Review

Distinct and common aspects of physical and psychological self-representation in the brain: A meta-analysis of self-bias in facial and self-referential judgements

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ABSTRACT

The neural representation of self is a fundamental question for brain research. Employing activation likelihood estimation (ALE) meta-analyses, we assessed the commonalities and distinctions between different components of the self by focusing on the 'physical' self and the 'psychological' self – assessed respectively through face processing and self-referential tasks. We first conducted ALE meta-analyses by computing the convergence of findings on brain activation in self-face recognition and self-referential studies respectively. Contrast and conjunction analyses of these two meta-analytic results were then applied to extract the distinctions and commonalities in self-face and self-reference tasks. Facial self processing was particularly associated with lateral brain regions with a right hemispheric dominance, while processing psychological self predominantly activated cortical midline structures, more specifically the anterior cingulate cortex/superior frontal cortex. In contrast, the conjunction analyses showed that the two aspects of self-processing recruit the dorsal anterior cingulate cortex and the left inferior frontal gyrus extending to the insula. A framework including both distinct and common neural representation of selfs is discussed.

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Contents

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1. Introduction

What is the self and what is the neural representation of the self in the brain? In the last three decades, psychologists and neuroscientists have repeatedly attempted to localize the neural underpinnings of the self by assessing different components of the self, including studies focused on the facial self, self embodiment, self ownership, self-related personality traits and so on, with many studies using functional Magnetic Resonance Imaging (fMRI) to evaluate the functional localization of self-related processing in these tasks (e.g., Gusnard et al., 2001; Kelley et al., 2002; Kircher et al., 2000; Sugiura et al., 2000). However, inconsistent findings across studies have led to contradictory views – for example, about whether there are self-specific modules in the human brain (Gillihan and Farah, 2005; Legrand and Ruby, 2009), and whether there are brain regions associated with all components of the self reflecting a common self-representation or representations specific to particular tasks?

To address these issues Northoff et al. (2006) conducted a meta-analysis of self-related neuroimaging studies and reported that self-relatedness was specifically processed in cortical midline structure (CMS), including the medial frontal cortex (MFC), anterior cingulate cortex (ACC), and posterior cingulate cortex (PCC). Several other meta-analyses have confirmed the role of CMS in processing self-related information (Araujo et al., 2013; Murray et al., 2012; Northoff et al., 2011; Qin and Northoff, 2011; van der Meer et al., 2010), with additional evidence suggesting the involvement of the anterior insula (AI, e.g., Northoff et al., 2011). A common aspect of these meta-analyses is the focus on contrasts comparing processing of the self-relative to the processing of information related to other people (self > other). However, all of these meta-analyses have treated the self as a single psychological entity, either by pooling different components of self-related processes as a whole (Northoff et al., 2011; Qin and Northoff, 2011) or by focusing only on one component of the self (Araujo et al., 2013; Martinelli et al., 2013; Murray et al., 2012; Platek et al., 2008), e.g., visual self recognition (Apps and Tsakiris, 2013; Devue and Brédart, 2011; Knoblich, 2002; Suddendorf and Butler, 2013, 2014), autobiographical memory (Cabeza and St Jacques, 2007), or self-evaluation (Schmitz and Johnson, 2007). These meta-analyses are limited however because they do not directly compare different components of the self.

In contrast to the emphasis on a single aspect of the self in these meta-analyses, many psychologists have distinguished different aspects of the self. For example, James (1890) distinguished different categories of the "self" including physical/material self, psychological self, and spiritual self. Following these lines, some neuroimaging studies have reported the distinction in brain activity between the physical and the psychological selves (Gillihan and Farah, 2005; Uddin, 2011). In those studies, the physical self refers to dissociating one's physical existence from the external environment and can be probed, for example, by tasks requiring a subject to discriminate his/her own face from the faces of strangers (Gillihan and Farah, 2005; Sugiura, 2013). In contrast, the psychological self is defined by personal attributes such as

personality traits as well as autobiographical memories and experiences (Gillihan and Farah, 2005; Murray et al., 2012; Northoff, 2011). Given the different definitions of the physical and psychological selves and disparities in previous findings, it is interesting to examine if physical and psychological aspects of the self are represented differentially in the brain, or if these contrasting aspects of the self largely overlap in the brain to form a core self-representation (Northoff and Bermpohl, 2004) (perhaps along also with some components specific to the different aspects of the self). Sui and Humphreys (2015) recently propose that there is an integrative self which can act as a glue to (i) bind information as a perceptual whole, (ii) link items to their context in memory, and (iii) integrate different levels of processing. This integrative capacity may be mediated by a core representation of the self, recruited in different tasks across. This is supported by neuropsychological evidence showing that selective brain lesions can modulate self-biases across a range of tasks (Sui et al., in press).

To address the above issues, we conducted meta-analyses by directly comparing the two key aspects of self-processing – reflecting the physical and psychological self, using activation likelihood estimation (ALE) meta-analyses of neuroimaging studies of self-biases in face recognition and referential judgements. ALE provides a quantitative measure of cross-study consistency that accommodates spatial uncertainty of activation data and allows statistically defensible conclusions to be formed (Fox et al., 2014; Laird et al., 2011). To take into account inconsistencies in the concept of the self (Legrand and Ruby, 2009), we first operationalized the physical and psychological selves, adopting relatively narrow definitions. The physical self was defined as the bodily-grounded self that dissociates one's physical existence from the external environment and may be probed by three major types of experiment – self-face recognition, self-body recognition and self-agency (Gillihan and Farah, 2005). Here we focused on studies of self-face recognition as the face is not only the most distinctive physical feature of the individual (Gallup, 1970; Suddendorf and Collier-Baker, 2009; Tsakiris, 2008) but also the attribute most commonly investigated (Platek et al., 2006; Sugiura et al., 2000, 2005; Uddin et al., 2005). The psychological self was taken to comprise self-related traits, autobiographical memory and judgements based on a first person perspective (Gillihan and Farah, 2005). In practice, the psychological self is often associated with the self-reference effect (SRE), which can be measured in terms of better memory for the trait words that refer to self than the trait words referring to others (Rogers et al., 1977). Most studies of both self-related traits and autobiographical memory have employed self-reference tasks, as defined by previous meta-analyses (Araujo et al., 2013; Kim, 2012; Martinelli et al., 2013; Spreng et al., 2009; Svoboda et al., 2006). Accordingly we chose studies using the self-reference task as representative of the psychological self, both because it has been widely used and because of its relevance to self-related traits and autobiographical memory. In contrast, studies of first person perspective were excluded because their linkage to self-representation is more ambiguous (Gillihan and Farah, 2005).

We first conducted ALE meta-analyses by computing the convergence of brain activation findings in self-face recognition and self-referential studies respectively. Contrast and conjunction analyses of these two meta-analytic results were then applied to assess the distinct and common neural correlated to the physical and psychological selves.

2. Methods

2.1. Literature search and study selection

Articles included in the present meta-analyses were identified by a systematic literature search using specific terms in PubMed and Google scholar (up to January 2015): "self face" or "own face" for self-face recognition studies, and "self-referential" or "self-reference" for self-referential studies; all these terms were combined ("AND") with "fMRI" or "PET" to identify relevant functional neuroimaging studies. For more complete coverage, articles were identified from recent meta-analyses (Araujo et al., 2013; Platek et al., 2008) and reviews (Devue and Brédart, 2011) as well. Additional studies were identified by searching through the reference lists of studies obtained through the initial search. The inclusion criteria for articles were the following:

(1) Only studies reporting whole brain analyses were included, while studies based on partial coverage or employing only region-of-interest analyses were excluded.
(2) Articles reporting results as coordinates in a standard reference frame (Talairach and Tournoux or MNI). Four articles were excluded due to unidentifiable coordinates (Ketay et al., 2014; Platek and Krill, 2009; Yoshimura et al., 2014; Yuan et al., 2013). To address problems caused by different coordinates used in studies, coordinates originally published in Talairach space were converted to MNI space using the Lancaster transformation (Lancaster et al., 2007).

(3) Studies included healthy subjects with no neurological, medical, or psychiatric disorders. Articles including patients were also selected if they reported results for a control group separately. Only studies including young and middle-aged adults (mean range, 18–59 years) were included to avoid effects due to aging changing self-related processes (Leshikar and Duarte, 2014).
(4) If the same dataset was reported in several articles, only one was used in the meta-analyses (e.g. Kircher et al., 2000, 2001).
(5) Only tasks using visual stimuli were included; any auditory, tactile, olfactory or gustatory paradigms were excluded from the meta-analyses (Apps et al., 2015).

Fig. 1 depicts the process of article selection in detail. There were 60 articles in total including: 23 articles (23 experiments 176 foci/451 subjects) in the self-face condition, and 37 articles (41 experiments, 215 foci/733 subjects) in the self-referential condition (Table 1 and supplementary information). Following previous meta-analyses, we used self > other condition to investigate the specificity of self-face and self-referential processing. If more than one self > other contrast was reported in the article, i.e., the self condition was compared to more than one type of 'other', we chose the contrast in which the self was compared with a familiar/close other, because the self > familiar/close others contrast more likely yields pure "self-specific" effects (Murray et al., 2012).

