and you will be guided stepwise through the creation and uploading of your files. The system automatically converts source files to a single PDF file of the article, which is used in the peer-review process. Please note that even though manuscript source files are converted to PDF files at submission for the review process, these source files are needed for further processing after acceptance. All correspondence, including notification of the Editor's decision and requests for revision, takes place by e-mail removing the need for a paper trail.

Referees

If a manuscript has been rejected by another journal in the Consortium, authors can now submit the manuscript to *NeuroImage* and indicate that the referees' reports from the first journal be made available to the Editors of *NeuroImage*.

N.B. Only manuscripts which were first submitted to another journal *after* the 1st January 2008 are eligible for the NPRC scheme.

The Editors of *NeuroImage* will use forwarded referees' reports at their discretion. The Editors may use the reports directly to make a decision, or they may request further reviews if they feel such are necessary.

PREPARATION

NEW SUBMISSIONS

Submission to this journal proceeds totally online and you will be guided stepwise through the creation and uploading of your files. The system automatically converts your files to a single PDF file, which is used in the peer-review process.
As part of the Your Paper Your Way service, you may choose to submit your manuscript as a single file to be used in the refereeing process. This can be a PDF file or a Word document, in any format or lay- out that can be used by referees to evaluate your manuscript. It should contain high enough quality figures for refereeing. If you prefer to do so, you may still provide all or some of the source files at the initial submission. Please note that individual figure files larger than 10 MB must be uploaded separately.

References

There are no strict requirements on reference formatting at submission. References can be in any style or format as long as the style is consistent. Where applicable, author(s) name(s), journal title/book title, chapter title/article title, year of publication, volume number/book chapter and the pagination must be present. Use of DOI is highly encouraged. The reference style used by the journal will be applied to the accepted article by Elsevier at the proof stage. Note that missing data will be highlighted at proof stage for the author to correct.

Formatting requirements

There are no strict formatting requirements but all manuscripts must contain the essential elements needed to convey your manuscript, for example Abstract, Keywords, Introduction, Materials and Methods, Results, Conclusions, Artwork and Tables with Captions.
If your article includes any Videos and/or other Supplementary material, this should be included in your initial submission for peer review purposes.
Divide the article into clearly defined sections.

Figures and tables embedded in text

Please ensure the figures and the tables included in the single file are placed next to the relevant text in the manuscript, rather than at the bottom or the top of the file.

REVISED SUBMISSIONS

Use of word processing software

Regardless of the file format of the original submission, at revision you must provide us with an editable file of the entire article. Keep the layout of the text as simple as possible. Most formatting codes will be removed and replaced on processing the article. The electronic text should be prepared in a way very similar to that of conventional manuscripts (see also the Guide to Publishing with Elsevier: http://www.elsevier.com/guidepublication). See also the section on Electronic artwork.
To avoid unnecessary errors you are strongly advised to use the 'spell-check' and 'grammar-check' functions of your word processor.

Article structure

Subdivision - numbered sections

Divide your article into clearly defined and numbered sections. Subsections should be numbered 1.1 (then 1.1.1, 1.1.2, ...), 1.2, etc. (the abstract is not included in section numbering). Use this numbering also for internal cross-referencing: do not just refer to 'the text'. Any subsection may be given a brief heading. Each heading should appear on its own separate line.

Introduction

State the objectives of the work and provide an adequate background, avoiding a detailed literature survey or a summary of the results.

Material and methods

Provide sufficient detail to allow the work to be reproduced. Methods already published should be indicated by a reference: only relevant modifications should be described.

Results

Results should be clear and concise.

Discussion

This should explore the significance of the results of the work, not repeat them. A combined Results and Discussion section is often appropriate. Avoid extensive citations and discussion of published literature.

Conclusions

The main conclusions of the study may be presented in a short Conclusions section, which may stand alone or form a subsection of a Discussion or Results and Discussion section.

