



Review

Person recognition and the brain: Merging evidence from patients and healthy individuals

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ABSTRACT

Recognizing other persons is a key skill in social interaction, whether it is with our family at home or with our colleagues at work. Due to brain lesions such as stroke, or neurodegenerative disease, or due to psychiatric conditions, abilities in recognizing even personally familiar persons can be impaired. The underlying causes in the human brain have not yet been well understood. Here, we provide a comprehensive overview of studies reporting locations of brain damage in patients impaired in person-identity recognition, and relate the results to a quantitative meta-analysis based on functional imaging studies investigating person-identity recognition in healthy individuals. We identify modality-specific brain areas involved in recognition from different person characteristics, and potential multimodal hubs for person processing in the anterior temporal, frontal, and parietal lobes and posterior cingulate. Our combined review is built on cognitive and neuroscientific models of face- and voice-identity recognition and revises them within the multimodal context of person-identity recognition. These results provide a novel framework for future research in person-identity recognition both in the clinical as well as basic neurosciences.

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1. Introduction

The ability to recognize the identity of other persons is a prerequisite for many social interactions in everyday life, and the inability to recognize persons is socially restricting (Gruter et al., 2008; Sasson et al., 2013; Schweich et al., 1992; Valentine et al., 2006). Impairments in person-identity recognition occur due to brain lesions with various aetiologies (e.g., stroke, tumour, or neurodegenerative disease), and psychiatric conditions, or also as selective congenital deficits (Gainotti, 2007a, 2011, 2013a; Gainotti et al., 2009; Gainotti and Marra, 2011; Gruter et al., 2008; Hailstone et al., 2010; Hailstone et al., 2011). Person-recognition disorders can occur selectively for faces, voices, and names as well as a combination of these different features (Gainotti, 2007a; Hailstone et al., 2011; Neuner and Schweinberger, 2000). In patients with brain lesions impairments of person-recognition abilities are relatively common: a behavioural study showed that more than a third of patients randomly selected from a neuropsychological rehabilitation ward was impaired in visual and/or auditory person recognition as compared to preserved object recognition (Neuner and Schweinberger, 2000). Person-recognition deficits due to congenital impairments are also frequent, for example, the prevalence for a congenital face-identity recognition deficit is about 2.5% (Kennerknecht et al., 2006, 2007).

Most of what we currently know about the neural basis of person-identity recognition is based on neuroscientific studies investigating face-identity recognition and its disorders, e.g., prosopagnosia (Bodamer, 1947; McConachie, 1976). Here, standardized testing tools are available (Benton et al., 1994; Duchaine and Nakayama, 2006; Warrington, 1984), which can be used on the clinical ward as well as in experimental neuroscience experiments (Arnott et al., 2008; Fox et al., 2008; Garrido et al., 2009b; Gruter et al., 2008; von Kriegstein et al., 2006). However, recent advances have also been made in our knowledge of voice-recognition mechanisms in healthy participants (Belin et al., 2002, 2004; von Kriegstein et al., 2003; von Kriegstein and Giraud, 2004, 2006) as well as voice-recognition deficits, e.g., phonagnosia (Garrido et al., 2009a; Van Lancker and Kreiman, 1987; Van Lancker and Canter, 1982; Van Lancker et al., 1989). Recognition of other persons based

on seeing their faces or hearing their voices is often considered successful when the name of the person is recalled (Bruce and Young, 1986). Names can, however, also be used as input information to recognize a person: for example, when we hear the name “Barack Obama”, we can immediately recall his face, voice, and person-related semantic information.

The aim of the present work is to advance our knowledge of the mechanisms of person-identity recognition by closing two major gaps in the literature. First, a systematic link between knowledge gained from patient studies and meta-analytic evidence from neuroimaging studies on healthy people is missing. Although excellent reviews on patient studies and descriptions of neuroimaging studies on face (Gainotti, 2007a,b, 2011; Gobbini and Haxby, 2007; Gross and Sergent, 1992; Stone and Valentine, 2003) and voice (Badcock and Chhabra, 2013; Belin et al., 2004) recognition exist, recent developments to analyse neuroimaging studies with meta-analytic techniques allow us to revisit and enrich the current understanding of person-identity recognition in the human brain. Closing the gap between patient studies and neuroimaging studies on healthy people would be important for making causal claims about specific activations found consistently in the neuroimaging literature. Second, person-identity recognition is essentially multimodal; however a systematic review of multimodal impairments in patients and multimodal neuroimaging investigations is missing. Here, we integrate the evidence of studies investigating person-identity recognition based on different modalities, i.e., faces, voices, names, and biographical information. Currently it is unclear whether some of the modality-specific networks overlap and how different modalities are integrated to afford recognition of famous, familiar, and unfamiliar persons (Blank et al., 2011; Gainotti et al., 2008, 2009; von Kriegstein and Giraud, 2006). For instance, recently an anterior face patch in the human brain that codes face identity has been reported (for review see Von Der Heide et al., 2013), however it is unknown whether the same area might also code identity in other modalities, like voice identity. A multimodal perspective on person-identity recognition is largely missing, but would be important for understanding the person-identity recognition network as a whole and the associated person-identity recognition impairments (Gainotti, 2013a). To

close these two gaps, we provide (i) a comprehensive overview of studies reporting locations of brain damage in patients impaired in person-identity recognition from several different modalities, and relate the results to (ii) a quantitative meta-analysis based on functional neuroimaging studies specifically investigating person-identity recognition in healthy individuals from several different modalities.

1.1. Approach

We performed systematic literature searches on studies investigating person-identity recognition (i.e., identification of other persons from faces, voices, or names; for details see Supplementary Methods). We specifically searched for studies reporting person-identity recognition impairments in patients with brain lesions and for neuroimaging studies (functional magnetic resonance imaging (fMRI) and positron emission tomography (PET)) involving healthy individuals. Person-identity recognition referred to all tasks that either required *explicit recognition* or *implicit recognition*. *Explicit recognition* could for example consist of providing the name of a previously learned person or judging whether a face is familiar among a set of novel and familiar faces. *Implicit recognition* could for example consist of detecting an inverted face in a sequence of famous and unfamiliar upright faces. For details about tasks and contrasts see Supplementary Tables 1 and 2. We complemented this approach with a review of studies on congenital disorders of person-identity recognition. As we specifically searched for studies investigating person-identity recognition, the literature review did not include studies that investigated perception of person-related information at lower levels, such as passive viewing of unfamiliar faces or listening to unfamiliar voices.

We performed three types of analyses. First, for patient case reports we provide a comprehensive overview of lesion location and associated impairment in person-identity recognition. Second, for single case as well as group patient studies (Supplementary Table 6) we investigated the hemispheric lateralization of person-identity recognition abilities; because many group studies provide only information about the affected hemisphere, but not the affected region (Supplementary Table 3). Third, the neuroimaging studies were analysed in a quantitative meta-analysis. For this, activation coordinates reported in fMRI/PET studies were analysed in ALE (activation likelihood estimation; <http://www.brainmap.org/ale/>; Supplementary methods).

We categorized all patient and neuroimaging studies according to the factors modality and familiarity. For the neuroimaging studies, 'modality' referred to studies investigating neuronal responses to face-, voice-, or name-identity recognition. These studies used various contrasts, e.g., "voice-identity recognition vs. speech recognition" or "face-identity recognition vs. detection of a fixation cross on scrambled faces" (see Supplementary Table 1). 'Familiarity' referred to recognition of personally familiar, famous, and newly learned persons (e.g., studies investigating neuronal responses to famous faces vs. unfamiliar faces, see Supplementary Table 2). In the patient studies, 'modality' referred to reports in which patients were impaired in recognizing other persons based on their voice, face, or name. 'Familiarity' referred to reports in which patients were impaired in recognizing familiar or unfamiliar persons (i.e., lacking feelings of familiarity for familiar persons, and hyper-familiarity with unfamiliar persons). Finally, we used the patient studies to differentiate between 'person-identity recognition' and 'discrimination of other persons'. 'Recognition' referred to tasks where recognition of either personal-familiar, famous, or previously learned faces was required. These tasks included for example selection of personal-familiar, famous, or previously learned faces from a mixed set of familiar and unfamiliar faces or matching names and faces of persons. 'Discrimination' referred

to tasks where recognition was not required, for example, in same-different response tasks using unfamiliar face images. A typical discrimination task is for example used in the Benton Facial Recognition Test with unfamiliar faces (Benton et al., 1983) in which participants select three out of six test faces that match in identity to a simultaneously presented target face. In these discrimination tasks presentation of the target face is either simultaneously or directly following the test faces.

We organized the review according to the factors modality and familiarity for both the neuroimaging studies and the patient studies and reported the results with reference to theoretical models of person recognition. In addition, we discuss impairments in recognition and discrimination of other persons. This integrated approach led to novel predictions about how the human brain processes person-related information from different modalities to enable person-identity recognition.