2.2. Meta-analyses

2.2.1. Activation likelihood estimation

All meta-analyses were performed using the revised activation likelihood estimation (ALE) algorithm for coordinate-based meta-analyses of neuroimaging results (Eickhoff et al., 2009; Laird et al., 2009a, 2009b; Turkeltaub et al., 2002) as implemented in GingerALE 2.3. This algorithm aims to identify areas showing a convergence of reported coordinates across experiments, which is
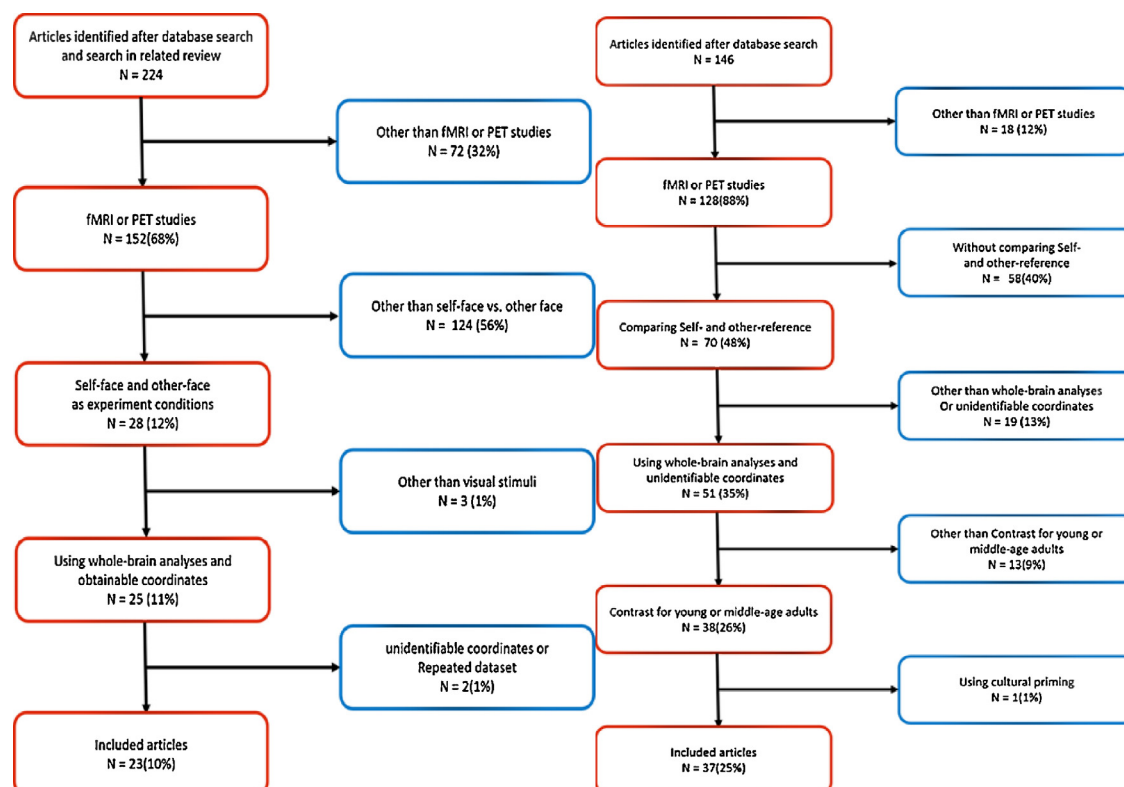

Fig. 1. Article selection process of neuroimaging studies of self-face (left) and self-referential process (right).

Table 1
Overview of studies and contrasts included in the present meta-analyses.

Articles	Model	Subjects (male)	Mean age	Stimuli	Contrast included
Devue et al. (2007)	fMRI	20 (0M)	22.1	Face	Self > familiar other (colleague)
Herwig et al. (2012)	fMRI	22 (5M)	23–41	Face	Self > other (known and unknown)
Kaplan et al. (2008)	fMRI	12 (6M)	26.6	Face	Self > familiar other (individualized)
Kircher et al. (2000)	fMRI	6 (6M)	31	Face	Self > familiar other (parent)
Morita et al. (2008)	fMRI	19 (9M)	26	Face	Self > unfamiliar other
Morita et al. (2011)	fMRI	15 (13M)	23.3	Face	Self > unfamiliar other
Morita et al. (2014)	fMRI	32 (16M)	21.3	Face	Self > unfamiliar other
Oikawa et al. (2012)	fMRI	28 (0M)	20.8	Face	Self > familiar other (friend)
Platek et al. (2004)	fMRI	5 (N/A)	N/A	Face	Self > public figure
Platek et al. (2009)	fMRI	12 (6M)	27.58	Face	Self > familiar other (friends)
Platek et al. (2006)	fMRI	12 (12M)	19.36	Face	Self > familiar other (fraternity brother)
Pujol et al. (2013)	fMRI	20 (6M)	24.4	Face	Self > unfamiliar other
Ramasubbu et al. (2011)	fMRI	10 (0M)	25	Face	Self > familiar other (friend)
Scheepers et al. (2013)	fMRI	41 (41M)	21	Face	Self > familiar other (individualized)
Sugiura et al. (2000)	PET	9 (9M)	19–23	Face	Self > unfamiliar other
Sugiura et al. (2012)	fMRI	23 (16M)	18–24	Face	Self > familiar other (friend)
Sugiura et al. (2008)	fMRI	29 (N/A)	18–24	Face	Self > familiar other (friend)
Sugiura et al. (2006)	fMRI	31 (21M)	18–24	Face	Self > familiar other (friend)
Sugiura et al. (2005)	fMRI	34 (26M)	18–26	Face	Self > unfamiliar other
Sugiura et al. (2015)	fMRI	20 (20M)	19–25	Face	Self > unfamiliar other
Sui et al. (2007)	fMRI	12 (6M)	24.3	Face	Self > familiar other (friend)
Taylor et al. (2009)	fMRI	10 (4M)	35.4	Face	Self > unfamiliar other
Uddin et al. (2005)	fMRI	10 (3M)	26.9	Face	Self > familiar other (friend or colleague)
Benoit et al. (2010)	fMRI	13 (8M)	24.2	Traits	Self > familiar other (friend)
Cikara et al. (2014)	fMRI	21 (10M)	23.1	Traits	Self > public figure (Obama)
D'Argembeau et al. (2007)	fMRI	17 (6M)	23	Traits	Self > close other
Fossati et al. (2003)	fMRI	10 (3M)	25.8	Traits	Self > other (general other)
Gutchess et al. (2007)	fMRI	19 (9M)	23.1	Traits	Self > public figure (Einstein)
Gutchess et al. (2010)	fMRI	17 (9M)	23.2	Traits	Self > public figure (Einstein)
Han et al. (2008)	fMRI	14 (8M)	22.5	Traits	Self > public figure (Zhu Rongji)
	fMRI	14 (6M)	23.6	Traits	Self > public figure (Zhu Rongji)
Han et al. (2010)	fMRI	14 (7M)	25.4	Traits	Self > public figure (Zhu Rongji)
Heatherton et al. (2006)	fMRI	30 (14M)	24	Traits	Self > familiar other (friend)
Jenkins et al. (2011)	fMRI	15 (5M)	21.2	Traits	Self > public figure (Bush)
Kelley et al. (2002)	fMRI	21 (12M)	20	Traits	Self > public figure (Bush)
Lombardo et al. (2010)	fMRI	33 (33M)	27.9	Traits	Self > public figure (British Queen)
Lou et al. (2004)	PET	13 (6M)	27	Traits	Self > public figure (Danish Queen)
Ma and Han (2011)	fMRI	23 (11M)	22	Traits	Self > public figure
Ma et al. (2014a)	fMRI	30 (15M)	22.7	Traits	Self > public figure
	fMRI	30 (15M)	25	Traits	Self > public figure
McAdams et al. (2014)	fMRI	18 (0M)	18–45	Traits	Self > familiar other (friend)
Modinos et al. (2009)	fMRI	16 (10M)	20.8	Traits	Self > familiar other (acquaintance)
Modinos et al. (2011)	fMRI	18 (10M)	20.8	Traits	Self > unfamiliar other
Moran et al. (2011)	fMRI	21 (8M)	24.3	Traits	Self > public figure (W. Bush)
Ochsner et al. (2005)	fMRI	16 (7M)	22.95	Traits	Self > familiar other (friend)
Pauly et al. (2014)	fMRI	13 (7M)	34.46	Traits	Self > familiar other (intimate one)
Pfeifer et al. (2007)	fMRI	12 (6M)	26.1	Traits	Self > familiar other (Harry Potter)
Powell et al. (2010)	fMRI	13 (4M)	20	Traits	Self > public figure (W. Bush)
Sarsam et al. (2013)	fMRI	14 (6M)	26.4	Traits	Self > public figure (Danish Queen)
Schmitz et al. (2004)	fMRI	18 (10M)	24	Traits	Self > significant other
Sul et al. (2011)	fMRI	19 (9M)	24	Traits	Self > other (famous entrepreneur)
van Buuren et al. (2010)	fMRI	19 (8M)	21.5	Traits	Self > public figure (a prime-minister)
van Buuren et al. (2012)	fMRI	18 (7M)	27.5	Traits	Self > public figure (a prime-minister)
Vanderwal et al. (2008)	fMRI	17 (10M)	21.5	Traits	Self > familiar other (mother)
Wang et al. (2012)	fMRI	32 (16M)	22.7	Traits	Self > public figure (Liu Xiang)
Wu et al. (2010a)	fMRI	16 (8M)	20.1	Traits	Self > public figure (Lu Xun)
	fMRI	15 (8M)	19.8	Traits	Self > other (Don-grub-rgyal)
J. Yang et al. (2012)	fMRI	17 (9M)	22.4	Traits	Self > public figure (brother)
W. Yang et al. (2013)	fMRI	25 (11M)	22.5	Traits	Self > public figure (Lu Xun)
Yoshimura et al. (2009)	fMRI	15 (7M)	23.3	Traits	Self > public figure (a prime-minister)
Zhang et al. (2006)	fMRI	7 (4M)	20.4	Traits	Self > public figure (Lu Xun)
Y. Zhu et al. (2007)	fMRI	13 (8M)	21.5	Traits	Self > public figure (Zhu Rongji)
	fMRI	13 (8M)	23.1	Traits	Self > public figure (Bill Clinton)
L. Zhu et al. (2012)	fMRI	14 (4M)	22.6	Traits	Self > public figure (Bruce Lee)

higher than expected under a random spatial association. The key idea behind ALE is to treat the reported foci not as single points, but rather as centers for 3D Gaussian probability distributions capturing the spatial uncertainty associated with each focus. The width of these uncertainty functions was determined based on empirical data on the between-subject and between-template variance, which represent the main components of this uncertainty. Importantly, the applied algorithm weights the between-subject variance by the number of examined subjects per study,

accommodating the notion that larger sample sizes should provide more reliable approximations of the 'true' activation effect and should therefore be modeled by 'smaller' Gaussian distributions (Eickhoff et al., 2009).