Appendices

If there is more than one appendix, they should be identified as A, B, etc. Formulae and equations in appendices should be given separate numbering: Eq. (A.1), Eq. (A.2), etc.; in a subsequent appendix, Eq. (B.1) and so on. Similarly for tables and figures: Table A.1; Fig. A.1, etc.

Essential title page information

- ***Title.*** Concise and informative. Titles are often used in information-retrieval systems. Avoid abbreviations and formulae where possible.
- ***Author names and affiliations.*** Where the family name may be ambiguous (e.g., a double name), please indicate this clearly. Present the authors' affiliation addresses (where the actual work was done) below the names. Indicate all affiliations with a lower-case superscript letter immediately after the author's name and in front of the appropriate address. Provide the full postal address of each affiliation, including the country name and, if available, the e-mail address of each author.
- ***Corresponding author.*** Clearly indicate who will handle correspondence at all stages of refereeing and publication, also post-publication. **Ensure that phone numbers (with country and area code) are provided in addition to the e-mail address and the complete postal address. Contact details must be kept up to date by the corresponding author.**
- ***Present/permanent address.*** If an author has moved since the work described in the article was done, or was visiting at the time, a 'Present address' (or 'Permanent address') may be indicated as a footnote to that author's name. The address at which the author actually did the work must be retained as the main, affiliation address. Superscript Arabic numerals are used for such footnotes.

Abstract

A concise and factual abstract is required. The abstract should state briefly the purpose of the research, the principal results and major conclusions. An abstract is often presented separately from the article, so it must be able to stand alone. For this reason, References should be avoided, but if essential, then cite the author(s) and year(s). Also, non-standard or uncommon abbreviations should be avoided, but if essential they must be defined at their first mention in the abstract itself.

Graphical abstract

A Graphical abstract is optional and should summarize the contents of the article in a concise, pictorial form designed to capture the attention of a wide readership online. Authors must provide images that clearly represent the work described in the article. Graphical abstracts should be submitted as a separate file in the online submission system. Image size: Please provide an image with a minimum of 531 × 1328 pixels (h × w) or proportionally more. The image should be readable at a size of 5 × 13 cm using a regular screen resolution of 96 dpi. Preferred file types: TIFF, EPS, PDF or MS Office files. See http://www.elsevier.com/graphicalabstracts for examples.

Authors can make use of Elsevier's Illustration and Enhancement service to ensure the best presentation of their images also in accordance with all technical requirements: Illustration Service.

Highlights

Highlights are mandatory for this journal. They consist of a short collection of bullet points that convey the core findings of the article and should be submitted in a separate file in the online submission system. Please use 'Highlights' in the file name and include 3 to 5 bullet points (maximum 85 characters, including spaces, per bullet point). See http://www.elsevier.com/highlights for examples.

Keywords

Immediately after the abstract, provide a maximum of 6 keywords, using American spelling and avoiding general and plural terms and multiple concepts (avoid, for example, 'and', 'of'). Be sparing with abbreviations: only abbreviations firmly established in the field may be eligible. These keywords will be used for indexing purposes.

Abbreviations

Define abbreviations that are not standard in this field in a footnote to be placed on the first page of the article. Such abbreviations that are unavoidable in the abstract must be defined at their first mention there, as well as in the footnote. Ensure consistency of abbreviations throughout the article.

Acknowledgements

Collate acknowledgements in a separate section at the end of the article before the references and do not, therefore, include them on the title page, as a footnote to the title or otherwise. List here those individuals who provided help during the research (e.g., providing language help, writing assistance or proof reading the article, etc.).

Units

Follow internationally accepted rules and conventions: use the international system of units (SI). If other units are mentioned, please give their equivalent in SI.

Database linking

Elsevier encourages authors to connect articles with external databases, giving their readers one-click access to relevant databases that help to build a better understanding of the described research. Please refer to relevant database identifiers using the following format in your article: Database: xxxx (e.g., TAIR: AT1G01020; CCDC: 734053; PDB: 1XFN). See http://www.elsevier.com/databaselinking for more information and a full list of supported databases.