1.2. Models of person recognition

Investigating person-identity recognition in patients as well as healthy subjects has been heavily influenced by cognitive and neuroscientific models of face and person recognition. Most of these person-identity recognition models were built on the well-known and highly-influential cognitive model of face recognition described by in Bruce and Young (1986). This model has been extended to include recognition of name and voice (Belin et al., 2004; Ellis et al., 1997; Neuner and Schweinberger, 2000; Young and Bruce, 2011). In these models, different hierarchically organized modules process voice, face, and name information entirely separately until it reaches the highest level: the so-called person identity node (PIN). The activation of modality-specific levels would already lead to feelings of familiarity without necessarily recognizing the person (e.g., feeling familiar with a face without recalling the identity of the person). The PIN as the highest level was defined as the store of person-specific semantic information, and its activation is thought to enable identification of a person independent of modality (Fig. 1A; Bruce and Young, 1986; Ellis et al., 1997). Detailed neuroanatomical research on patients with brain lesions and neuroimaging studies on healthy individuals, led to a reformulation of this model in neuroanatomical terms (Belin et al., 2004; Gainotti, 2007a; Gainotti et al., 2009, 2010; Gainotti and Marra, 2011; Hailstone et al., 2011; Haxby et al., 2000). In this view, early face processing takes place in 'core face regions' located in the occipital face area (OFA); face-identity recognition in the fusiform face area (FFA); and identity recognition within an 'extended system' in the anterior temporal lobe (Haxby et al., 2000). A similar posterior-to-anterior processing pathway has been suggested for voice-sensitive areas in the right superior temporal sulcus (STS), with the posterior STS processing acoustic information and the anterior STS coding voice identity (Belin and Zatorre, 2003; Nakamura et al., 2001; von Kriegstein et al., 2003; von Kriegstein and Giraud, 2004).

Recent evidence from behavioural, neuroimaging, and patient studies questions the serial and by-and-large bottom-up processing view of the original cognitive person-identity recognition models (Bruce and Young, 1986; Ellis et al., 1997). First, for faces as well as voices, there is evidence that recognition is based on representations of stored 'prototypes'. Prototypes are averaged representations of voices or faces within a multidimensional space (Latinus and Belin, 2011; Leopold et al., 2001; Rhodes and Jeffery, 2006). Recognition is accomplished by comparing the incoming stimulus to the stored representation and reflects the interaction of bottom-up and top-down processes. Such a procedure contradicts strict serial processing that proceeds from the sensory input level to more abstract cognitive levels, because the representation of the sensory input is influenced by the stored

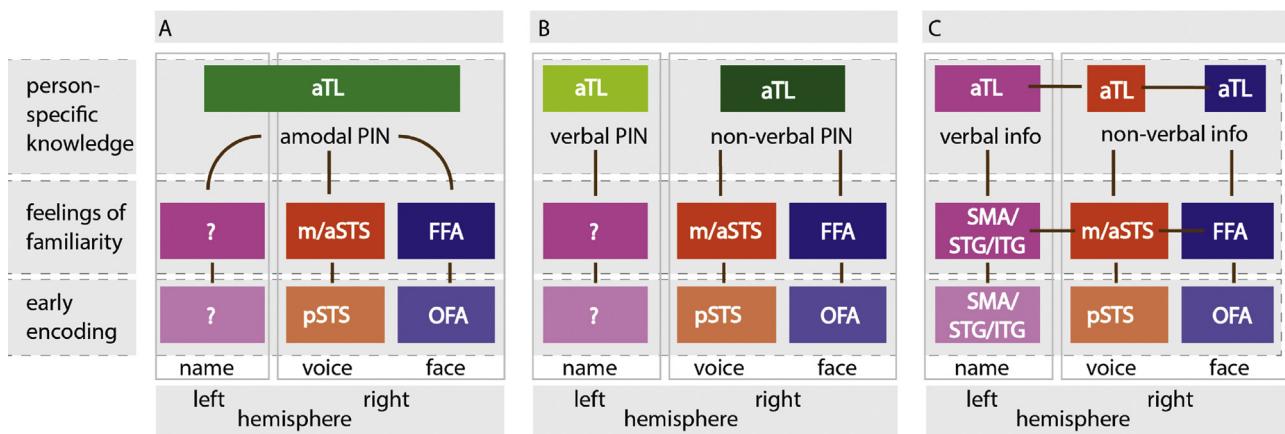


Fig. 1. Models of person recognition. (A) Model of face-identity recognition (blue) adapted from Bruce and Young (1986), and complemented with similar models of voice (red) and name (pink) recognition (Ellis et al., 1997; Neuner and Schweinberger, 2000): during person recognition feelings of familiarity are generated in modality-specific recognition units, and person-specific knowledge is accessed in the modality-free person identity node (PIN in green). Anatomical brain labels are taken from (Haxby et al., 2000) for faces and from (Belin et al., 2004; von Kriegstein and Giraud, 2004) for voices. (B) Person-identity recognition models adapted in accordance with proposals by Snowden et al. (2004) and Gainotti (2007b); in this model person identity is represented differently within the two hemispheres in the brain, where the left hemisphere processes verbal and the right hemisphere non-verbal (mainly visual) person-specific information (Gainotti, 2007a; Gainotti et al., 2003; Snowden et al., 2004). (C) An alternative model that assumes an interconnected network of brain regions without a single modality-free hub. In this view, interconnected regions process person-related information from different modalities (e.g., face and voice) and are potentially interconnected by a region which processes information from different modalities. [posterior/middle/anterior superior temporal sulcus (p/m/a STS), anterior temporal lobe (aTL), occipital face area (OFA), fusiform face area (FFA), supplementary motor area (SMA), inferior temporal gyrus (ITG)]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

prototype. Strict serial processing is also difficult to reconcile with findings that the FFA can be activated before or even without ipsilateral OFA (Atkinson and Adolphs, 2011; Jiang et al., 2011; Rossion et al., 2003b; Steeves et al., 2006), and that both regions might share processing of face identity and lower level facial properties (Eger et al., 2004; Grill-Spector et al., 2004; Kriegeskorte et al., 2007; Nestor et al., 2011; Pourtois et al., 2005a; Rotshtein et al., 2005; Xu et al., 2009).

Recent findings also challenge the traditional idea that successful recognition is only accomplished by activation of a single modality-free PIN (Bruce and Young, 1986; Ellis et al., 1997). First, evidence from patient studies contradicts a single modality-free PIN and suggests different roles of the two hemispheres, with the left hemisphere processing verbal, and the right visual person information (Gainotti, 2007a; Gainotti et al., 2003; Snowden et al., 2004) (Fig. 1B). Second, in contrast to the traditional position that the PIN is the first stage of multimodal interaction, recent neuroimaging studies provide evidence of early, direct interaction of visual and auditory information during voice-identity recognition (Blank et al., 2011; Schall et al., 2013; von Kriegstein et al., 2005, 2008; von Kriegstein and Giraud, 2006). Taken to extreme, in such an interconnected system a PIN might not be necessary (Fig. 1C).

2. Recognizing other persons based on different modalities

2.1. Face-identity recognition and prosopagnosia

We will start our review with the modality that is most often used to investigate person-identity recognition in both patients and healthy volunteers: faces. Face-identity recognition is easy to measure because face pictures are readily available on the internet, and there are a host of databases for face images and also standardized face-recognition tests (Benton et al., 1994; Warrington, 1984). Several meta-analyses have reported on the neural mechanisms involved in face-processing in patients (e.g., Bouvier and Engel, 2006) and healthy subjects (Fusar-Poli et al., 2009; Von Der Heide et al., 2013). We focus our review on those studies that explicitly tested recognition of face identity (in contrast to processing of other facial properties or unfamiliar faces) and on integrating findings from patients and neuroimaging.

2.1.1. Patient case reports

When we plotted the lesion locations reported in patient studies (Table 1) on a brain template, we found that eight individuals with a single lesion located in the right temporal lobe were impaired in face-identity recognition (stars in light blue in Fig. 2A). However, the analysis also revealed that face-identity recognition deficits are associated with lesion sites in almost all areas of cortex (light blue in Fig. 2A). One explanation for this is that few of the studies also tested person-identity recognition from other modalities. This leaves open the possibility that the recognition deficit is not caused by a specific face-identity recognition disorder, but by a more general person-identity recognition deficit encompassing more than one modality. When we plotted only those studies that tested for specificity of the face-identity recognition deficit (i.e., person-identity recognition in other modalities was tested and was normal), we found that these specific deficits were associated with lesions predominantly located in temporal and occipital lobes, as well as frontal and hippocampal areas (dark blue in Fig. 2A). Some patients who were impaired on face-identity recognition nevertheless showed increased feelings of familiarity for faces. This means that patients were not able to identify faces, but judged many, even unfamiliar, faces as familiar. Such a pattern of person-identity recognition disorders was associated with lesions in the right temporal, parietal, and frontal lobes (olive in Fig. 2A).

2.1.2. Patient group studies and hemispheric lateralization

Impaired face-identity recognition was primarily associated with damage of the right hemisphere, but also often occurred with bilateral brain damage (light blue in Fig. 2B).