The probabilities of all foci reported in a given experiment were then combined for each voxel, resulting in a modeled activation (MA) map (Turkeltaub et al., 2012). Taking the union across these MA maps yielded voxel-wise ALE scores describing the convergence of results across experiments at each particular location in

the brain. To distinguish 'true' convergence between studies from random convergence (i.e., noise), ALE scores were compared to an empirical null-distribution reflecting a random spatial association between experiments. In this comparison a random-effects inference is invoked, focusing on inference on the above-chance convergence between studies, not the clustering of foci within a particular study. Computationally, deriving this null-hypothesis involved sampling a voxel at random from each of the MA maps and taking the union of these values in the same manner as done for the (spatially contingent) voxels in the original analyses, a process which can be solved analytically (Eickhoff et al., 2012). The *p*-value of the "true" ALE was then given by the proportion of equal or higher values obtained under the null-distribution. The resulting non-parametric *p*-values were then thresholded at Cluster-Level $p < 0.05$ (Eickhoff et al., 2012), with 5000 threshold permutations for uncorrected $p < 0.001$. All significant clusters were reported, included the volume, weighted center and locations and *Z*-scores at peaks within the region.

2.2.2. Conjunctions and comparison of individual meta-analyses

Conjunction analyses identify voxels where a significant effect was present in all separate analyses. Specifically, we took the individual *Z*-maps of the ALE results in self-face and self-referential tasks, and conducted a minimum conjunction (Nichols et al., 2005), then applied a voxel level threshold of $p < 0.001$ (uncorrected). We conducted the conjunction analysis with the 'image calculator' utility in SPM8 (www.fil.ion.ucl.ac.uk).

Differences between the conditions were tested by first performing separate ALE analyses for each condition and computing the voxel-wise differences between the ensuing ALE maps. All experiments contributing to either set of analyses were then pooled and randomly divided into two groups of the same size as the two original sets of experiments reflecting the contrasting ALE analyses (Eickhoff et al., 2011; Rottschy et al., 2012). ALE-scores for these two randomly assembled groups were calculated and the difference between these ALE-scores was recorded for each voxel in the brain. Repeating this process 25,000 times then yielded a null-distribution of differences in ALE-scores between the two conditions. The "true" difference in ALE scores was subsequently tested against this voxel-wise null-distribution of label-exchangeability and thresholded at $p < 0.01$ (FDR corrected).

2.2.3. Data visualization

The resulting areas were anatomically labeled by reference to probabilistic cytoarchitectonic maps of the human brain (Eickhoff et al., 2005, 2006, 2007). For visualization purposes, we used Brain-Net Viewer (Xia et al., 2013) to present the meta-analytical results.

3. Results

### 3.1. Individual meta-analyses

3.1.1. Self-face vs. other face processing

The regions with greater activations in self-face processing contrasted against other-face processing are shown in Fig. 2A and Table 2. The largest areas of convergence were in the right superior occipital gyrus/angular gyrus, the bilateral inferior frontal gyrus, and the bilateral fusiform gyrus/inferior temporal gyrus. Four large areas of convergent activation were also found in the bilateral insula, right postcentral gyrus/supramarginal gyrus and right ACC. The left middle occipital gyrus and right inferior occipital gyrus were also consistently activated in these studies.

3.1.2. Self-referential vs. other-referential processing

The regions with enhanced activations in self-referential processing compared to other-referential processing are illustrated in
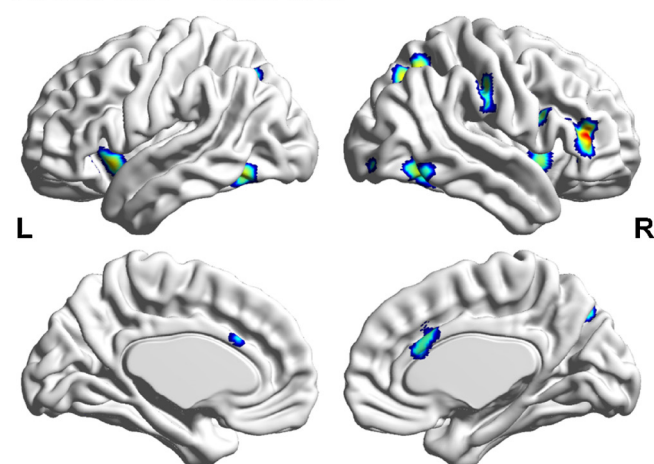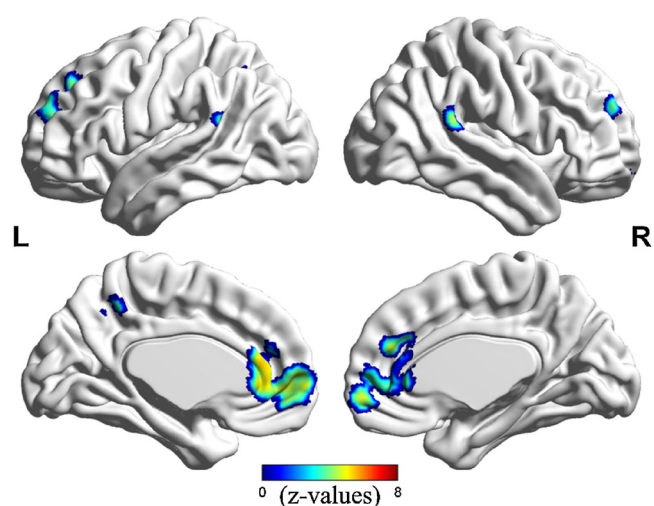

Fig. 2. ALE meta-analyses of neuroimaging studies on self-face and self-reference (*z*-value). (A) Brain regions activated more by self-face than by other-face; (B) brain regions activated more by self-referential processing than by other-referential processing. *Note*: L means left hemisphere, R means right hemisphere.

Fig. 2B and Table 2. Areas comprising the cortical midline structure (the bilateral ACC/medial frontal gyrus, left precuneus) were reliably activated in this contrast. Other brain regions such as left middle frontal gyrus, inferior parietal lobule and bilateral superior temporal gyrus were also more activated during self-referential processing than other-referential processing.

3.2. Common and distinct brain areas of self-face and self-referential processing

To investigate common and distinct neural regions involved in self-face and self-referential processing, we compared the ALE results for self-face processing relative to self-referential processing. The conjunction analysis of the two ALE meta-analytic results showed that the ACC and left inferior frontal gyrus (IFG) extending to the insula were activated in both self-face and self-referential tasks (Table 3 and Fig. 4). The contrast analyses showed that the right inferior frontal gyrus, the right superior occipital gyrus, the right temporal gyrus (fusiform gyrus), and the postcentral gyrus were more likely to be activated in self-face processing (Table 3

Table 2
Results of meta-analyses for individual contrast condition.

| Cluster no.	Macroanatomical location	MNI coordinates			Volume (mm³)	Maximum z-value
		X	Y	Z		
Self-face > other-face						
1	R superior occipital gyrus/angular gyrus	28	−66	45	3864	5.89
2	R inferior frontal gyrus/fusiform gyrus	46	37	9	3376	7.36
3	R inferior temporal gyrus	48	−58	−12	2848	5.31
4	L insula lobe	−37	18	−6	1752	5.29
5	R inferior frontal gyrus	50	8	26	1656	5.64
6	R postcentral gyrus/supramarginal gyrus	57	−23	38	1256	4.86
7	Anterior cingulate cortex	4	21	28	1168	3.89
8	L fusiform gyrus	−46	−61	−14	1056	4.84
9	R insula lobe	37	10	−4	824	4.41
10	L middle occipital gyrus	−22	−68	45	480	3.99
11	R inferior occipital gyrus	36	−85	−7	456	4.13
Self-referential > other-referential						
1	Anterior cingulate cortex	−1	47	6	15,680	5.66
2	L middle frontal gyrus	−25	49	28	2360	4.34
3	R superior temporal gyrus	65	−39	20	744	4.68
4	R middle frontal gyrus	29	53	27	728	4.29
5	Precuneus	−3	−51	47	680	4.56
6	L superior temporal gyrus	−61	−47	20	456	3.72
7	L inferior parietal lobule	−38	−58	51	432	4.13

All peaks were assigned to the most probable brain area by using the SPM Anatomy Toolbox.

Table 3
Contrast and conjunction analyses of self-face and self-referential processing.

Cluster no.	Macroanatomical location	MNI coordinates			Volume	Maximum z-value
		X	Y	Z		
(Self-face > other-face) > (self-referential > other-referential)						
1	R superior occipital gyrus	27	−67	43	3376	3.89
2	R inferior frontal gyrus	46	38	10	2544	3.89
3	R inferior temporal gyrus	50	−56	−14	1656	3.89
4	R inferior frontal gyrus	51	9	27	624	3.72
5	R postcentral gyrus	54	−22	41	280	3.89
(Self-referential > other-referential) > (self-face > other-face)						
1	Anterior cingulate cortex	−1	53	−1	8264	3.89
(Self-face > other-face) ∩ (self-referential > other-referential)						
1	Anterior cingulate cortex	1	35	19	136	3.42
2	L inferior frontal gyrus and insula	−35	12	−6	80	3.38

All peaks were assigned to the most probable brain area by using the SPM Anatomy Toolbox. R, right; L, left.