Math formulae

Present simple formulae in the line of normal text where possible and use the solidus (/) instead of a horizontal line for small fractional terms, e.g., X/Y. In principle, variables are to be presented in italics. Powers of e are often more conveniently denoted by exp. Number consecutively any equations that have to be displayed separately from the text (if referred to explicitly in the text).

Footnotes

Footnotes should be used sparingly. Number them consecutively throughout the article. Many wordprocessors build footnotes into the text, and this feature may be used. Should this not be the case, indicate the position of footnotes in the text and present the footnotes themselves separately at the end of the article. Do not include footnotes in the Reference list.

Table footnotes

Indicate each footnote in a table with a superscript lowercase letter.

Artwork *Electronic artwork General points*

- Make sure you use uniform lettering and sizing of your original artwork.
- Preferred fonts: Arial (or Helvetica), Times New Roman (or Times), Symbol, Courier.

- Number the illustrations according to their sequence in the text.
- Use a logical naming convention for your artwork files.
- Indicate per figure if it is a single, 1.5 or 2-column fitting image.
- For Word submissions only, you may still provide figures and their captions, and tables within a single file at the revision stage.
- Please note that individual figure files larger than 10 MB must be provided in separate source files.

A detailed guide on electronic artwork is available on our website:
http://www.elsevier.com/artworkinstructions.

You are urged to visit this site; some excerpts from the detailed information are given here.

Formats

Regardless of the application used, when your electronic artwork is finalized, please 'save as' or convert the images to one of the following formats (note the resolution requirements for line drawings, halftones, and line/halftone combinations given below):

EPS (or PDF): Vector drawings. Embed the font or save the text as 'graphics'.

TIFF (or JPG): Color or grayscale photographs (halftones): always use a minimum of 300 dpi. TIFF (or JPG): Bitmapped line drawings: use a minimum of 1000 dpi.

TIFF (or JPG): Combinations bitmapped line/half-tone (color or grayscale): a minimum of 500 dpi is required.

Please do not:

- Supply files that are optimized for screen use (e.g., GIF, BMP, PICT, WPG); the resolution is too low.
- Supply files that are too low in resolution.
- Submit graphics that are disproportionately large for the content.

Color artwork

Please make sure that artwork files are in an acceptable format (TIFF (or JPEG), EPS (or PDF) or MS Office files) and with the correct resolution. If, together with your accepted article, you submit usable color figures then Elsevier will ensure, at no additional charge, that these figures will appear in color on the Web (e.g., ScienceDirect and other sites) in addition to color reproduction in print. For further information on the preparation of electronic artwork, please see http://www.elsevier.com/artworkinstructions.

Illustration services

Elsevier's WebShop (http://webshop.elsevier.com/illustrationservices) offers Illustration Services to authors preparing to submit a manuscript but concerned about the quality of the images accompanying their article. Elsevier's expert illustrators can produce scientific, technical and medical-style images, as well as a full range of charts, tables and graphs. Image 'polishing' is also available, where our illustrators take your image(s) and improve them to a professional standard. Please visit the website to find out more.

Figure captions

Ensure that each illustration has a caption. A caption should comprise a brief title (**not** on the figure itself) and a description of the illustration. Keep text in the illustrations themselves to a minimum but explain all symbols and abbreviations used.

Tables

Number tables consecutively in accordance with their appearance in the text. Place footnotes to tables below the table body and indicate them with superscript lowercase letters. Avoid vertical rules. Be sparing in the use of tables and ensure that the data presented in tables do not duplicate results described elsewhere in the article.

References

Citation in text

Please ensure that every reference cited in the text is also present in the reference list (and vice versa). Any references cited in the abstract must be given in full. Unpublished results and personal communications are not recommended in the reference list, but may be mentioned in the text. If these references are included in the reference list they should follow the standard reference style of the journal and should include a substitution of the publication date with either 'Unpublished results' or 'Personal communication'. Citation of a reference as 'in press' implies that the item has been accepted for publication.