2.1.3. Neuroimaging meta-analysis

In healthy individuals the meta-analysis revealed clusters in the temporal and occipital as well as frontal lobes and parahippocampus (blue in Fig. 2C, Table 2(1), and Supplementary Table 1.1). The temporal region ($x=40, y=-51, z=-21$) was located in right fusiform gyrus in a location similar to FFA based on comparison with coordinates of published FFA localizers (Kanwisher et al., 1997). Although the FFA is one of the regions most frequently investigated in the human brain, there is still an on-going discussion as to whether the FFA processes primarily facial properties

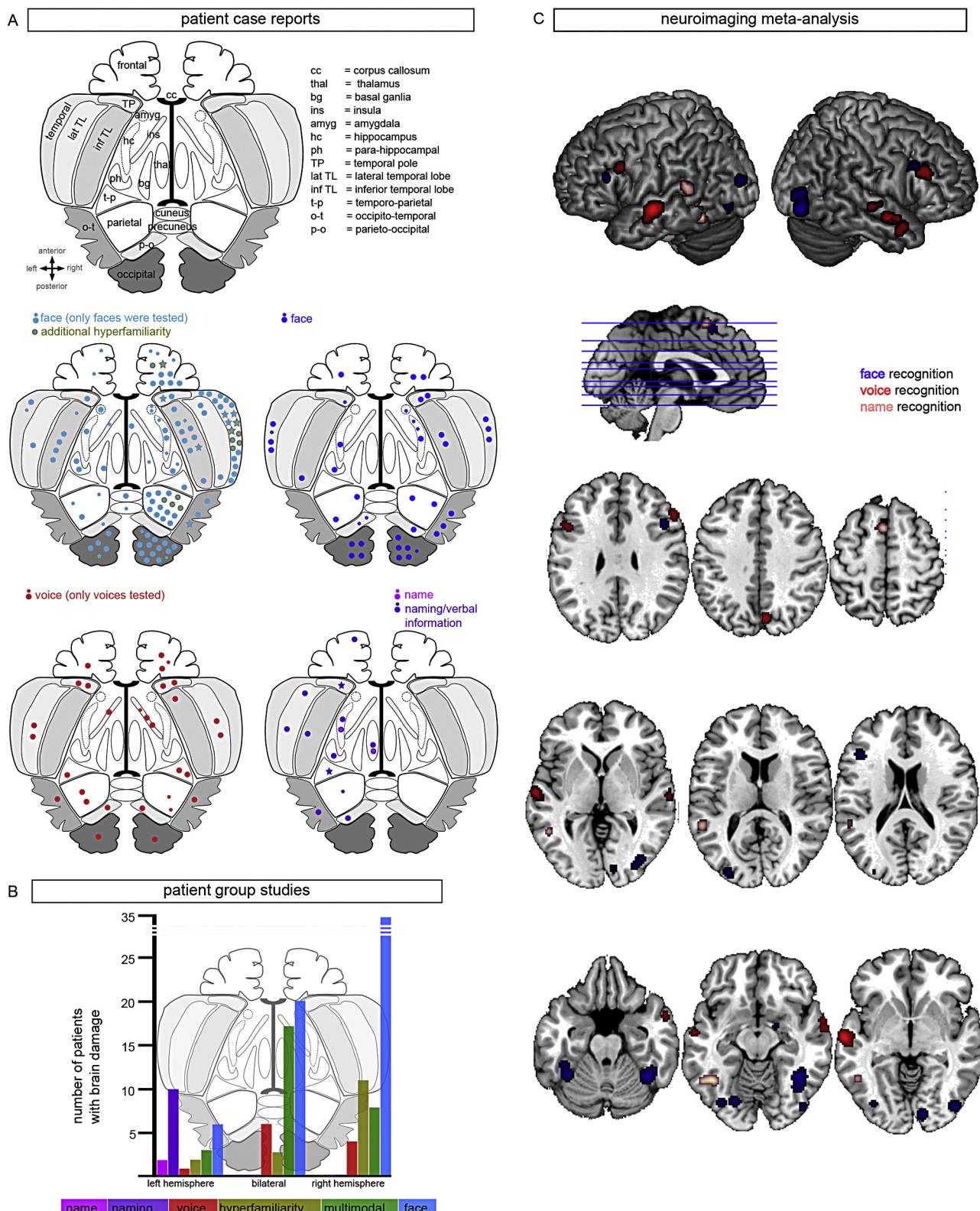


Fig. 2. Overview of sites involved in person-identity recognition from different modalities. (A) Patient case reports. Colours code the modality or type of recognition disorder (blue: face; red: voice; olive: hyperfamiliarity and name; pink: naming/verbal information). Each dot represents one lesion. Small dots represent lesions that were explicitly reported as being small. Large dots represent all other lesions. The colour used to fill the dot corresponds to modality or type of recognition disorder; the colour used to outline the dot corresponds to additional specification of recognition disorder (e.g., dot with blue fill and green circle corresponds to 'impaired face recognition with hyperfamiliarity'). If there is only a single lesion per patient, the corresponding location is marked by a star instead of a dot. (B) **Contributions of the right and left hemisphere to different modalities of person-identity recognition.** The plot includes all patients for which information about both the side of the damaged hemisphere and the person-recognition deficit were available. Colours correspond to impaired modality or type of recognition disorder (name recognition, naming, voice, hyperfamiliarity, multimodal, and face) and are grouped according to damage of the hemisphere (left, bilateral, right). (C) **Meta-analysis:** (side view of rendered brain and transversal sliced view, neurological convention). Brain regions involved in recognition of face (blue), voice (red), and name (light pink) as identified by a meta-analysis on neuroimaging studies in healthy subjects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Patient studies grouped according to the modality of person recognition disorder (studies included in Fig. 2) [(number) behind reference indicates number of patients per study, '+' indicates additional hyperfamiliarity, [] around reference indicates that the patient was not included in the figures because the lesion location was to unspecific].

Multimodal	Hyperfamiliarity	Face
Barton (2008) (1)	Feinberg et al. (1999) (1 + multimodal)	Anaki et al. (2007) (1)
Busigny et al. (2009) (1)	Francis et al. (2002) (1 + multimodal)	Barton et al. (2002) (4)
Ellis et al. (1989) (1)	Hailstone et al. (2010) (1 + multimodal)	[Benson et al. (1974) (1)]
Eslinger et al. (1996) (2)	Rapcsak et al. (1996) (3, 4 + face)	Bukach et al. (2006) (1)
Evans et al. (1995) (1)	Rapcsak et al. (1994) (2)	Carlesimo et al. (1998) (1)
Feinberg et al. (1999) (1 + hyperfamiliarity)	Rapcsak et al. (1998) (1)	Clarke et al. (1997) (1)
Foerstl (1990) (1)	Vuilleumier et al. (2003) (1)	[Cohn et al. (1977) (2)]
Francis et al. (2002) (1 + hyperfamiliarity)	Ward et al. (1999) (1)	Delvenne et al. (2004) (1)
Gainotti et al. (2003) (1)	[Young et al. (1993) (1)]	De Renzi et al. (1991) (3)
Gainotti et al. (2008) (1)		De Renzi et al. (1994) (3)
Gentileschi et al. (1999) (1)		Etcoff et al. (1991) (1)
Gentileschi et al. (2001) (1)		Gainotti et al. (2010) (1)
Gorno-Tempini et al. (2004) (1)		Gloning et al. (1970) (1)
Hailstone et al. (2010) (2, 1 + hyperfamiliarity)		Haslam et al. (2001) (1)
Hanley et al. (1989) (1)		[Hecaen et al. (1957) (1)]
Joubert et al. (2006) (3)		[Heidenhain (1927) (1)]
Mattson et al. (2000) (1)		Heutink et al. (2012) (1)
McNeil and Warrington (1991) (1)		Lhermitte et al. (1972) (1)
Thompson et al. (2004) (1)		Malone et al. (1982) (1)
Ward et al. (1999) (1)		Marotta et al. (2001) (2)
		McNeil and Warrington (1991) (2)
		Mendez and Ghajarnia (2001) (1)
		Nakachi et al. (2007) (1)
		[Pevzner et al. (1962) (1)]
		Rapcsak et al. (1996) (11, 4 + hyperfamiliarity)
		Rapcsak et al. (1994) (2, 2 + hyperfamiliarity)
		Riddoch et al. (2008) (1)
		Rosson et al. (2003a) (1)
		Schweinberger et al. (1995) (1)
		Sergent and Poncet (1990) (1)
		Sergent and Villemure (1989) (1)
		Sergent and Signoret (1992) (3)
		Takahashi et al. (1995) (4)
		Van Lancker and Klein (1990) (1)
		Verstichel and Chia (1999) (1)
		Wada and Yamamoto (2001) (1)
		[Wilbrand (1892) (1)]
		Williams et al. (2006) (1)
		Young et al. (1995) (1)
Naming	Name	Voice
Flude et al. (1989) (1)	Verstichel et al. (1996) (1)	Van Lancker et al. (1988) (3)
Giovanello et al. (2003) (1)		Peretz et al. (1994) (2)
Lucchelli et al. (1997) (1)		
Miceli et al. (2000) (1)		
Otsuka et al. (2005) (1)		
Semenza et al. (1998) (1)		
Verstichel et al. (1996) (1)		

or face identity, or both (Grill-Spector et al., 2004; Kriegeskorte et al., 2007; Nestor et al., 2011; Pourtois et al., 2005a; Rotshtein et al., 2005; Xu et al., 2009). The results of our analysis confirm the involvement of the FFA during face-identity recognition. The occipital region ($x=44$, $y=-81$, $z=-10$) was located in occipital gyrus similar in location to OFA (Pitcher et al., 2011). There are two possible explanations why the ALE analysis revealed the involvement of FFA and OFA during person-identity recognition: (i) in contrast to the assumption that OFA is only involved in low-level face processing, OFA is essentially involved in higher-level face-identity recognition, and/or (ii) studies may not have used a sufficient high-level control condition to remove activation to facial features. For example, investigating face-identity recognition in the experimental condition, but contrasting it against scrambled versions of the faces, or voices (as e.g., Brambati et al., 2010; Relander and Rama, 2009).