A. Self-face > Self-referential
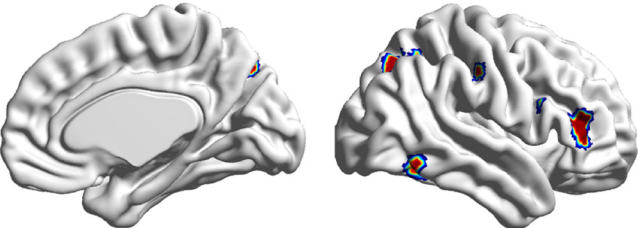
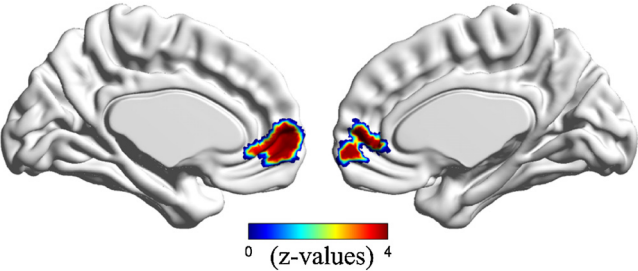B. Self-referential > Self-face

Fig. 3. Meta-analytical results of contrast analyses (z-value). (A) Brain regions activated more by self-face than self-referential processing (in the right hemisphere); (B) brain regions activated more by self-referential than self-face processing.

L   R
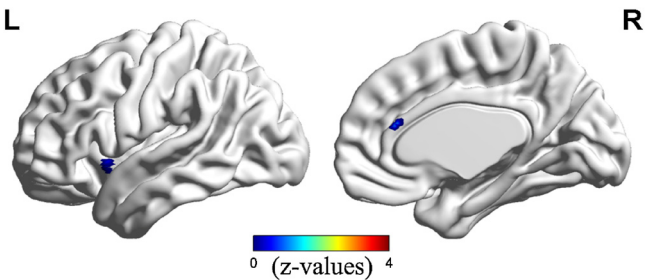
Fig. 4. Meta-analytical results of conjunction analyses (z-value). Brain regions activated by both self-face and self-referential processing.

and Fig. 2). In contrast, regions around perigenual anterior cingulate/medial prefrontal cortex were more likely to be activated by self-referential processing (Table 3 and Fig. 3).

4. Discussion

The current meta-analyses aimed at delineating the neural basis for 'physical self' judgements (to the participant's own vs. another face) and 'psychological self' judgements (when stimuli are referred

to the self rather than another person). The ALE results demonstrated that the ACC and left IFG/insula gyrus link to both self-face and self-referential processing, reflecting a common neural representation of self. In contrast the analyses specific to self-face recognition revealed a widely-distributed brain network, with the dominance of the right hemisphere, consistent with prior reviews (Devue and Brédart, 2011). The analyses in self-referential judgements showed that the CMS was associated with processing related to the 'psychological self', congruent with previous meta-analyses (Araujo et al., 2013; Murray et al., 2012; Northoff et al., 2006; Qin and Northoff, 2011). In addition, the contrast analyses also revealed effects specific to the different tasks, which we review below.

4.1. The neural representation of the physical self

The meta-analysis of facial self judgements we presented is the first comprehensive quantitative review of neuroimaging studies on this topic. The analysis revealed that a widely-distributed brain network was involved in the processing of the participant's own vs. another face, including the right IFG, the bilateral fusiform gyrus/inferior temporal gyrus, the bilateral insula, the right postcentral gyrus/supramarginal gyrus and the ACC, the right superior occipital gyrus/angular gyrus, the right inferior occipital gyrus and the left middle occipital gyrus. The right IFG, inferior temporal gyrus/fusiform gyrus, ACC and right insula lobe have previously been linked to self-face processing in a meta-analyses (Platek et al., 2008) and an ALE meta-analysis containing fewer studies than here (Veluw and Chance, 2014). Also, the present meta-analysis extended previous studies by showing the engagement of several visual processing areas (the right superior occipital gyrus/angular gyrus, the right inferior occipital gyrus, the left middle occipital gyrus) along with the right postcentral gyrus/supramarginal gyrus, and left insula lobe, putatively involved in self-representation.

In previous behavioral and neuroimaging studies, self-face recognition has been used as an index of stimulus-driven self-awareness (Gallup, 1982; Gallup et al., 2014; Veluw and Chance, 2014, though see Suddendorf and Butler, 2013, 2014). A more recent view, however, is that there is modulation of both bottom-up and top-down processes by the self, in self-face processing (Apps and Tsakiris, 2013; Legrand and Ruby, 2009; Sugiura, 2015; Sui et al., 2012). Our meta-analytic results tended to support this last view. We present three lines of support.

Firstly, we found that visual sensory cortices were more activated by the participant's own self. These results were not only found in the single ALE results, but also in the contrast analyses of the ALE results when self-referential processing was excluded: for example, the right superior occipital gyrus/angular gyrus, bilateral occipital gyrus, right postcentral gyrus/supramarginal gyrus, the left middle occipital gyrus, and the fusiform gyrus bilaterally, were all more activated by the self-face than another face (Fig. 1). Also, self-face processing specifically activated the right fusiform gyrus/inferior temporal gyrus, the right superior occipital gyrus/angular, and the right postcentral gyrus/supramarginal gyrus (Fig. 2). The involvement of the sensory cortex could be explained by the interaction of bottom-up and top-down processing. The activation of right superior occipital gyrus and the left middle occipital gyrus likely reflect stimulus-driven processing. The superior occipital gyrus includes both parts of visual cortex whilst activation of the right angular gyrus has been reported in studies of self-action perception (Farrer et al., 2008). The right occipital gyrus is also associated with location coding (Haxby et al., 1994) and sensory differentiation (Sadato et al., 2004). Importantly, the sensory cortex receives top-down modulation from higher-order cortex and sub-cortical structures, with stronger activation in the self-face than

another face condition. Behavioral studies have found that self-face can attract more attention than other stimuli (Tong and Nakayama, 1999), even when they are not targets (Devue and Brédart, 2008). EEG results have also shown that images of our own faces elicit a larger N170 component over posterior brain regions, relative to the faces of other people (Keyes et al., 2010). Other researchers have shown that brain potentials evoked by one own face are not affected by attention (Sui et al., 2006). There is however enhanced attention toward self-face images, indexed by the early anterior N2 component (Sui et al., 2012, 2013), similar to evidence on enhanced attention to reward (Anderson et al., 2011) and to in-group members (Moradi et al., 2015; Van Bavel et al., 2011).

Second, we also found that the right IFG was selectively activated by self-faces, when compared with self-referential processes. The right IFG has been consistently activated across studies of self-face processing, and researchers have proposed that the right IFG, in particular, is involved in differencing the self from others (Devue et al., 2007; Uddin et al., 2005), in self-evaluation (Morita et al., 2008), and in enhanced attention to self-related stimuli (Sugiura et al., 2000). Research on executive control shows that the IFG is part of a fronto-parietal attention network and plays an important role in cognitive inhibition (Aron et al., 2004, 2014; Hampshire et al., 2010). Here we speculate that activation of right IFG may reflect the increased demands on cognitive control when processing the self-face.

Third, the bilateral anterior insula lobe and the dorsal anterior cingulate cortex (dACC) were activated more when participants processed their own faces compared with the faces of familiar others. These brain regions were shown to be part of the CMS in previous meta-analyses of the self (Feinberg, 2011; Murray et al., 2014; Northoff et al., 2011). Interestingly, activation in these regions was not reliable when self-referential judgements were made. In addition, the anterior insula is crucial for social-emotional processing, including the processing of interoceptive information (Craig, 2009), emotional awareness (Gu et al., 2013), and empathy (Singer et al., 2009). It has also been reported that the salience network, of which the fronto-insula circuit is a core part, may compare the relative salience of different external inputs to determine which are more likely to capture attention (Uddin, 2014). Some researchers have also argued that the anterior insula may be critical for switching between the default model network (DMN) and the task network (Di and Biswal, 2014; Sridharan et al., 2008). We note too that the dACC is part of the CMS and is reported to be part of the self-related network (Murray et al., 2012). These two regions may be involved in assigning salience to the physical self (i.e., the participant's own face).

At a more general level, the current meta-analytic results showed a right dominance in self-face recognition. The lateralization of self-face processing has long been debated (Keenan and Gorman, 2007; Keenan et al., 2005; Morin, 2007). Studies on split-brain patients suggest that the left hemisphere may be critical (Morin, 2007; Turk et al., 2002). On the other hand, other neurological studies report that the right hemisphere is necessary for self-face recognition (Keenan et al., 1999, 2001) and a recent review of self-face processing has argued that the right hemisphere is particularly engaged (Devue and Brédart, 2011). The current study provides quantitative evidence for this last view.

In sum, the present meta-analytic results found that seeing our own faces activated brain regions associated with sensory processing, cognitive control and the evaluation of stimulus salience. Taken together we suggest that there is an interaction of bottom-up and top-down processing when distinguishing the physical self from the external environment. For example, that hypotheses 'suggested' by early perceptual processing of stimuli are confirmed through attentional feedback to enhance stimulus salience (see Sui and Humphreys, 2015).

4.2. The neural basis of the psychological self

For this review, the psychological self was defined by personal attributes such as personality traits, as well as autobiographical memories and experiences, and self-referential studies were used as an index. The current meta-analysis demonstrated that the psychological self was correlated with stronger activation in the anterior cingulate cortex (extending to the medial frontal cortex), the left middle frontal gyrus, the right superior temporal gyrus, the right middle frontal gyrus, the left precuneus, the left superior temporal gyrus, and the left inferior parietal lobule.

On the one hand, these results are in line with previous meta-analyses of self-related neuroimaging studies (Araujo et al., 2013; Martinelli et al., 2013; Northoff et al., 2006, 2011; Qin et al., 2012; Qin and Northoff, 2011), showing that the cortical midline structures (medial frontal gyrus/anterior cingulate gyrus, precuneus) are more activated for processing self-related stimuli compared with stimuli linked to other people. These studies, however, did not distinguish between physical and psychological aspects of the self and largely included self-referential studies in their analyses.