Reference links
Increased discoverability of research and high quality peer review are ensured by online links to the sources cited. In order to allow us to create links to abstracting and indexing services, such as Scopus, CrossRef and PubMed, please ensure that data provided in the references are correct. Please note that incorrect surnames, journal/book titles, publication year and pagination may prevent link creation. When copying references, please be careful as they may already contain errors. Use of the DOI is encouraged.

Web references
As a minimum, the full URL should be given and the date when the reference was last accessed. Any further information, if known (DOI, author names, dates, reference to a source publication, etc.), should also be given. Web references can be listed separately (e.g., after the reference list) under a different heading if desired, or can be included in the reference list.

References in a special issue
Please ensure that the words 'this issue' are added to any references in the list (and any citations in the text) to other articles in the same Special Issue.

Reference formatting
There are no strict requirements on reference formatting at submission. References can be in any style or format as long as the style is consistent. Where applicable, author(s) name(s), journal title/book title, chapter title/article title, year of publication, volume number/book chapter and the pagination must be present. Use of DOI is highly encouraged. The reference style used by the journal will be applied to the accepted article by Elsevier at the proof stage. Note that missing data will be highlighted at proof stage for the author to correct. If you do wish to format the references yourself they should be arranged according to the following examples:

Reference style
Name and year style in the text
Text: All citations in the text should refer to:
1. *Single author:* the author's name (without initials, unless there is ambiguity) and the year of publication;
2. *Two authors:* both authors' names and the year of publication;
3. *Three or more authors:* first author's name followed by 'et al.' and the year of publication. Citations may be made directly (or parenthetically). Groups of references should be listed first alphabetically, then chronologically.

Examples: 'as demonstrated (Allan, 2000a, 2000b, 1999; Allan and Jones, 1999). Kramer et al. (2010) have recently shown ...'
List: References should be arranged first alphabetically and then further sorted chronologically if necessary. More than one reference from the same author(s) in the same year must be identified by the letters 'a', 'b', 'c', etc., placed after the year of publication. Note that any (consistent) reference style and format may be used: the Publisher will ensure that the correct style for this journal will be introduced for the proof stages, the final print version and the PDF files for electronic distribution.

Journal abbreviations source
Journal names should be abbreviated according to the
List of title word abbreviations: http://www.issn.org/2-22661-LTWA-online.php.

Video data
Elsevier accepts video material and animation sequences to support and enhance your scientific research. Authors who have video or animation files that they wish to submit with their article are strongly encouraged to include links to these within the body of the article. This can be done in the same way as a figure or table by referring to the video or animation content and noting in the body text where it should be placed. All submitted files should be properly labeled so that they directly relate to the video file's content. In order to ensure that your video or animation material is directly usable, please provide the files in one of our recommended file formats with a preferred maximum size of 50 MB. Video and animation files supplied will be published online in the electronic version of your article in Elsevier Web products, including ScienceDirect: http://www.sciencedirect.com. Please supply 'stills' with your files: you can choose any frame from the video or animation or make a separate image. These will be used instead of standard icons and will personalize the link to your video data. For more detailed instructions please visit our video instruction pages at

http://www.elsevier.com/artworkinstructions. Note: since video and animation cannot be embedded in the print version of the journal, please provide text for both the electronic and the print version for the portions of the article that refer to this content.

AudioSlides

The journal encourages authors to create an AudioSlides presentation with their published article. AudioSlides are brief, webinar-style presentations that are shown next to the online article on ScienceDirect. This gives authors the opportunity to summarize their research in their own words and to help readers understand what the paper is about. More information and examples are available at http://www.elsevier.com/audioslides. Authors of this journal will automatically receive an invitation e-mail to create an AudioSlides presentation after acceptance of their paper.