In contrast to the patient studies in which lesions affected predominantly the right hemisphere, clusters found in the neuroimaging meta-analyses were bilateral. We speculate that this co-activation of the left hemisphere is not absolutely essential

for performing successfully on face-identity recognition tests. For example, it has been proposed that the right FFA processes faces at a holistic level while the left FFA processes faces at a more part-based level (Rosson, 2008). Therefore, lesions in face-sensitive regions of the left hemisphere might impair fine-grained discrimination of face parts, which is not commonly tested in patient studies, while those to the right hemisphere might impair face-identity recognition.

2.1.4. Merging evidence from patients and healthy volunteers

Both neuroimaging and patient studies showed that not only core-face regions in ventral occipito-temporal cortex, known as fusiform and occipital face areas (Gauthier et al., 2000; Kanwisher et al., 1997, for review see Haxby et al., 2000), are required during face-identity recognition, but also frontal regions and the anterior temporal lobe. The frontal regions were located in left and right inferior frontal gyrus (BA 9 and 46, right pars opercularis, left pars triangularis). Involvement of prefrontal cortex in face-identity recognition was also found in macaques during passive fixation without an active task (O'Scalaidhe et al., 1997; Tsao et al., 2008).

Table 2

Brain regions involved in recognition of face, voice, and name as identified by a meta-analysis on healthy subjects.

(1) Face-identity recognition				
Region	BA	Weighted centre coordinates whole brain	Weighted centre coordinates all studies	Size (mm ³)
Frontal lobe				
Right inferior frontal gyrus (p. Opercularis)	9		45 17 28	448
Left inferior frontal gyrus (p. Triangularis)	9, 46	−43 23 19	−43 23 20	672
Left SMA	6, 8, 32		−2 19 50	416
Temporal lobe				
Right fusiform gyrus	20, 37	40 −51 −21	41 −53 −19	4152
Left fusiform gyrus	20, 36, 37	−37 −48 −24	−38 −49 −22	2520
Left fusiform gyrus	18, 19		−28 −77 −11	1512
Limbic lobe				
Right parahippocampal gyrus	28, 34		19 −4 −18	672
Occipital lobe				
Right lingual gyrus	17, 18		12 −88 −5	568
Right inferior occipital gyrus	18, 19	44 −81 −10	40 −81 −5	1992
Left middle occipital gyrus	18, 19		−30 −90 12	400
(2) Voice-identity recognition				
Region	BA	Weighted centre coordinates whole brain	Weighted centre coordinates all studies	Size (mm ³)
Frontal lobe				
Right inferior frontal gyrus (p. Triangularis)	9, 46	55 24 27	53 26 26	760
Left inferior frontal gyrus (p. Triangularis)	9		−48 14 29	352
Temporal lobe				
Left middle temporal gyrus	21, 22	−62 −13 −7	−61 −14 −7	2072
Right middle temporal gyrus	21, 22, 38	65 −4 −12	65 −4 −12	704
Right superior temporal gyrus	21, 22		66 −19 −2	216
Right middle temporal gyrus	21, 38	57 6 −24	57 6 −24	392
Parietal lobe				
Right precuneus	7, 18, 19		7 −74 39	456
(3) Name-identity recognition				
Region	BA	Weighted centre coordinates whole brain	Weighted centre coordinates all studies	Size (mm ³)
Frontal lobe				
Left SMA	6		−4 12 56	464
Temporal lobe				
Left superior temporal gyrus	13, 22	−6 12 59	−55 −44 12	528
Left inferior temporal gyrus	19, 21, 22, 37	−51 −56 −16	−47 −55 −13	2032

The role of these frontal regions in face-identity recognition is currently unclear. Decreased activity in inferior frontal cortex after presentation of face images with different views was interpreted as an abstract, non-visual representation of identity in this region (Pourtois et al., 2005b). Neuroimaging studies show that anterior temporal lobe responses to faces are also view-independent (Garrido et al., 2009b; Kriegeskorte et al., 2007; Von Der Heide et al., 2013). Several patient studies report lesions in the anterior temporal lobe associated with face-identity recognition deficits (light and dark blue in Fig. 2A). However, since most of these studies only tested face-identity recognition abilities (light blue in Fig. 2A), it remains unclear how modality-specific the role of the anterior temporal lobe is. We did not find an anterior temporal lobe cluster in the meta-analysis on face-identity recognition. This could be because the anterior temporal lobe is not specifically involved in face-identity recognition for all faces, but only those of personally familiar or famous persons (Von Der Heide et al., 2013; see also Section ‘3 Evidence for a multimodal hub of person-identity recognition’ below).

2.1.5. Congenital prosopagnosia

Additional evidence that core-face regions but also other regions are involved in face-identity recognition comes from studies on persons with congenital (or developmental) prosopagnosia, i.e., impairment in face-identity recognition from birth without apparent underlying brain damage (Behrmann and Avidan, 2005;

McConachie, 1976). The initial studies on this population were surprising: most fMRI studies revealed a normal activation level within “core-face regions” in ventral occipito-temporal cortex in congenital prosopagnosics as compared to healthy participants across various contrasts investigating face-identity recognition (Avidan and Behrmann, 2009; Avidan et al., 2005; Hasson et al., 2003; Van den Stock et al., 2008). However, recent studies on larger congenital prosopagnosia groups using more subtle experimental paradigms or analysis methods show differential activation or grey matter density of fusiform gyrus between prosopagnosics and controls (Garrido et al., 2009b; von Kriegstein et al., 2008).

The regions outside the core network are not yet entirely consistently reported in neuroimaging studies of congenital prosopagnosia. One study showed that precuneus, posterior cingulate, and anterior paracingulate cortex were more activated in neurotypical participants, but not in congenital prosopagnosics, during a same–different identity judgment on a pair of sequentially presented face images (Avidan and Behrmann, 2009). Another recent study found regions in medial prefrontal regions to be more active in congenital prosopagnosia than in healthy patients during gender identification for faces (Dinkelacker et al., 2011). In addition, in prosopagnosics compared to healthy individuals, there is reduced functional and structural connectivity between core-regions and extended face-identity recognition regions in anterior temporal and frontal cortices (Thomas et al., 2009; von Kriegstein et al., 2006). However, it is unclear which of these differences in

activity and connectivity result from life-long difficulties with face recognition, and which are causal for impaired face-identity recognition abilities.

2.2. Voice-identity recognition

2.2.1. Patient case reports

There are only a few case reports on voice-identity recognition deficits, i.e., acquired phonagnosia (Table 1). This is surprising because voice-identity recognition impairments in patients with brain lesions are frequent: from 36 patients randomly selected from a rehabilitation ward, 8 were specifically impaired in voice-identity recognition (Neuner and Schweinberger, 2000). One reason for this lack of studies might be that voice-identity recognition tests are not as readily available as face-identity recognition tests. Furthermore, voice-identity recognition deficits might not be as socially impairing as face-identity recognition deficits. Only two studies reported voice-identity recognition impairments and corresponding brain lesions at the single patient level (Peretz et al., 1994; Van Lancker et al., 1988). In these patients, lesions were distributed along bilateral temporal, frontal, parietal, and occipital lobes (red in Fig. 2A). Only in one of these patients was performance in other modalities (i.e., face-identity recognition) tested, and the deficit was found to be specific to the voice (Peretz et al., 1994). A recent study analysed voice-recognition abilities in two groups of dementia patients (Hailstone et al., 2011). It showed that voice-identity recognition was more impaired in patients with a temporal variant of frontotemporal lobe degeneration; and voice perception (i.e., voice discrimination and perception of gender and size of the speaker) was more impaired in patients with Alzheimer's disease. The deficits were however not entirely specific to voices: both patient groups were additionally impaired in face- and name-identity recognition. The severity of the voice-identity recognition and discrimination deficits as well as the multimodal person-identity recognition deficits were correlated with the amount of grey matter density in the right anterior temporal lobe.

2.2.2. Patient group studies and hemispheric lateralization

Impairments in voice-recognition were related to brain damage in the right hemisphere or bilateral lesions (red in Fig. 2B) (Lang et al., 2009; Van Lancker and Canter, 1982; Van Lancker et al., 1989). Unfortunately, there is not enough evidence about regions essential for voice-recognition to make a strong conclusion about lateralization, although the current results suggest that voice-identity recognition is supported by both hemispheres or the right hemisphere.