Besides the CMS, we also found that the middle frontal gyrus (bilaterally), the bilateral superior temporal gyrus and the left inferior parietal lobule were also more strongly activated for judgements related to the self compared with others. This again replicates prior reviews (Northoff et al., 2006; Qin and Northoff, 2011). These brain regions have been proposed to engage in higher-level cognition including working memory (Leung et al., 2002), verbal rehearsal (Bigler et al., 2007; Morosan et al., 2005) and judgements about agency (Chaminade and Decety, 2002), all of which may contribute to self-reference effects in memory (Northoff et al., 2006).

On the other hand, it should be noted that our meta-analytic results differed from the conclusions drawn from previous studies in that we found that only the 'psychological self' activated the CMS, while the 'physical self' did not. This pattern of results was confirmed in two sets of our results. Firstly, the ALE results on the psychological self converged on the perigenual anterior cingulate cortex, and the pACC/medial frontal cortex, while the physical self activated the dorsal part of the ACC. Secondly, the contrast analyses of the ALE results for the psychological and physical selves further confirmed that pACC/medial frontal cortex was specifically activated by the psychological self, but not by the physical self. These results are consistent with the findings on autistic individuals who manifest deficits related to the psychological self but not to processing of physical aspects of the self (Uddin, 2011).

The specific activation of pACC/MFC could be accounted for in several ways. First, the psychological self may reflect the internal representation of self, which is internally oriented and closely related to the default mode network. The pACC is part of a default model network (DMN), activated when people are at rest and deactivated when engaged in cognitive tasks (Biswal et al., 1995). Previous meta-analyses of self-related processing have found that the pACC is activated in both self-specific processing and the default module network (Qin and Northoff, 2011). A similar meta-analyses by Murray et al. (2012) also reported that the 'conceptual self-representation', by which they referred to abstract mental representations of personal traits, emotions, beliefs, values and attitudes (Murray et al., 2014), activated the pACC. A meta-analytic connectivity model (MACM), using the pACC as a seed area for conceptual self processing, found that this region is primarily linked with emotion and interoception (Murray et al., 2014). Therefore, the activation of the pACC/medial frontal cortex has been linked to an internal representation for conceptual aspects of the self related to emotion (Qin and Northoff, 2011).

Second, the self-referential task contains an implicit evaluation of the self, likely including an emotional evaluation of the self, which may be absent in other-referential tasks and in self-face recognition. In typical self-referential tasks, participants are asked to judge whether or not a personal trait could describe them (e.g., Fossati et al., 2003), and usually there is a bias to link positive traits toward the self (Watson et al., 2007). This self-evaluation process may involve the MFC, which has been linked with social cognitive processes (Stanley and Adolphs, 2013) including social decision making (Ruff and Fehr, 2014), emotion regulation (Winecoff et al., 2013) and moral judgements (Hu and Jiang, 2014; Shenhav and Greene, 2014). A recent theoretical account suggested that the unified role of the MFC was to assign "value" to a stimuli according to the survival of organism (Roy et al., 2012). Taken together, the specific activation of the dACC/MFC may reflect internal and evaluative aspects of the self.

In summary, our meta-analyses confirmed the role of the CMS in making psychological judgements about the self. The activation of higher-order cortical regions also confirmed the link between the psychological self and more complex aspects of cognition including the association with emotion.

4.3. The common self-representation in the brain

Our conjunction analysis found that the ACC and left IFG/insula were associated with both physical self processing and psychological self processing. These results are compatible with the "supramodularity" view of CMS, which suggests that the CMS is activated by self-referential stimuli regardless of the sensory modality (Northoff et al., 2006). Gillihan and Farah (2005) concluded that the neuroimaging evidence for a specific neural system for self-face recognition was mixed and the evidence for neural specificity of the psychological self was even more complicated. The current meta-analyses however showed that processing of the physical and psychological self activated common neural networks (the ACC, left IFG and insula), suggesting a core self-representation in the brain.

The left insula is thought to play an important role in self-awareness. It has been reported that the anterior insula is specifically associated with self-processing (Northoff et al., 2011), and creating internal bodily self-representations (Feinberg, 2011). A recent meta-analyses found that insula, particularly the anterior sections, was crucial in self-agency (Sperduti et al., 2011). Prior meta-analytic connectivity modeling has also shown that the insula is segregated into different subdivisions and the interior-ventral parts are correlated with social-emotional tasks (Kurth et al., 2010; Uddin et al., 2013).

As noted in Section 1, a recent neuropsychological study has also reported that a patient with damage to the ACC and left IFG/insula lesions failed to show self-biased responses in memory as well as in perceptual matching (Sui et al., in press). The data indicate that the ACC and left IFG/insula are associated with a common self-representation. Damage to these regions consequently leads to common cognitive impairments in self-processing. This is also consistent with the idea that the activation of self-representations generates a central integrative function in information processing, enhancing binding within perception and memory and also linking perceptual to memorial processes (Sui and Humphreys, 2015). We propose that access to a core self-representation, accessed across different tasks and responding to both physical and psychological aspects of the self, serves this integrative function.

4.4. Limitation

Several limitations of the current study should be noted. First, meta-analyses are necessarily based on the available literature and

hence may be affected by the potential publication-bias disfavoring null results (Jennings and Horn, 2012). Second, to set a clear standard to select studies, we used narrow definitions for both the physical and the psychological self.

Related to the physical self, only self-face recognition studies were included as indices of physical self judgements while body-recognition and self-agency were excluded. Studies on self-agency were excluded because they are associated with the psychological self as well as the physical self (Gillihan and Farah, 2005), and could not be classified as the representation of the physical self only. Another line of research on the psychical self concerns self embodiment, for example studies on the rubber hand illusion (e.g. Tsakiris et al., 2007). These studies were not covered because this type of research typically deals with the relations between body-recognition, self-agency and first-person perspective coding (Tsakiris et al., 2010), going beyond representation of the physical self per se. In addition, we would assume that to include the research in self-body recognition (excluding the rubber hand illusions) would not change the results of present study, because both self-body recognition and self-face recognition recruit the right frontal cortex and insula lobe (Devue et al., 2007). However, if we included studies on self-body recognition, then sensorimotor areas would be involved due to the representation of the self-body being co-activated due to associated body movement (Ferri et al., 2012; Tsakiris, 2010), this is out of the scope of the current study.

As to the psychological self, we only included studies using self-reference judgements while first person perspective judgements were excluded, in order to stress the significance of self-referential processing for the psychological self (Northoff, 2015; Northoff and Bermpohl, 2004), while eliminating ambiguity of definition between these two aspects (Gillihan and Farah, 2005). Previous meta-analyses have found that different autobiographic memory systems all activate the MPFC, though they typically involve distinct parts of the MPFC (Martinelli et al., 2013; Svoboda et al., 2006). Other self-related studies, demanding self-regulation and self-movement were not included either, because they are not directly associated with self-representation. Moreover, we did not further distinguish the different control conditions used to contrast with self processing, i.e., self vs. close other and self vs. non-close others. Therefore, we did not further consider whether any self-related effects were domain-specific or reflected a more general factor such as stimulus familiarity. However, the results in the current study are consistent with previous meta-analyses demonstrating that the self vs. close other also activated the CMS (Araujo et al., 2013). Future studies could be more inclusive and further specify the contrast (e.g., between the self and others) to delineate the neural correlates of self.

5. Conclusion

A self-concept is central to our lives, and we may build-up different aspects of the self through our lives. The present meta-analytic review found that face-based judgements about the physical self activated the cortex responsible for sensory processing, cognitive control and the evaluation of stimulus salience, suggesting an interaction of bottom-up and top-down processing when distinguishing the physical self from the external environment. In contrast to this, self-reference judgements (judgements about the psychological self) activated both the CMS and higher-level cortical regions, indicating the internal and evaluative nature of the psychological self. Moreover, the physical and psychological selves both activated the ACC and left IFG/insula supporting the idea of a core self-representation in the brain.

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.2015.12.003.

References

Anderson, B.A., Laurent, P.A., Yantis, S., 2011. Value-driven attentional capture. Proc. Natl. Acad. Sci. U. S. A. 108 (25), 10367–10371, http://dx.doi.org/10.1073/pnas.1104047108.

Apps, M.A.J., Tajadura-Jiménez, A., Sereno, M., Blanke, O., Tsakiris, M., 2015. Plasticity in unimodal and multimodal brain areas reflects multisensory changes in self-face identification. Cereb. Cortex 25 (1), 46–55, http://dx.doi.org/10.1093/cercor/bht199.

Apps, M.A.J., Tsakiris, M., 2013. The free-energy self: a predictive coding account of self-recognition. Neurosci. Biobehav. Rev. 41, 85–97, http://dx.doi.org/10.1016/j.neubiorev.2013.01.029.

Araujo, H.F., Kaplan, J., Damasio, A., 2013. Cortical midline structures and autobiographical-self processes: an activation-likelihood estimation (ALE) meta-analysis. Front. Hum. Neurosci. 7, http://dx.doi.org/10.3389/fnhum.2013.00548.

Aron, A.R., Robbins, T.W., Poldrack, R.A., 2004. Inhibition and the right inferior frontal cortex. Trends Cogn. Sci. 8 (4), 170–177, http://dx.doi.org/10.1016/j.tics.2004.02.010.

Aron, A.R., Robbins, T.W., Poldrack, R.A., 2014. Inhibition and the right inferior frontal cortex: one decade on. Trends Cogn. Sci. 18 (4), 177–185, http://dx.doi.org/10.1016/j.tics.2013.12.003.

Bigler, E.D., Mortensen, S., Neeley, E.S., Ozonoff, S., Krasny, L., Johnson, M., Lu, J., Provencal, S.L., McMahon, W., Lainhart, J.E., 2007. Superior temporal gyrus, language function, and autism. Dev. Neuropsychol. 31 (2), 217–238, http://dx.doi.org/10.1080/87565640701190841.