Supplementary data

Elsevier accepts electronic supplementary material to support and enhance your scientific research. Supplementary files offer the author additional possibilities to publish supporting applications, high-resolution images, background datasets, sound clips and more. Supplementary files supplied will be published online alongside the electronic version of your article in Elsevier Web products, including ScienceDirect: http://www.sciencedirect.com. In order to ensure that your submitted material is directly usable, please provide the data in one of our recommended file formats. Authors should submit the material in electronic format together with the article and supply a concise and descriptive caption for each file. For more detailed instructions please visit our artwork instruction pages at http://www.elsevier.com/artworkinstructions.

**NEW* Inline supplementary material*

Articles in *NeuroImage* have offered the possibility to include supplementary material for some time. This has now been improved, as supplementary material can now be added inline. This means that the supplementary figures or tables will appear within the text of the online (HTML) article in an expandable viewing box- delivering the supplementary information in a contextual and valuable way to readers.

Submission of inline supplementary material (ISM) is very similar to submitting regular supplementary material. The main difference is you will now need to indicate where the Inline Supplementary Material should appear within your article, by including an instruction such as: 'Insert Supplementary Table 1 here' or by referencing the Inline Supplementary Material in the body of the text e.g. 'see Inline Supplementary Table 1'. When submitting, you need to also indicate that the attachment is Inline Supplementary material by choosing the corresponding file type from the drop down menu in EES. For more information and to see an example visit http://www.elsevier.com/ism.

MATLAB FIG files

MATLAB FIG files (optional): You can enrich your online articles by providing supplementary MATLAB figure files with the .FIG file extension. These files will be visualized using an interactive viewer that allows readers to explore your figures within the article. The FIG files can be uploaded in our online submission system, and will be made available to download from your online article on ScienceDirect. For more information, please see http://www.elsevier.com/matlab.

3D neuroimaging

You can enrich your online articles by providing 3D neuroimaging data in NIfTI format. This will be visualized for readers using the interactive viewer embedded within your article, and will enable them to: browse through available neuroimaging datasets; zoom, rotate and pan the 3D brain reconstruction; cut through the volume; change opacity and color mapping; switch between 3D and 2D projected views; and download the data. The viewer supports both single (.nii) and dual (.hdr and .img) NIfTI file formats. Recommended size of a single uncompressed dataset is 100 MB or less. Multiple datasets can be submitted. Each dataset will have to be zipped and uploaded to the online submission system via the '3D neuroimaging data' submission category. Please provide a short informative description for each dataset by filling in the 'Description' field when uploading a dataset. Note: all datasets will be available for downloading from the online article on ScienceDirect. If you have concerns about your data being downloadable, please provide a video instead. For more information see: http://www.elsevier.com/3DNeuroimaging.

Submission checklist

The following list will be useful during the final checking of an article prior to sending it to the journal for review. Please consult this Guide for Authors for further details of any item.

Ensure that the following items are present:

One author has been designated as the corresponding author with contact details:

- E-mail address
- Full postal address
- Telephone

All necessary files have been uploaded, and contain:

- Keywords
- All figure captions
- All tables (including title, description, footnotes) Further considerations
- Manuscript has been 'spell-checked' and 'grammar-checked'
- All references mentioned in the Reference list are cited in the text, and vice versa
- Permission has been obtained for use of copyrighted material from other sources (including the Web)
- Color figures are clearly marked as being intended for color reproduction on the Web (free of charge) and in print, or to be reproduced in color on the Web (free of charge) and in black-and-white in print
- If only color on the Web is required, black-and-white versions of the figures are also supplied for printing purposes

For any further information please visit our customer support site at http://support.elsevier.com.

Guidelines for Comments and Controversies

NeuroImage is happy to consider a range of comments and controversy articles. The format of these pieces can include:

- A single commentary, editorial or opinion piece.
- A target article, with between one and four commentaries. If the number of commentaries is greater than one, we would normally expect these not to exceed 2000 words in length.
- A target article, commentary (or commentaries) and a response by the original authors. This response would not normally exceed 2000 words in length.