2.2.3. Neuroimaging meta-analysis

For voice-identity recognition in healthy individuals we identified significant clusters in bilateral middle/superior temporal gyrus, bilateral inferior frontal gyrus, and right precuneus (red in Fig. 2C, Table 2(2), and Supplementary Table 1(2)). The clusters in the temporal lobe are located in the middle and anterior portions of the STG/STS. This is in line with the suggestion that these regions specifically are involved in voice-identity recognition (Andics et al., 2010; Belin and Zatorre, 2003; von Kriegstein et al., 2003; von Kriegstein and Giraud, 2004). In contrast, more posterior regions in the temporal lobe have been implicated in processing acoustic properties of voices (von Kriegstein and Giraud, 2004; von Kriegstein et al., 2007). Similarly to face processing, it has been suggested that there is a posterior to anterior gradient in the temporal lobe, from representations of sensory information to representations which are independent of the auditory sensory input but represent voice identity (Belin and Zatorre, 2003; von Kriegstein et al., 2003; von Kriegstein and Giraud, 2006). The meta-analysis did not reveal posterior voice clusters in the STS, supporting the view that the

posterior STS is primarily involved in processing acoustic features of the voice, but not representing the voice identity.

The clusters in bilateral inferior frontal gyrus for voice-identity recognition (red in Fig. 2C) were directly adjacent to the clusters found for face-identity recognition (blue in Fig. 2C). We performed a conjunction analysis to investigate whether these face and voice regions overlap; this was not the case. Neurons in macaques' prefrontal cortex also respond to both faces and vocalizations (Sugihara et al., 2006, for review see Romanski, 2012) and to presentations of vocalizations only (although macaques only performed a visual fixation task without voice-identity recognition; Romanski et al., 2005; Romanski and Goldman-Rakic, 2002).

2.2.4. Merging evidence from patients and healthy volunteers

Combined evidence from patient studies and from the meta-analysis of healthy individuals suggests that voice-identity recognition involves both hemispheres, specifically in frontal and temporal lobes. There are currently, to our knowledge, only five patients reported as single cases specifically impaired in voice-identity recognition (Peretz et al., 1994; Van Lancker et al., 1988); and seven neuroimaging studies (see Supplementary Table 1.2) investigating voice-identity recognition in healthy individuals. Therefore, the results, of the meta-analysis especially, have to be interpreted with caution. Voice-identity recognition represents a unique window to further understand the process of person-identity recognition, since it allows, in combination with face-recognition research, differentiation of those processes that are modality-specific and those that generalize across modalities. This calls for a more systematic test in patients with brain damage as well as more neuroimaging studies, for example, comparing person-identity recognition from different modalities.

2.2.5. Congenital phonagnosia

Only recently, Garrido and colleagues reported the first case of congenital phonagnosia (Garrido et al., 2009a): KH. Despite serious impairments in recognition of voice-identity, KH performed normally with tasks measuring face-identity recognition, vocal affect, and vocal gender recognition. In addition, her music perception, recognition of environmental sounds, and comprehension of speech without background noise was normal. These findings confirm and extend earlier findings in patients with lesions (Van Lancker et al., 1988, 1989) that the recognition of a speaker's vocal identity is separable from those mechanisms used to recognize other information from the voice or non-vocal auditory stimuli. Currently, there are no studies investigating possible brain mechanisms underlying congenital phonagnosia.

2.3. Name-identity recognition, naming, and providing verbal person-related information during person-identity recognition

In addition to faces and voices, names and biographical information can be considered as further "input channels" to enable person-identity recognition (Ellis et al., 1997; Neuner and Schweinberger, 2000). Access to names and biographical information are also often used as "output channels" to evaluate successful person-identity recognition, for example, based on face or voice (Bruce and Young, 1986; Burton et al., 1990; Neuner and Schweinberger, 2000), because verbal articulation of names and biographical information is easy to test, especially in the clinical environment. We here refer to these two different tasks using the labels "name" (for recognition of given names) and "naming/verbal information" (for generation of person-related information after successful recognition). What both tasks have in common is that person-related, verbal information has to be recognized or retrieved.

2.3.1. Patient case reports

We found that impaired recognition of names and difficulties in naming other persons were associated with lesions specifically in the left hemisphere at the individual patient level (pink in Fig. 2A). This was also the case for difficulties in providing verbal information about other persons, for example, providing information about biographical details. The associated lesions were located in left temporal lobe (including lateral temporal and hippocampal areas), occipital, and parietal lobe as well as thalamus (purple in Fig. 2A, Table 1).

2.3.2. Patient group studies and hemispheric lateralization

Impaired name-identity recognition and naming of persons was selectively associated with damage of the left hemisphere (pink and purple in Fig. 2B, Table 1, Supplementary Table 3).

2.3.3. Neuroimaging meta-analysis

For ‘name-identity recognition’ (without recognition of biographical information because this was rarely tested) in healthy individuals, we identified a left-hemispheric network containing significant clusters in left supplementary motor area and the left posterior superior and inferior temporal gyrus (light pink in Fig. 2C, Table 2(3); Supplementary Table 1.3).

2.3.4. Merging evidence from patients and healthy volunteers

In summary, evidence from both patient studies and the meta-analysis on healthy individuals supports the view that names and person-specific verbal information are processed in the left temporal lobe. There is still a lack of systematic, consistent results in patients about whether recognition and generation of names and person-specific verbal information can be impaired separately (Haslam et al., 2002). However, a single case study reported a dissociation of the ability to name other persons and to recognize persons based on their given names and biographical information when these two abilities were tested separately and naming of other categories was intact (Verstichel et al., 1996).

3. Evidence for a multimodal hub of person-identity recognition: Recognition of personally familiar, famous, and unfamiliar persons

Most models of person-identity recognition propose that different modalities are processed entirely independently until they are integrated at a multimodal hub, the person identity node (PIN; Bruce and Young, 1986; Burton et al., 1990; Ellis et al., 1997) (Fig. 1A). The PIN was either considered a pure merging zone of different modalities (Burton et al., 1990) or an additional store of person-related semantic information (Bruce and Young, 1986). Whether such a PIN, a modality-free or multimodal hub which provides access to person-related semantic information, exists in the human brain is still unclear. We used two approaches to test and identify whether there is a region in the human brain that could correspond to a multimodal hub of person-identity recognition. First, we tested the assumption that this multimodal hub could be activated as a common region during recognition via different modalities presented separately (e.g., face- or voice-identity recognition) (Section 3.1). Second, we tested the hypothesis that a multimodal hub is activated during recognition of personally familiar and famous persons, because personally familiar and famous persons are inherently represented in more than one modality and are always associated with semantic information (Section 3.2). A lesion of such a region would be associated with person-identity recognition impairments in multiple or all modalities and/or deficits in feeling familiar with a person in multiple or all modalities.

3.1. Multimodal testing and representations

3.1.1. Patient case reports

Most of the patient studies which tested person-identity recognition abilities in different modalities also found multimodal impairments, for example, impaired recognition of both faces and voices (review (Gainotti, 2011; Hailstone et al., 2011)). These individuals with impaired multimodal person-identity recognition had brain damage in bilateral temporal lobes, especially in the anterior parts (Fig. 3A). In addition, lesions in bilateral lingual gyri, several medial temporal lobe structures (bilateral hippocampus, right amygdala), and the right insula were associated with multimodal person-identity recognition impairments. These multimodal identity-recognition impairments can occur independently from perceptual difficulties with faces. A detailed assessment of a patient with focal atrophy of the anterior temporal lobe predominantly within the right hemisphere showed impaired person-identity recognition from faces, voices, and names with spared abilities for identification of famous places, famous events, and flowers (Busigny et al., 2009).

3.1.2. Patient group studies and hemispheric lateralization

Impaired recognition abilities from multiple modalities were most often associated with bilateral brain lesions (green in Fig. 2B). Several patient group studies have shown that the right and left hemisphere serve different functions. For example, semantic dementia patients with predominant left temporal lobe atrophy showed worse recognition of names than faces, while patients with right temporal predominance showed the reverse pattern (Snowden et al., 2004, 2012). Another study showed that patients with left temporal lobe epilepsy (prior to surgery) were specifically only impaired in naming faces, while patients with right temporal lobe epilepsy were impaired in all face-related recognition tests (Seidenberg et al., 2002). A similar hemispheric specialization was also shown for learning of unfamiliar faces paired with names and biographical information (Moran et al., 2005). Correspondingly, for feelings of familiarity, patients with right unilateral temporal lobe epilepsy (Viskontas et al., 2002) or atrophy (Gainotti et al., 2010) were impaired in judging familiarity specifically from faces. The pattern of impairment associated with these regions suggests that they integrate several modalities or represent person identity independent of modality. However, usually the impairment is not restricted to persons and is also present for other semantic categories, such as identification of famous places (Busigny et al., 2009; Gentileschi et al., 2001; Gorno-Tempini et al., 2004; Joubert et al., 2003).

3.1.3. Neuroimaging meta-analysis on multiple modalities

We tested with a conjunction analysis whether identity recognition based on different modalities (faces, names, voices) overlapped. This was not the case, suggesting that the regions found in the analyses of person-identity recognition from different modalities (Fig. 2C) are modality-specific, i.e., are not candidate areas for a multimodal hub.