Biswal, B., Yetkin, F.Z., Haughton, V.M., Hyde, J.S., 1995. Functional connectivity in the motor cortex of resting human brain using echo-planar MRI. Magn. Reson. Med. 34 (4), 537–541, http://dx.doi.org/10.1002/mrm.1910340409.

Cabeza, R., St Jacques, P., 2007. Functional neuroimaging of autobiographical memory. Trends Cogn. Sci. 11 (5), 219–227, http://dx.doi.org/10.1016/j.tics.2007.02.005.

Chaminade, T., Decety, J., 2002. Leader or follower? Involvement of the inferior parietal lobule in agency. NeuroReport 13 (15), 1975–1978.

Craig, A.D., 2009. How do you feel – now? The anterior insula and human awareness. Nat. Rev. Neurosci. 10 (1), 59–70, http://dx.doi.org/10.1038/nrn2555.

Devue, C., Brédart, S., 2008. Attention to self-referential stimuli: can I ignore my own face? Acta Psychol. 128 (2), 290–297, http://dx.doi.org/10.1016/j.actpsy.2008.02.004.

Devue, C., Brédart, S., 2011. The neural correlates of visual self-recognition. Conscious. Cogn. 20 (1), 40–51, http://dx.doi.org/10.1016/j.concog.2010.09.007.

Devue, C., Collette, F., Balteau, E., Degueldre, C., Luxen, A., Maquet, P., Brédart, S., 2007. Here I am: the cortical correlates of visual self-recognition. Brain Res. 1143, 169–182, http://dx.doi.org/10.1016/j.brainres.2007.01.055.

Di, X., Biswal, B.B., 2014. Modulatory interactions between the default mode network and task positive networks in resting-state. PeerJ 2, e367, http://dx.doi.org/10.7717/peerj.367.

Eickhoff, S.B., Bzdok, D., Laird, A.R., Kurth, F., Fox, P.T., 2012. Activation likelihood estimation meta-analysis revisited. NeuroImage 59 (3), 2349–2361, http://dx.doi.org/10.1016/j.neuroimage.2011.09.017.

Eickhoff, S.B., Bzdok, D., Laird, A.R., Roski, C., Caspers, S., Zilles, K., Fox, P.T., 2011. Co-activation patterns distinguish cortical modules, their connectivity and functional differentiation. NeuroImage 57 (3), 938–949, http://dx.doi.org/10.1016/j.neuroimage.2011.05.021.

Eickhoff, S.B., Heim, S., Zilles, K., Amunts, K., 2006. Testing anatomically specified hypotheses in functional imaging using cytoarchitectonic maps. NeuroImage 32 (2), 570–582, http://dx.doi.org/10.1016/j.neuroimage.2006.04.204.

Eickhoff, S.B., Laird, A.R., Grefkes, C., Wang, L.E., Zilles, K., Fox, P.T., 2009. Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: a random-effects approach based on empirical estimates of spatial uncertainty. Hum. Brain Mapp. 30 (9), 2907–2926, http://dx.doi.org/10.1002/hbm.20718.

Eickhoff, S.B., Paus, T., Caspers, S., Grosbras, M.-H., Evans, A.C., Zilles, K., Amunts, K., 2007. Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. NeuroImage 36 (3), 511–521, http://dx.doi.org/10.1016/j.neuroimage.2007.03.060.

Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. NeuroImage 25 (4), 1325–1335, http://dx.doi.org/10.1016/j.neuroimage.2004.12.034.

Farrer, C., Frey, S.H., Van Horn, J.D., Tunik, E., Turk, D., Inati, S., Grafton, S.T., 2008. The angular gyrus computes action awareness representations. Cereb. Cortex 18 (2), 254–261, http://dx.doi.org/10.1093/cercor/bhm050.

Feinberg, T.E., 2011. The nested neural hierarchy and the self. Conscious. Cogn. 20 (1), 4–15, http://dx.doi.org/10.1016/j.concog.2010.09.016.

Ferri, F., Frassinetti, F., Ardizzi, M., Costantini, M., Gallese, V., 2012. A sensorimotor network for the bodily self. J. Cogn. Neurosci. 24 (7), 1584–1595, http://dx.doi.org/10.1162/jocn_a_00230.

Fossati, P., Hevenor, S.J., Graham, S.J., Grady, C., Keightley, M.L., Craik, F., Mayberg, H., 2003. In search of the emotional self: an fMRI study using positive and negative emotional words. Am. J. Psychiatry 160 (11), 1938–1945, http://dx.doi.org/10.1176/appi.ajp.160.11.1938.

Fox, P.T., Lancaster, J.L., Laird, A.R., Eickhoff, S.B., 2014. Meta-analysis in human neuroimaging: computational modeling of large-scale databases. Annu. Rev. Neurosci. 37 (1), 409–434, http://dx.doi.org/10.1146/annurev-neuro-062012-170320.

Gallup Jr., G.G., 1970. Chimpanzees: self-recognition. Science 167 (3914), 86–87, http://dx.doi.org/10.1126/science.167.3914.86.

Gallup Jr., G.G., 1982. Self-awareness and the emergence of mind in primates. Am. J. Primatol. 2 (3), 237–248, http://dx.doi.org/10.1002/ajp.1350020302.

Gallup Jr., G.G., Platek, S.M., Spaulding, K.L., 2014. The nature of visual self-recognition revisited. Trends Cogn. Sci. 18 (2), 57–58, http://dx.doi.org/10.1016/j.tics.2013.10.012.

Gillihan, S.J., Farah, M.J., 2005. Is self special? A critical review of evidence from experimental psychology and cognitive neuroscience. Psychol. Bull. 131 (1), 76–97, http://dx.doi.org/10.1037/0033-2909.131.1.76.

Gu, X., Hof, P.R., Friston, K.J., Fan, J., 2013. Anterior insular cortex and emotional awareness. J. Comp. Neurol. 521 (15), 3371–3388, http://dx.doi.org/10.1002/cne.23368.

Gusnard, D.A., Akbudak, E., Shulman, G.L., Raichle, M.E., 2001. Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. Proc. Natl. Acad. Sci. U. S. A. 98 (7), 4259–4264, http://dx.doi.org/10.1073/pnas.071043098.

Hampshire, A., Chamberlain, S.R., Monti, M.M., Duncan, J., Owen, A.M., 2010. The role of the right inferior frontal gyrus: inhibition and attentional control. NeuroImage 50 (3), 1313–1319, http://dx.doi.org/10.1016/j.neuroimage.2009.12.109.

Haxby, J., Horwitz, B., Ungerleider, L., Maisog, J., Pietrini, P., Grady, C., 1994. The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. J. Neurosci. 14 (11), 6336–6353.

Hu, C., Jiang, X., 2014. An emotion regulation role of ventromedial prefrontal cortex in moral judgment. Front. Hum. Neurosci. 8, http://dx.doi.org/10.3389/fnhum.2014.00873.

James, W., 1890. The Principles of Psychology. New York, Henry Holt.

Jennings, R., Horn, J., 2012. Publication bias in neuroimaging research: implications for meta-analyses. Neuroinformatics 10 (1), 67–80, http://dx.doi.org/10.1007/s12021-011-9125-y.

Keenan, J.P., Gorman, J., 2007. The causal role of the right hemisphere in self-awareness: it is the brain that is selective. Cortex 43 (8), 1074–1082, http://dx.doi.org/10.1016/S0010-9452(08)70705-6.

Keenan, J.P., McCutcheon, B., Freund, S., Gallup Jr., G.G., Sanders, G., Pascual-Leone, A., 1999. Left hand advantage in a self-face recognition task. Neuropsychologia 37 (12), 1421–1425, http://dx.doi.org/10.1016/S0028-3932(99)00025-1.

Keenan, J.P., Nelson, A., O'Connor, M., Pascual-Leone, A., 2001. Neurology: self-recognition and the right hemisphere. Nature 409 (6818), 305, http://dx.doi.org/10.1038/35053167.

Keenan, J.P., Rubio, J., Racioppi, C., Johnson, A., Barnacz, A., 2005. The right hemisphere and the dark side of consciousness. Cortex 41 (5), 695–704, http://dx.doi.org/10.1016/S0010-9452(08)70286-7.

Kelley, W.M., Macrae, C.N., Wyland, C.L., Caglar, S., Inati, S., Heatherton, T.F., 2002. Finding the self? An event-related fMRI study. J. Cogn. Neurosci. 14 (5), 785–794, http://dx.doi.org/10.1162/08989290260138672.

Ketay, S., Hamilton, H.K., Haas, B.W., Simeon, D., 2014. Face processing in depersonalization: an fMRI study of the unfamiliar self. Psychiatry Res.: Neuroimaging 222 (1), 107–110, http://dx.doi.org/10.1016/j.pscychresns.2014.02.003.

Keyes, H., Brady, N., Reilly, R.B., Foxe, J.J., 2010. My face or yours? Event-related potential correlates of self-face processing. Brain Cogn. 72 (2), 244–254, http://dx.doi.org/10.1016/j.bandc.2009.09.006.

Kim, H., 2012. A dual-subsystem model of the brain's default network: self-referential processing, memory retrieval processes, and autobiographical memory retrieval. NeuroImage 61 (4), 966–977, http://dx.doi.org/10.1016/j.neuroimage.2012.03.025.

Kircher, T.T.J., Senior, C., Phillips, M.L., Benson, P.J., Bullmore, E.T., Brammer, M., Simmons, A., Williams, S.C., Bartels, M., David, A.S., 2000. Towards a functional neuroanatomy of self processing: effects of faces and words. Cogn. Brain Res. 10 (1–2), 133–144, http://dx.doi.org/10.1016/S0926-6410(00)00036-7.