The target article, in all cases can be invited by an Editor, a member of the Editorial Board or can be endorsed by either following an unsolicited request from an author. Before proceeding with the target article, it would be appropriate to secure the title, abstract and anticipated time-frame for submission Furthermore, suggested reviewers and commentators should be considered. It is generally a good idea to clarify in advance who will be the reviewers of the target article and commentaries and who will be commentators. The commentators are usually chosen through dialogue with the author, with the final responsibility resting with the Handling Editor. When these details have been finalised the Editorial Office should be notified, so that we can coordinate and help with logistics.
Submission of the invited target article should follow the procedures detailed under Invitation to submit an article in the author tutorial. Similarly, commentators should be invited to submit a commentary on a manuscript using the protocol under Submitting a commentary.

AFTER ACCEPTANCE

Use of the Digital Object Identifier

The Digital Object Identifier (DOI) may be used to cite and link to electronic documents. The DOI consists of a unique alpha-numeric character string which is assigned to a document by the publisher upon the initial electronic publication. The assigned DOI never changes. Therefore, it is an ideal medium for citing a document, particularly 'Articles in press' because they have not yet received their full bibliographic information. Example of a correctly given DOI (in URL format; here an article in the journal *Physics Letters B*):
http://dx.doi.org/10.1016/j.physletb.2010.09.059
When you use a DOI to create links to documents on the web, the DOIs are guaranteed never to change.

Proofs

One set of page proofs (as PDF files) will be sent by e-mail to the corresponding author (if we do not have an e-mail address then paper proofs will be sent by post) or, a link will be provided in the e-mail so that authors can download the files themselves. Elsevier now provides authors with PDF proofs which can be annotated; for this you will need to download Adobe Reader version 7 (or higher) available free from http://get.adobe.com/reader. Instructions on how to annotate PDF files will accompany the proofs (also given online). The exact system requirements are given at the Adobe site: http://www.adobe.com/products/reader/tech-specs.html.

If you do not wish to use the PDF annotations function, you may list the corrections (including replies to the Query Form) and return them to Elsevier in an e-mail. Please list your corrections quoting line number. If, for any reason, this is not possible, then mark the corrections and any other comments (including replies to the Query Form) on a printout of your proof and return by fax, or scan the pages and e-mail, or by post. Please use this proof only for checking the typesetting, editing, completeness and correctness of the text, tables and figures. Significant changes to the article as accepted for publication will only be considered at this stage with permission from the Editor. We will do everything possible to get your article published quickly and accurately – please let us have all your corrections within 48 hours. It is important to ensure that all corrections are sent back to us in one communication: please check carefully before replying, as inclusion of any subsequent corrections cannot be guaranteed. Proofreading is solely your responsibility. Note that Elsevier may proceed with the publication of your article if no response is received.

Offprints

The corresponding author, at no cost, will be provided with a PDF file of the article via e- mail (the PDF file is a watermarked version of the published article and includes a cover sheet with the journal cover image and a disclaimer outlining the terms and conditions of use). For an extra charge, paper offprints can be ordered via the offprint order form which is sent once the article is accepted for publication. Both corresponding and co-authors may order offprints at any time via Elsevier's WebShop (http://webshop.elsevier.com/myarticleservices/offprints). Authors requiring printed copies of multiple articles may use Elsevier WebShop's 'Create Your Own Book' service to collate multiple articles within a single cover (http://webshop.elsevier.com/myarticleservices/offprints/myarticlesservices/booklets).

AUTHOR INQUIRIES

For inquiries relating to the submission of articles (including electronic submission) please visit this journal's homepage. For detailed instructions on the preparation of electronic artwork, please visit http://www.elsevier.com/artworkinstructions. Contact details for questions arising after acceptance of an article, especially those relating to proofs, will be provided by the publisher. You can track accepted articles at http://www.elsevier.com/trackarticle. You can also check our Author FAQs at http://www.elsevier.com/authorFAQ and/or contact Customer Support via http://support.elsevier.com.