3.2. Familiarity testing and representations

Recognition of another person is usually accompanied by feeling familiar with this person. In patients, the ability to generate feelings of familiarity was most often tested with familiarity judgments. For example, patients were asked to judge whether a personally familiar, famous, or unfamiliar face was familiar or not. In the following, we review reports that describe patients who are impaired at such familiarity judgements. To link these results to healthy individuals, we compared the evidence from patient studies with the

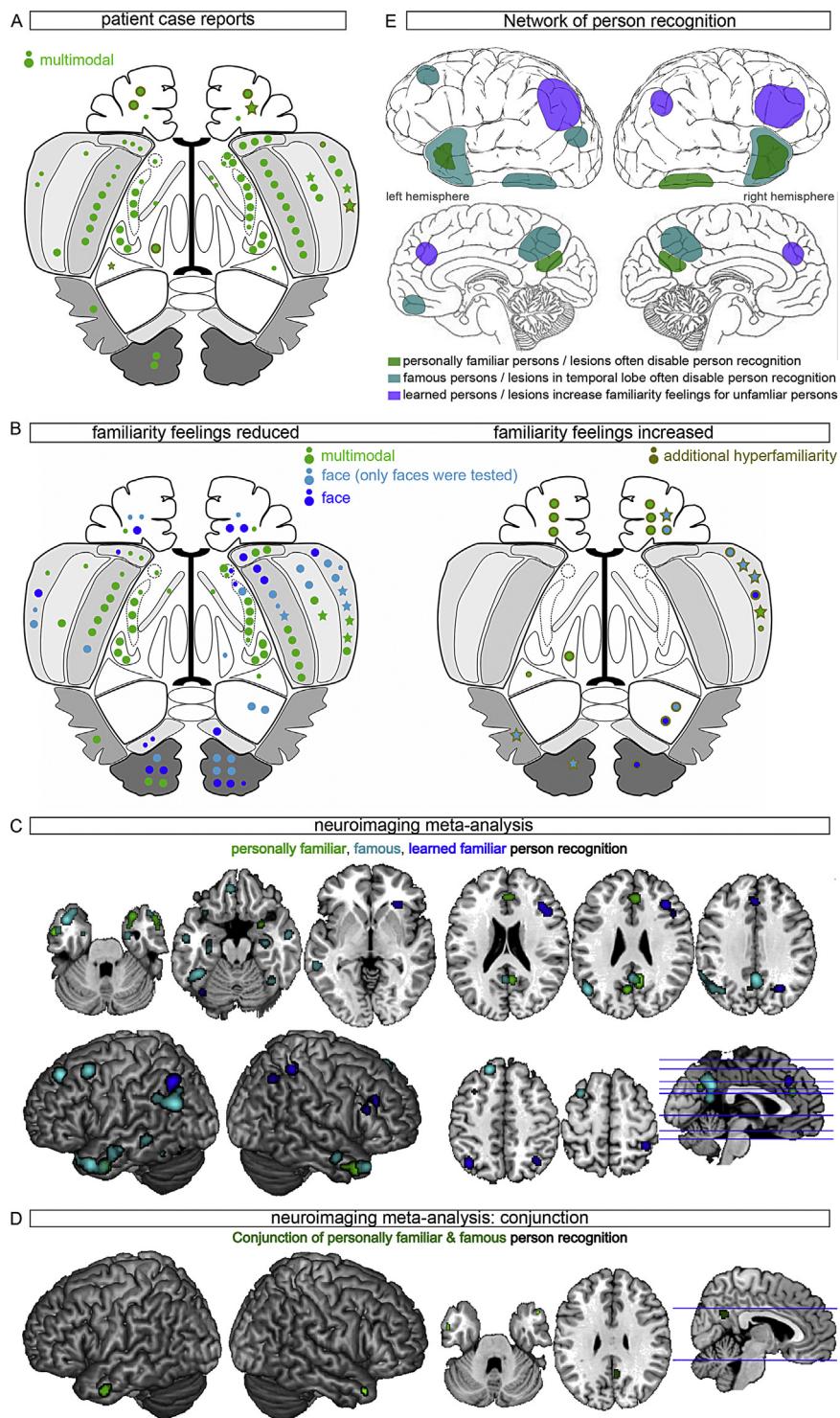


Fig. 3. Overview of sites involved in multimodal person-identity recognition and in processing different familiarities during person-identity recognition. (A) Patient case reports. Each dot represents one lesion. Small dots represent lesions that were explicitly reported as being small. Large dots represent all other lesions. If there is only a single lesion per patient, the corresponding location is marked by a star instead of a dot. (B) Location of lesions in studies that explicitly tested feelings of familiarity during person-identity recognition. (left: reduced and right: increased feelings of familiarity). Each dot represents one lesion. Small dots represent lesions that were explicitly reported as being small. If there is only a single lesion per patient, the corresponding dot is marked by a star instead of a dot. (C) Meta-analysis: brain regions involved in recognition of personally familiar (light green), famous (cyan), and learned-familiar (dark blue) persons as identified by a meta-analysis on healthy subjects (transversal sliced and side view of rendered brain, neurological convention). (D) Conjunction analysis: Conjunction of personally familiar and famous person-identity recognition revealed an overlap in bilateral anterior temporal lobe and right precuneus/posterior cingulate (transversal sliced view and side view of rendered brain). (E) Network of person recognition in the human brain. Famous and personally familiar persons activate a similar network of brain regions (fusiform gyrus, posterior cingulate, and anterior temporal lobes) and lesions in these regions are related to impaired person-identity recognition from several modalities. In contrast, newly learned persons involve anterior cingulate cortex, right frontal and bilateral parietal lobes and lesions in these regions lead to increased feelings of familiarity for unfamiliar persons. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

neuroimaging meta-analyses on personally familiar and famous persons as well as persons learned in the course of the experiments.

3.2.1. Patient case reports

Decreased feelings of familiarity in patients are commonly identified by testing patients' responses to personally familiar or famous person material. Decreased feelings of familiarity, for example, when patients reported that they did not feel familiar with relatives, were caused by lesions in bilateral hippocampi (predominantly on the right), and bilateral lateral temporal, occipito-temporal, occipital, and frontal lobes (cyan in Fig. 3B).

In patients with increased feelings of familiarity (hyperfamiliarity) to unfamiliar persons, brain damage was present in bilateral frontal and parietal lobes, and temporal and occipital lobes of the right hemisphere (olive in Fig. 3B). Of these regions, the right temporal lobe appeared to be especially important since exclusive damage to this area was sufficient to cause hyperfamiliarity in four patients.

3.2.2. Patient group studies and hemispheric lateralization

The lateralization analysis revealed that hyperfamiliarity to unfamiliar persons appeared to be primarily related to damage in the right hemisphere, and occurred rarely with bilateral damage or damage to the left hemisphere (olive in Fig. 2F, Supplementary Table 5). In patient-group studies, Rapcsak et al. (1996) showed that damage of right prefrontal lobe caused hyperfamiliarity to unfamiliar faces, but spared recognition abilities of famous faces. Moreover, these patients produced more false alarms to unfamiliar faces; however this study contained no control for false alarms in general (Rapcsak et al., 2001).

3.2.3. Neuroimaging meta-analysis of different familiarities

The meta-analysis for 'personally familiar person-identity recognition' revealed an extended brain network in the right anterior and medial temporal lobe, left inferior temporal gyrus and the clusters in midbrain structures of which the weighted centres were located in the right anterior cingulate cortex, the right precuneus, and the left cuneus (Fig. 3D, Supplementary Table 2). For 'famous person-identity recognition', we identified a network of regions involving the bilateral temporal lobes, the bilateral posterior and left anterior cingulate cortex, and furthermore several regions in bilateral fusiform gyrus, bilateral limbic, left temporal, left parietal, and left frontal lobes (cyan in Fig. 3C, Table 3). The famous and personally familiar person-identity networks partly overlapped. This was confirmed in a conjunction analysis which revealed overlapping regions in left and right anterior temporal lobe and right precuneus/posterior cingulate (Fig. 3D). In contrast, recognition of persons learned in the course of the experiment (i.e., 'newly learned persons') revealed bilateral frontal, parietal, and temporal lobes as involved regions (dark blue in Fig. 3C, Table 3). These regions did not overlap with regions activated during recognition of personally familiar and famous persons.

3.2.4. Merging evidence from patients and healthy volunteers

On visual inspection, the pattern of lesions associated with hyperfamiliarity to unfamiliar persons and the results of the neuroimaging meta-analysis on recognition of newly learned persons were similar (Fig. 3E). We speculate that hyperfamiliarity to unfamiliar persons emerges when erroneously evoked feelings of familiarity are not suppressed. The similarity of the network involved in unfamiliar person-identity recognition and the network associated with hyperfamiliarity could indicate that 'recognition of newly learned persons' requires similar mechanisms as the 'rejecting recognition of unfamiliar persons'.

We compared the lesions associated with decreased familiarity feelings to regions activated during recognition of personally

familiar and famous persons in healthy individuals, because damage to brain regions activated during recognition of personally familiar and famous persons should cause decreased feelings of familiarity to these persons. Together, both patient studies and neuroimaging studies on healthy individuals suggest that precuneus/posterior cingulate, temporal and, as indicated by the patient studies, frontal lobes are especially critical for feeling familiar with known persons (Fig. 3B/C/D).

The traditional models of face-identity recognition propose that feelings of familiarity are initiated in modality-specific recognition units (Bruce and Young, 1986) or at a higher-level, modality-free recognition stage (Burton et al., 1990). Patient studies reporting increased or decreased feelings of familiarity show the involvement of modality-specific regions (e.g., in occipital and temporal lobes) as well as higher-level, potentially modality-independent regions (e.g., in anterior temporal and frontal lobes). This was also the case for the meta-analysis of neuroimaging findings for recognition of familiar and famous persons, e.g., fusiform areas were identified for identity recognition of famous persons.