Kircher, T.T.J., Senior, C., Phillips, M.L., Rabe-Hesketh, S., Benson, P.J., Bullmore, E.T., Brammer, M., Simmons, A., Bartels, M., David, A.S., 2001. Recognizing one's own face. Cognition 78 (1), B1–B15, http://dx.doi.org/10.1016/S0010-0277(00)00104-9.

Knoblich, G., 2002. Self-recognition: body and action. Trends Cogn. Sci. 6 (11), 447–449, http://dx.doi.org/10.1016/S1364-6613(02)01995-2.

Kurth, F., Zilles, K., Fox, P., Laird, A., Eickhoff, S., 2010. A link between the systems: functional differentiation and integration within the human insula revealed by meta-analysis. Brain Struct. Funct. 214 (5–6), 519–534, http://dx.doi.org/10.1007/s00429-010-0255-z.

Laird, A.R., Eickhoff, S., Fox, P.M., Uecker, A., Ray, K., Saenz, J., McKay, D.R., Bzdok, D., Laird, R.W., Robinson, J.L., Turner, J.A., Turkeltaub, P.E., Lancaster, J.L., Fox, P.T., 2011. The BrainMap strategy for standardization, sharing, and meta-analysis of neuroimaging data. BMC Res. Notes 4 (1), 349, http://dx.doi.org/10.1186/1756-0500-4-349.

Laird, A.R., Eickhoff, S.B., Kurth, F., Fox, P.M., Uecker, A.M., Turner, J.A., Robinson, J.L., Lancaster, J.L., Fox, P.T., 2009a. ALE meta-analysis workflows via the Brain-Map database: progress towards a probabilistic functional brain atlas. Front. Neuroinform. 3, http://dx.doi.org/10.3389/neuro.11.023.2009.

Laird, A.R., Lancaster, J.L., Fox, P.T., 2009b. Lost in localization? The focus is meta-analysis. NeuroImage 48 (1), 18–20, http://dx.doi.org/10.1016/j.neuroimage.2009.06.047.

Lancaster, J.L., Tordesillas-Gutiérrez, D., Martinez, M., Salinas, F., Evans, A., Zilles, K., Mazziotta, J.C., Fox, P.T., 2007. Bias between MNI and Talairach coordinates analyzed using the ICBM-152 brain template. Hum. Brain Mapp. 28 (11), 1194–1205, http://dx.doi.org/10.1002/hbm.20345.

Legrand, D., Ruby, P., 2009. What is self-specific? Theoretical investigation and critical review of neuroimaging results. Psychol. Rev. 116 (1), 252–282, http://dx.doi.org/10.1037/a0014172.

Leshikar, E., Duarte, A., 2014. Medial prefrontal cortex supports source memory for self-referenced materials in young and older adults. Cogn. Affect. Behav. Neurosci. 14 (1), 236–252, http://dx.doi.org/10.3758/s13415-013-0198-y.

Leung, H.C., Gore, J.C., Goldman-Rakic, P.S., 2002. Sustained mnemonic response in the human middle frontal gyrus during on-line storage of spatial memoranda. J. Cogn. Neurosci. 14 (4), 659–671, http://dx.doi.org/10.1162/08989290260045882.

Martinelli, P., Sperduti, M., Piolino, P., 2013. Neural substrates of the self-memory system: new insights from a meta-analysis. Hum. Brain Mapp. 34 (7), 1515–1529, http://dx.doi.org/10.1002/hbm.22008.

Moradi, Z., Sui, J., Hewstone, M., Humphreys, G., 2015. In-group modulation of perceptual matching. Psychon. Bull. Rev., 1–23, http://dx.doi.org/10.3758/s13423-014-0798-8.

Morin, A., 2007. Self-awareness and the left hemisphere: the dark side of selectively reviewing the literature. Cortex 43 (8), 1068–1073, http://dx.doi.org/10.1016/S0010-9452(08)70704-4.

Morita, T., Itakura, S., Saito, D.N., Nakashita, S., Harada, T., Kochiyama, T., Sadato, N., 2008. The role of the right prefrontal cortex in self-evaluation of the face: a functional magnetic resonance imaging study. J. Cogn. Neurosci. 20 (2), 342–355, http://dx.doi.org/10.1162/jocn.2008.20024.

Morosan, P., Schleicher, A., Amunts, K., Zilles, K., 2005. Multimodal architectonic mapping of human superior temporal gyrus. Anat. Embryol. 210 (5–6), 401–406, http://dx.doi.org/10.1007/s00429-005-0029-1.

Murray, R.J., Debbané, M., Fox, P.T., Bzdok, D., Eickhoff, S.B., 2014. Functional connectivity mapping of regions associated with self- and other-processing. Hum. Brain Mapp., http://dx.doi.org/10.1002/hbm.22703.

Murray, R.J., Schaer, M., Debbané, M., 2012. Degrees of separation: a quantitative neuroimaging meta-analysis investigating self-specificity and shared neural activation between self- and other-reflection. Neurosci. Biobehav. Rev. 36 (3), 1043–1059, http://dx.doi.org/10.1016/j.neubiorev.2011.12.013.

Nichols, T., Brett, M., Andersson, J., Wager, T., Poline, J.-B., 2005. Valid conjunction inference with the minimum statistic. NeuroImage 25 (3), 653–660, http://dx.doi.org/10.1016/j.neuroimage.2004.12.005.

Northoff, G., 2011. Self and brain: what is self-related processing? Trends Cogn. Sci. 15 (5), 186–187, http://dx.doi.org/10.1016/j.tics.2011.03.001.

Northoff, G., 2015. Is the self a higher-order or fundamental function of the brain? The "basis model of self-specificity" and its encoding by the brain's spontaneous activity. Cogn. Neurosci., http://dx.doi.org/10.1080/17588928.2015.1111868.

Northoff, G., Bermpohl, F., 2004. Cortical midline structures and the self. Trends Cogn. Sci. 8 (3), 102–107, http://dx.doi.org/10.1016/j.tics.2004.01.004.

Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., Panksepp, J., 2006. Self-referential processing in our brain—a meta-analysis of imaging studies on the self. NeuroImage 31 (1), 440–457, http://dx.doi.org/10.1016/j.neuroimage.2005.12.002.

Northoff, G., Qin, P., Feinberg, T.E., 2011. Brain imaging of the self – conceptual, anatomical and methodological issues. Conscious. Cogn. 20 (1), 52–63, http://dx.doi.org/10.1016/j.concog.2010.09.011.

Platek, S.M., Krill, A.L., 2009. Self-face resemblance attenuates other-race face effect in the amygdala. Brain Res. 1284, 156–160, http://dx.doi.org/10.1016/j.brainres.2009.05.076.

Platek, S.M., Loughead, J.W., Gur, R.C., Busch, S., Ruparel, K., Phend, N., Panyavin, I.S., Langleben, D.D., 2006. Neural substrates for functionally discriminating self-face from personally familiar faces. Hum. Brain Mapp. 27 (2), 91–98, http://dx.doi.org/10.1002/hbm.20168.

Platek, S.M., Wathne, K., Tierney, N.G., Thomson, J.W., 2008. Neural correlates of self-face recognition: an effect-location meta-analysis. Brain Res. 1232, 173–184, http://dx.doi.org/10.1016/j.brainres.2008.07.010.

Qin, P., Liu, Y., Shi, J., Wang, Y., Duncan, N., Gong, Q., Weng, X., Northoff, G., 2012. Dissociation between anterior and posterior cortical regions during self-specificity and familiarity: a combined fMRI–meta-analytic study. Hum. Brain Mapp. 33 (1), 154–164, http://dx.doi.org/10.1002/hbm.21201.

Qin, P., Northoff, G., 2011. How is our self related to midline regions and the default-mode network? NeuroImage 57 (3), 1221–1233, http://dx.doi.org/10.1016/j.neuroimage.2011.05.028.

Rogers, T.B., Kuiper, N.A., Kirker, W.S., 1977. Self-reference and the encoding of personal information. J. Personal. Soc. Psychol. 35 (9), 677–688, http://dx.doi.org/10.1037/0022-3514.35.9.677.

Rottschy, C., Langner, R., Dogan, I., Reetz, K., Laird, A.R., Schulz, J.B., Fox, P.T., Eickhoff, S.B., 2012. Modelling neural correlates of working memory: a coordinate-based meta-analysis. NeuroImage 60 (1), 830–846, http://dx.doi.org/10.1016/j.neuroimage.2011.11.050.

Roy, M., Shohamy, D., Wager, T.D., 2012. Ventromedial prefrontal-subcortical systems and the generation of affective meaning. Trends Cogn. Sci. 16 (3), 147–156, http://dx.doi.org/10.1016/j.tics.2012.01.005.

Ruff, C.C., Fehr, E., 2014. The neurobiology of rewards and values in social decision making. Nat. Rev. Neurosci., http://dx.doi.org/10.1038/nrn3776 (advance online publication).

Sadato, N., Okada, T., Kubota, K., Yonekura, Y., 2004. Tactile discrimination activates the visual cortex of the recently blind naive to Braille: a functional magnetic resonance imaging study in humans. Neurosci. Lett. 359 (1–2), 49–52, http://dx.doi.org/10.1016/j.neulet.2004.02.005.

Schmitz, T.W., Johnson, S.C., 2007. Relevance to self: a brief review and framework of neural systems underlying appraisal. Neurosci. Biobehav. Rev. 31 (4), 585–596, http://dx.doi.org/10.1016/j.neubiorev.2006.12.003.

Shenhav, A., Greene, J.D., 2014. Integrative moral judgment: dissociating the roles of the amygdala and ventromedial prefrontal cortex. J. Neurosci. 34 (13), 4741–4749, http://dx.doi.org/10.1523/JNEUROSCI.3390-13.2014.

Singer, T., Critchley, H.D., Preuschoff, K., 2009. A common role of insula in feelings, empathy and uncertainty. Trends Cogn. Sci. 13 (8), 334–340, http://dx.doi.org/10.1016/j.tics.2009.05.001.

Sperduti, M., Delaveau, P., Fossati, P., Nadel, J., 2011. Different brain structures related to self- and external-agency attribution: a brief review and meta-analysis. Brain Struct. Funct. 216 (2), 151–157, http://dx.doi.org/10.1007/s00429-010-0298-1.

Spreng, R.N., Mar, R.A., Kim, A.S.N., 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. J. Cogn. Neurosci. 21 (3), 489–510, http://dx.doi.org/10.1162/jocn.2008.21029.

Sridharan, D., Levitin, D.J., Menon, V., 2008. A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. Proc. Natl. Acad. Sci. U. S. A. 105 (34), 12569–12574, http://dx.doi.org/10.1073/pnas.0800005105.

Stanley, D.A., Adolphs, R., 2013. Toward a neural basis for social behavior. Neuron 80 (3), 816–826, http://dx.doi.org/10.1016/j.neuron.2013.10.038.

Suddendorf, T., Butler, D.L., 2013. The nature of visual self-recognition. Trends Cogn. Sci. 17 (3), 121–127, http://dx.doi.org/10.1016/j.tics.2013.01.004.

Suddendorf, T., Butler, D.L., 2014. Are rich interpretations of visual self-recognition a bit too rich? Trends Cogn. Sci. 18 (2), 58–59, http://dx.doi.org/10.1016/j.tics.2013.11.004.

Suddendorf, T., Collier-Baker, E., 2009. The evolution of primate visual self-recognition: evidence of absence in lesser apes. Proc. R. Soc. B: Biol. Sci. 276 (1662), 1671–1677, http://dx.doi.org/10.1098/rspb.2008.1754.

Sugiura, M., 2013. Associative account of self-cognition: extended forward model and multi-layer structure. Front. Hum. Neurosci. 7, http://dx.doi.org/10.3389/fnhum.2013.00535.

Sugiura, M., 2015. Three faces of self-face recognition: potential for a multi-dimensional diagnostic tool. Neurosci. Res. 90, 56–64, http://dx.doi.org/10.1016/j.neures.2014.10.002.

Sugiura, M., Kawashima, R., Nakamura, K., Okada, K., Kato, T., Nakamura, A., Hatano, K., Itoh, K., Kojima, S., Fukuda, H., 2000. Passive and active recognition of one's own face. NeuroImage 11 (1), 36–48, http://dx.doi.org/10.1006/nimg.1999.0519.

Sugiura, M., Watanabe, J., Maeda, Y., Matsue, Y., Fukuda, H., Kawashima, R., 2005. Cortical mechanisms of visual self-recognition. NeuroImage 24 (1), 143–149, http://dx.doi.org/10.1016/j.neuroimage.2004.07.063.

Sui, J., Enock, F., Ralph, J., Humphreys, G.W., 2015. Dissociating hyper and hypoself biases to a core self-representation. Cortex, http://dx.doi.org/10.1016/j.cortex.2015.04.024 (in press).

Sui, J., He, X., Humphreys, G.W., 2012. Perceptual effects of social salience: evidence from self-prioritization effects on perceptual matching. J. Exp. Psychol.: Hum. Percept. Perform. 38 (5), 1105–1117, http://dx.doi.org/10.1037/a0029792.

Sui, J., Humphreys, G.W., 2015. The integrative self: how self-reference integrates perception and memory. Trends Cogn. Sci., http://dx.doi.org/10.1016/j.tics.2015.08.015.

Sui, J., Rotshtein, P., Humphreys, G.W., 2013. Coupling social attention to the self forms a network for personal significance. Proc. Natl. Acad. Sci. U. S. A. 110 (19), 7607–7612, http://dx.doi.org/10.1073/pnas.1221862110.

Sui, J., Zhu, Y., Han, S., 2006. Self-face recognition in attended and unattended conditions: an event-related brain potential study. NeuroReport 17 (4), 423–427, http://dx.doi.org/10.1097/01.wnr.0000203357.65190.61.

Svoboda, E., McKinnon, M.C., Levine, B., 2006. The functional neuroanatomy of autobiographical memory: a meta-analysis. Neuropsychologia 44 (12), 2189–2208, http://dx.doi.org/10.1016/j.neuropsychologia.2006.05.023.

Tong, F., Nakayama, K., 1999. Robust representations for faces: evidence from visual search. J. Exp. Psychol.: Hum. Percept. Perform. 25 (4), 1016–1035, http://dx.doi.org/10.1037/0096-1523.25.4.1016.

Tsakiris, M., 2008. Looking for myself: current multisensory input alters self-face recognition. PLoS ONE 3 (12), e4040, http://dx.doi.org/10.1371/journal.pone.0004040.

Tsakiris, M., 2010. My body in the brain: a neurocognitive model of body-ownership. Neuropsychologia 48 (3), 703–712, http://dx.doi.org/10.1016/j.neuropsychologia.2009.09.034.

Tsakiris, M., Hesse, M.D., Boy, C., Haggard, P., Fink, G.R., 2007. Neural signatures of body ownership: a sensory network for bodily self-consciousness. Cereb. Cortex 17 (10), 2235–2244, http://dx.doi.org/10.1093/cercor/bhl131.

Tsakiris, M., Longo, M.R., Haggard, P., 2010. Having a body versus moving your body: neural signatures of agency and body-ownership. Neuropsychologia 48 (9), 2740–2749, http://dx.doi.org/10.1016/j.neuropsychologia.2010.05.021.

Turk, D.J., Heatherton, T.F., Kelley, W.M., Funnell, M.G., Gazzaniga, M.S., Macrae, C.N., 2002. Mike or me? Self-recognition in a split-brain patient. Nat. Neurosci. 5 (9), 841–842, http://dx.doi.org/10.1038/nn907.

Turkeltaub, P.E., Eden, G.F., Jones, K.M., Zeffiro, T.A., 2002. Meta-analysis of the functional neuroanatomy of single-word reading: method and validation. NeuroImage 16 (3), 765–780, http://dx.doi.org/10.1006/nimg.2002.1131.

Turkeltaub, P.E., Eickhoff, S.B., Laird, A.R., Fox, M., Wiener, M., Fox, P., 2012. Minimizing within-experiment and within-group effects in activation likelihood estimation meta-analyses. Hum. Brain Mapp. 33 (1), 1–13, http://dx.doi.org/10.1002/hbm.21186.

Uddin, L.Q., 2011. The self in autism: an emerging view from neuroimaging. Neurocase 17 (3), 201–208, http://dx.doi.org/10.1080/13554794.2010.509320.

Uddin, L.Q., 2014. Salience processing and insular cortical function and dysfunction. Nat. Rev. Neurosci., http://dx.doi.org/10.1038/nrn3857 (advance online publication).

Uddin, L.Q., Kaplan, J.T., Molnar-Szakacs, I., Zaidel, E., Iacoboni, M., 2005. Self-face recognition activates a frontoparietal "mirror" network in the right hemisphere: an event-related fMRI study. NeuroImage 25 (3), 926–935, http://dx.doi.org/10.1016/j.neuroimage.2004.12.018.

Uddin, L.Q., Kinnison, J., Pessoa, L., Anderson, M.L., 2013. Beyond the tripartite cognition–emotion–interoception model of the human insular cortex. J. Cogn. Neurosci., 1–12, http://dx.doi.org/10.1162/jocn_a_00462.

Van Bavel, J.J., Packer, D.J., Cunningham, W.A., 2011. Modulation of the fusiform face area following minimal exposure to motivationally relevant faces: evidence of in-group enhancement (not out-group disregard). J. Cogn. Neurosci. 23 (11), 3343–3354, http://dx.doi.org/10.1162/jocn_a_00016.

van der Meer, L., Costafreda, S., Aleman, A., David, A.S., 2010. Self-reflection and the brain: a theoretical review and meta-analysis of neuroimaging studies with implications for schizophrenia. Neurosci. Biobehav. Rev. 34 (6), 935–946, http://dx.doi.org/10.1016/j.neubiorev.2009.12.004.

Veluw, S., Chance, S., 2014. Differentiating between self and others: an ALE meta-analysis of fMRI studies of self-recognition and theory of mind. Brain Imaging Behav. 8 (1), 24–38, http://dx.doi.org/10.1007/s11682-013-9266-8.

Watson, L.A., Dritschel, B., Obonsawin, M.C., Jentzsch, I., 2007. Seeing yourself in a positive light: brain correlates of the self-positivity bias. Brain Res. 1152, 106–110, http://dx.doi.org/10.1016/j.brainres.2007.03.049.

Winecoff, A., Clithero, J.A., Carter, R.M., Bergman, S.R., Wang, L., Huettel, S.A., 2013. Ventromedial prefrontal cortex encodes emotional value. J. Neurosci. 33 (27), 11032–11039, http://dx.doi.org/10.1523/jneurosci.4317-12.2013.

Xia, M., Wang, J., He, Y., 2013. BrainNet Viewer: a network visualization tool for human brain connectomics. PLOS ONE 8 (7), e68910, http://dx.doi.org/10.1371/journal.pone.0068910.

Yoshimura, S., Okamoto, Y., Onoda, K., Matsunaga, M., Okada, G., Kunisato, Y., Yoshino, A., Ueda, K., Suzuki, S., Yamawaki, S., 2014. Cognitive behavioral therapy for depression changes medial prefrontal and ventral anterior cingulate cortex activity associated with self-referential processing. Soc. Cogn. Affect. Neurosci. 9 (4), 487–493, http://dx.doi.org/10.1093/scan/nst009.

Yuan, C., Zhang, Z., Wang, Z., Liao, W., Chen, G., Northoff, G., Lu, G., 2013. Impaired self-referential processing in mesial temporal lobe epilepsy: a functional MRI study. Neurosci. Lett. 555, 187–192, http://dx.doi.org/10.1016/j.neulet.2013.09.054.