In summary, evidence from both patient studies and the meta-analysis on healthy controls consistently supports the important role of the (anterior) temporal lobes (predominantly in the right hemisphere) and the frontal and parietal lobes in multimodal person-identity recognition. The comparison, however, also revealed inconsistencies between these two sources of evidence: the conjunction meta-analysis, but not the review of the patient reports, identified the precuneus as a central region involved in person-identity recognition. Below, we discuss the potential role of the regions as candidate regions for a multimodal hub of person-identity recognition.

4. Recognition vs. discrimination of other persons

To gain further insight into which brain regions are specifically involved during person-identity recognition (as compared to other tasks), we took advantage of several patient studies which tested performance in recognition of person-related characteristics in comparison to discrimination (the simple differentiation of other persons, e.g., saying that two faces depicted in different views belong to the same or a different person, Supplementary Table 4). In the majority of these studies, both recognition of person identity and discrimination were impaired and the brain was predominantly damaged in the right hemisphere (Fig. 4A). Are recognition and discrimination nevertheless dissociable? Several studies reported patients who were only impaired in person-identity recognition while discrimination was spared. This is in line with traditional models that assume that discrimination precedes recognition (Bruce and Young, 1986; Burton et al., 1990). Most of these patients had right hemispheric lesions (Fig. 4B). Interestingly, selective damage of the right (anterior) temporal lobe was sufficient to specifically impair identity-recognition but not discrimination in two patients, indicating a major role of this region for person-identity recognition (Evans et al., 1995; Gainotti et al., 2010). Second, it was also found that person-identity recognition can be spared, while discrimination is impaired: Van Lancker and Kreiman (1987) explicitly tested voice discrimination and voice-identity recognition in patients with damage to either the left or right hemisphere (Van Lancker et al., 1989). They showed a dissociation of voice discrimination and recognition by finding high voice-identity recognition abilities in three subjects who were impaired in discriminating voices (Van Lancker and Kreiman, 1987) (Fig. 4C). Deficiency in famous voice-identity recognition was associated with damage in the right hemisphere, specifically in the right parietal lobe. Impairments in voice discrimination were associated with temporal-lobe damage in either hemisphere (Van Lancker

Table 3

Brain regions involved in recognition of personally familiar, famous, and newly learned persons as identified by a meta-analysis on healthy subjects.

(1) Personally familiar person-identity recognition				
Region	BA	Weighted centre coordinates whole brain	Weighted centre coordinates all studies	Size (mm ³)
Limbic lobe				
Right Precuneus	23, 31, 30		7 –57 25	1416
Right anterior cingulate cortex	9, 24		3 35 23	896
Temporal lobe				
Right temporal pole	28, 34, 47	26 4 –26	28 10 –28	1360
Left inferior temporal gyrus	20		–56 –3 –29	640
Right medial temporal pole	21, 38		53 11 –33	696
Occipital lobe				
Left cuneus	23, 31		–5 –66 27	720
(2) Famous person-identity recognition				
Region	BA	Weighted centre coordinates whole brain	Weighted centre coordinates all studies	Size (mm ³)
Frontal lobe				
Left rectal gyrus	10, 11, 32	–7 47 –17	–7 47 –17	1152
Left superior frontal gyrus	6, 8	–16 38 46	–15 38 45	1080
Left middle frontal gyrus	6	–31 13 54	–32 13 54	904
Limbic lobe				
Precuneus	7, 23, 29, 30, 31	1 –56 32	0 –56 29	3552
Left Parahippocampal gyrus	35		–28 –24 –18	1032
Right Parahippocampal gyrus	28, 35, 36	27 –12 –28	31 –15 –24	624
Right Parahippocampal gyrus	28, 35, 36	27 –12 –28	24 –6 –33	600
Left fusiform gyrus/hippocampus	28, 35, 36		–26 –4 –35	544
Temporal lobe				
Left fusiform gyrus	20, 37	–42 –50 –22	–43 –40 –21	1664
Right fusiform gyrus	20, 37		39 –56 –18	640
Left angular gyrus	19, 39, 40	–49 –65 28	–49 –63 30	2656
Right medial temporal pole	38, 47		44 20 –34	768
Left middle temporal gyrus	20, 21, 22, 47	–55 –10 –18	–46 4 –27	3944
Left middle temporal gyrus	20, 21, 22, 37		–59 –39 –5	512
Right middle temporal gyrus	20, 21, 38	57 –6 –22	57 –6 –21	480
(3) Learned familiar person-identity recognition				
Region	BA	Weighted centre coordinates whole brain	Weighted centre coordinates all studies	Size (mm ³)
Frontal lobe				
Right inferior frontal gyrus (p. Triangularis)	9, 13, 46	41 25 21	41 25 21	1920
Left superior medial gyrus	6, 8, 32	–1 32 34	–1 32 34	640
Temporal lobe				
Right sub-lobar. Claustrum, Insula	13, 45	30 27 –4	30 27 –4	512
Left fusiform gyrus			–37 –70 –18	376
Parietal lobe				
Left angular gyrus	7, 19, 39	–38 –63 44	–38 –63 44	1104
	7, 13	27 –65 34	27 –65 34	488
Right superior parietal lobule	7, 40	40 –45 58	40 –45 58	488
Right angular gyrus	7, 19, 39		36 –62 47	336
(4) Conjunction analysis: Personally familiar and famous person-identity recognition				
Region	BA	Weighted centre coordinates	Size (mm ³)	
Parietal lobe				
Right precuneus	23, 31	5 –56 26	400	
Temporal lobe				
Left middle temporal gyrus	20, 21	–53 –2 –30	200	
Right medial temporal pole	38	51 15 –32	48	

et al., 1989). Similar findings were reported in the visual domain, suggesting that the dissociation of recognition and discrimination is not only a phenomenon in voice-identity recognition: Recognition and discrimination dissociation was found in a patient who could recognize famous faces but was unable to discriminate unfamiliar faces (Malone et al., 1982).

The double dissociation between recognition and discrimination provides a new perspective on models of person-identity recognition that assume a serial processing in which discrimination precedes recognition (Bruce and Young, 1986; Burton et al., 1990).

It rather suggests that there might be at least partially separable pathways that mediate discrimination and recognition.

5. Discussion

In this review, we provided a systematic link between knowledge gained from patient studies and meta-analytic evidence from neuroimaging studies on healthy people. The review showed that person-identity recognition employs a whole network of brain regions which process different modalities and different

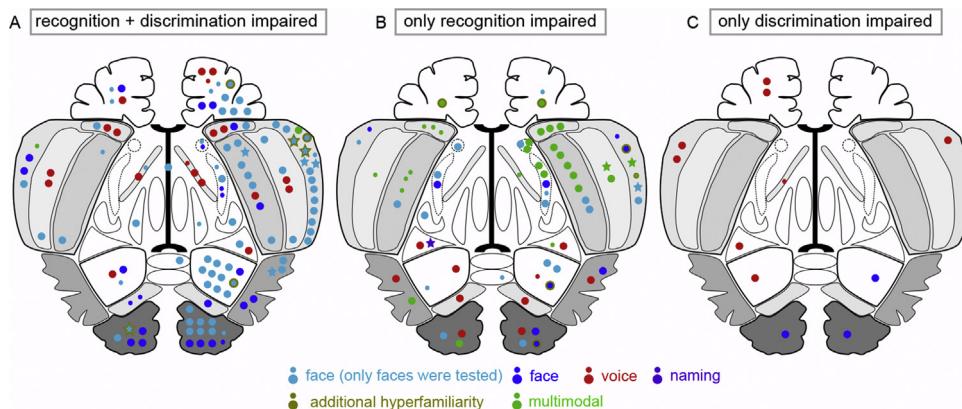


Fig. 4. Location of lesions in patients who were explicitly tested on recognition and discrimination of person related information. Subpanels are grouped according to which tests were impaired: (A) Recognition and discrimination were impaired, (B) Only recognition was impaired (discrimination was tested and unimpaired), and (C) Only discrimination was impaired (recognition was tested and unimpaired). Each dot represents one lesion. Small dots represent lesions that were explicitly reported as being small.

familiarities during person-identity recognition (Fig. 3E). In line with cognitive models of person-identity recognition, there are modality-specific non-overlapping regions involved in face, voice, and name-identity recognition. While for some regions the function has been relatively well investigated (e.g., FFA in face-identity recognition), the function of other areas still remains elusive (e.g., frontal areas in voice- and face-identity recognition).

5.1. PIN—Is there a multimodal hub for person-identity recognition?

There is no final evidence for a single multimodal hub of person-identity recognition in the human brain. Such a multimodal hub would have been indicated by a lesion to a single specific brain region in a patient who could recognize and feel familiar with faces, names, and voices separately, but not retrieve semantic information about that person, and not associate the names, faces, and voices. Furthermore, if a PIN is independent from a general semantic storage, the deficit should be specific for person-identity recognition but absent for other categories (e.g., non-person information such as knowledge about sights or cities). Nevertheless, the neuroimaging meta-analysis revealed several potential candidate areas of a multimodal hub of person-identity recognition in the human brain. We now discuss these, starting with the most promising candidate region: the anterior temporal lobe.

5.1.1. Anterior temporal lobe

The anterior temporal lobe has been repeatedly related to memory of person identity (Ellis et al., 1989; Gorno-Tempini et al., 1998; Rotstein et al., 2005; Sergent et al., 1992; Sugiura et al., 2009; Tsukiura et al., 2008) and person-related knowledge (Simmons et al., 2010). The anterior temporal lobe is also a central region for modality-free general semantic processing for categories other than persons (Guo et al., 2013; Patterson et al., 2007; Ralph et al., 2010; Visser et al., 2010). Damage to the temporal lobes frequently caused deficits in multimodal person-identity recognition (Fig. 3A) although, in most of the studies reviewed, not all modalities were tested. In healthy individuals the anterior temporal lobe was involved in recognition of personally familiar and famous persons (Fig. 3C). These findings suggest the anterior temporal lobe is the best candidate region for a multimodal hub. It is a consistent finding that the two hemispheres are asymmetrically involved depending on the modality of the information used to recognize other persons (e.g., left hemisphere for names vs. right hemisphere

for faces) (Figs. 1B/C and 2) (Gainotti, 2007a, 2013b; Gainotti and Marra, 2011; Seidenberg et al., 2002; Snowden et al., 2004, 2012; Tranel, 2006; Tranel et al., 1997; Wong and Gallate, 2012). Also, fMRI studies in healthy individuals showed that the left anterior temporal lobe is involved in associating person-related semantic information with names, and the right anterior temporal lobe is involved in associating person-related semantic information with faces (Tsukiura et al., 2008). However, another study showed that similar anterior temporal lobe regions are involved when learning to associate voices with names or voices with faces of unfamiliar persons (von Kriegstein and Giraud, 2006). This suggests that the right anterior temporal lobe processes not purely visual but rather multisensory information (reviewed in Gainotti and Marra, 2011). How multisensory person identity is represented in the right anterior temporal lobe is still an open question and there are two fundamentally different possible answers: (1) the anterior temporal lobe could contain a single multimodal/modality-free region (PIN) in which evidence from different modalities (e.g., face and voice) is merged (Fig. 1B). This possibility is supported by both patient studies showing impaired person-identity recognition from several modalities (Fig. 3A), and the common activation of the anterior temporal lobe for recognition of famous and personally familiar persons in healthy individuals (Fig. 3C). However, both sources of evidence are constrained because no patient was reported in which a lesion of the anterior temporal lobe caused a recognition impairment of all modalities specifically for person-identity. In addition, most of the neuroimaging studies investigated recognition of famous and personally familiar persons with face stimuli or stimuli that were associated with faces (e.g., voices learned with corresponding faces), so that it is difficult to define whether this region is a truly multimodal, or rather face-specific region which is cross-modally activated, for example, during voice-identity recognition. (2) Recent evidence for direct connections between face- and voice-recognition areas (Blank et al., 2011; Focker et al., 2011; Schall et al., 2013; von Kriegstein et al., 2005) and the discussion of different modality-specific sub-regions within the temporal lobe (Bonner and Price, 2013; Gainotti, 2011; Skipper et al., 2011) question the apparently redundant role of a single multimodal/modality-free region which merges person-identity information from different modalities. We speculate that person identity information might be stored in different sub-regions of the anterior temporal lobe: face-identity might be processed in right ventral, and voice-identity in more lateral anterior temporal lobe; with both possibly being connected directly or via a multimodal person-identity region which provides access to person-related semantics (Fig. 1C).

5.1.2. Medial parietal lobe (precuneus) and posterior cingulate

The posterior cingulate/precuneus was associated with identity recognition of familiar and famous persons, and activation differed between congenital prosopagnosics and healthy individuals (Avidan and Behrmann, 2009; Dinkelacker et al., 2011). The region is not only involved in person-identity recognition, but also encoding of person-identity (Kosaka et al., 2003; Simmons et al., 2010). However, impairments in person-identity recognition were only rarely associated with lesions in precuneus and posterior cingulate. This could be because focal lesions in these regions are rare and, when present, cause other, more noticeable impairments such as severe general memory impairments (Minoshima et al., 1997; Wagner et al., 2005). The posterior cingulate is classically seen as part of the default network and is activated during social cognition, emotional processing, and unconstrained cognition tasks (Cavanna and Trimble, 2006; Schilbach et al., 2012). This is interesting because potentially person-related cognitive processes occur during these non-demanding or social tasks.

5.1.3. Lateral parietal lobes

The lateral parietal lobes were associated with recognition of newly learned and famous persons in the neuroimaging meta-analysis, and increased as well as decreased familiarity feelings (Fig. 3B). However, they were not involved in identity-recognition of personally familiar persons, so are unlikely to correspond to a PIN. Based on these findings, we speculate that the lateral parietal lobes combine person-related information from several modalities especially during those stages of person-identity recognition in which the person to be recognized has not been learned very well (Campanella et al., 2001; Joassin et al., 2011). Potentially, the lateral parietal lobes are not required during recognition of personally familiar persons, because access to information about these personally known persons is provided by other regions (e.g., anterior temporal lobe). This specific involvement of the parietal lobes in recognition of newly learned persons indicates that person recognition depends on the familiarity of the recognized person, and that different熟悉ities are represented differently in the brain. This suggests that models of person recognition have to differentiate between recognition of (personally) familiar persons and recognition of unfamiliar/newly learned persons (Gobbini and Haxby, 2007).

5.1.4. Frontal lobes

Frontal lobe regions were involved in many person-identity recognition functions, including face- and voice-identity recognition as well as recognition of famous and learned-familiar persons. Lesions in the frontal lobe lead to both increased and decreased feelings of familiarity (Fig. 3B). However, the frontal lobes were not indicated in recognition of personally familiar persons, and there was dissociation between hemispheres with recognition of famous persons in the left hemisphere and of learned-familiar persons in the right frontal lobe (Fig. 3C/F). This is not compatible with a PIN; and it might be that the frontal lobes are rather involved in top-down control during recognition processes in general (Rapcsak and Edmonds, 2011).

5.2. General discussion with implications for cognitive models of person-identity recognition

There are two separate networks for recognition of newly learned persons and recognition of personally familiar and famous persons. One interpretation of the network for unfamiliar persons could be that identity-recognition of unfamiliar persons is usually more difficult than recognition of familiar persons (Hancock et al., 2000; Klatzky and Forrest, 1984; Young et al., 1985). However, lesions in similar sites lead to hyperfamiliarity, suggesting a more

specific role in identity-recognition of unfamiliar persons. These findings indicate that models of person-identity recognition have to differentiate between recognition of newly learned persons and famous and personally familiar persons, in line with earlier suggestions (Ellis et al., 1979; Gobbini and Haxby, 2007; Johnston and Edmonds, 2009).

There is evidence of brain regions that combine information of different modalities and relate it, for example, to person-specific semantic information: several focal brain regions caused impairments in person-identity recognition affecting several modalities (although in most studies not all modalities were tested and impaired). The anterior temporal lobes are the most promising candidate regions for person-identity recognition independent of modality. This independence is relative because left and right anterior temporal lobes are involved in different functions. Cross-talk between modality-specific regions (for example, via direct functional and structural connections between face and voice-identity recognition areas (Blank et al., 2011; Schall et al., 2013; von Kriegstein and Giraud, 2006; von Kriegstein et al., 2005)) would potentially make a region for integration of multisensory information redundant (Fig. 1C).

Although recognition of persons, and predominantly of faces, has been investigated extensively in both lesion studies and neuroimaging in healthy participants, the results from the previous literature are still quite diverse. The neural representation of person recognition therefore remains relatively ill-defined. A reason for the many brain regions found to be involved in person-identity recognition could be the use of insufficient control tasks. In neuroimaging studies these often include low-level controls (e.g. person vs. object stimuli); in patient studies person recognition is often only tested in one modality.

Some guidelines on investigating person-identity recognition might help to advance the knowledge about neuronal mechanisms in the future. For example, in patient studies, diagnostics for person-identity recognition should always include systematic behavioural tests of different modalities (faces, names, and especially also voices), recognition of other objects or categories, and performance in basic perceptual properties (as in (Busigny et al., 2009)). Behavioural testing and diagnostics have to be combined with advanced neuroimaging techniques to localize lesions in patients, so that impairments in person-identity recognition can be related to the corresponding brain region causing the impairment. A more precise localization within the temporal lobe would be especially valuable, because the temporal lobe seems to be central for person-identity recognition. So far many patient studies only reported the temporal lobes as lesion location without further classification into specific subregions.

Similarly, for experimental neuroimaging studies it would be important to test person-identity recognition in more than one modality, and to use high-level baselines to separate person-identity recognition from low-level processing and recognition of other categories (e.g., objects or sites). In addition, advanced imaging techniques are needed to reliably acquire data from the anterior temporal lobe, currently the most promising region for a multimodal hub for person-identity recognition in the brain.

6. Conclusions

The present review localized a network of modality-specific as well as multimodal/modality-free regions in the human brain that enable recognition of person identity. It highlighted the importance of investigating person-identity recognition from multiple modalities in both patients and healthy individuals. The results revised several assumptions of traditional cognitive and neuroscientific models of person-identity recognition and provide a

model-driven framework for testing patients in clinical settings as well as basic experimental research to further advance our understanding of person-identity recognition.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.neubiorev.2014.10.022>.

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