

## Different brain structures related to self- and external-agency attribution: a brief review and meta-analysis

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**Abstract** Several neuroimaging studies have consistently shown activations of areas surrounding the temporo-parietal junction (TPJ) during tasks exploring the sense of agency. Beyond TPJ, activations in different structures, such as the dorsolateral prefrontal cortex (dLPFC), the pre-supplementary motor area (pre-SMA), the insula and the precuneus have been reported. Moreover, a possible dissociation between self- and external-agency attribution has been suggested. To test the hypothesis of distinct neural correlates for self- and external-agency attribution a quantitative meta-analysis, based on activation likelihood estimation (ALE) method, across 15 PET and fMRI studies (228 subjects) was conducted. Results show converging activations including the TPJ, pre-SMA, precuneus and dorsomedial prefrontal cortex (dMPFC) in external-agency, while insula activation was related to self-agency. We discuss these findings, highlighting the role of the insula, and calling for the use of alternative paradigms such as intentional binding and interactive imitation to study agency.

**Keywords** Agency · Insula · fMRI · PET · Meta-analysis

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### Introduction

A growing number of neuroimaging studies explore the brain correlates of self- and other-agency. Self-agency is a fundamental process and a basic step to draw a primary distinction between self-monitored and externally caused events. As such it is involved in any kind of self-environment exchange, and especially in social interaction, where correctly attributing the origin of an action to self or to others covers a primary role in regulating efficiently an interaction.

However, the tasks designed rarely allow discriminating a sense of self-agency from the sense of other-agency (Gallagher 2007). Indeed, they are mostly inspired by the comparator model, firstly proposed to account for sensorimotor control (Wolpert et al. 1995; Wolpert and Miall 1996) and later extended as a cognitive model of agency (Frith et al. 2000). The comparator methodology compares two conditions: intact visual perception of own movements and manipulated perception. The model states that to reach a certain goal the motor system specifies a sequence of motor commands. An efferent copy of these commands is used to build a forward model that predicts the next state of the system. Reafferent sensory inputs are used to estimate the actual state of the system. The actual and predicted states are then compared. In case of congruency between predicted and actual states, agency is attributed to self, on the contrary, if incongruence is detected, the origin of the action is attributed to an external causation. The objection by Tsakiris and Haggard (2005) is that the task requires active movements in the two conditions, thus preventing to address self-ownership.

Several neuroimaging experiments have been conducted within this framework to assess the neural correlates of the sense of agency. Most of these studies have manipulated

the action–effect coupling by systematically varying the delay (Leube et al. 2003a), the morphology (David et al. 2007; Farrer et al. 2003) or the congruence (Farrer and Frith 2002; Kontaris et al. 2009) of the visual feedback. By doing so they disrupt the sense of self-agency or induce an external attribution or judgment of action effect.

Activations in areas surrounding the TPJ, in the dLPFC and in the SMA/pre-SMA have been constantly reported (David et al. 2007; Farrer and Frith, 2002; Farrer et al. 2003; Fink et al. 1999; Nahab et al. 2010; Yomogida et al. 2010), and thus a pivotal role in agency processes has been assigned to these structures.

It is important to note, however, as stressed by Moore and colleagues (2010), that these regions are more involved in non-agency experience under ambiguous feedback or in “this is not my action” feeling. Regions underpinning self-agency experience should be more active during coherent feedback and in conditions in which subjects feel in control of actions outcomes.

While there is a great consensus on structures involved in non-agency experience or in external-agency attribution, results concerning self-agency experience under coherent action–effect coupling are more controversial. For example Farrer and Frith (2002) and Farrer et al. (2003) reported greater insula activation for self- versus other-agency attribution, Leube and coworkers (2003a, b) found a negative correlation between putamen activity and the extent of temporal delay of the visual feedback, Kontaris et al. (2009) showed activation in parieto-occipital sulcus for congruent compared to incongruent feedback while other studies did not report any significant activation when directly comparing conditions of coherent versus distorted feedback (Bralslev et al. 2006; David et al. 2007; Nahab et al. 2010).

So while current evidence strongly supports a dissociation between external-agency attribution and a feeling or attribution of self-agency, areas involved in the latter process are still a matter of debate.

The aim of this paper is to investigate this dissociation and possibly to shed light on the neural correlates of proper self-agency experience. With this aim we conducted a whole brain quantitative meta-analysis based on activation likelihood estimation (ALE) (Laird et al. 2005; Turkeltaub et al. 2002) which allows the integration of results across available neuroimaging studies on agency.

## Materials and methods

### Studies selection

Twenty-four studies were identified through two recent meta-analyses (Decety and Lamm, 2007; Spengler et al.

2009) and a review (David et al. 2008) on the sense of agency. We further used a systematic literature search in large databases (PubMed, PsychInfo, and Web of sciences) for English-language manuscripts of neuroimaging studies published till September 2010. The search keywords were “agency”, “brain imaging”, “fMRI”, “PET”. In addition, we used the “related articles” function on PubMed to identify additional papers. This search revealed seven additional papers (Corradi-Dell’Acqua et al. 2008; Kontaris et al. 2009; Matsuzawa et al. 2005; Nahab et al. 2010; Spengler et al. 2009; Yomogida et al. 2010; Tsakiris et al. 2010) making a total of 31 studies.

Between these papers we included in our analysis only studies that responded to the following criteria:

- Involved healthy adults (27 out of the 31 studies met this criterion).
- Reported results of whole-brain analyses as coordinates in a standard reference space (Talairach/Tournoux, MNI), papers reporting only ROI analyses were excluded (26 out of the 27 studies met this criterion).
- Required subject to execute finger or hand movements, thus, excluding mental simulation or observation of actions only (23 out of the 26 studies met this criterion).
- Assessed brain correlates of the sense of agency using either a temporal, angular or congruency distortion of the visual feedback (15 out of the 23 studies met this criterion).

We considered two conditions to carry on two meta-analyses: the self-agency (i.e. judgment or implicit attribution of the perceived movement to oneself) and the external-agency (i.e. judgment or implicit attribution of the perceived movement to an external agent). Description of the included contrasts is provided on Table 1.

All foci were accepted when reported as significant according to the criteria designated in each individual study, works reporting *p* values that were not corrected for multiple comparisons were equally included. Where necessary coordinates originally published in Talairach space were converted to MNI space using the Lancaster transformation (Lancaster et al. 2007).

### Contrasts selection

Fifteen studies (13 fMRI and 2 PET studies) were included for a total of 228 subjects (see Table 1 for descriptions of included studies).

Two separate ALE analyses were conducted to investigate brain activations related to self- and external-agency. The first analysis concerned self-agency and pooled results of contrasts comparing conditions of real versus distorted feedback (13 experiments, 53 foci). The second analysis referred to external-agency and pooled results of contrasts

**Table 1** Overview of the 15 studies included in the two meta-analyses

Study	Subjects	Imaging method	Contrast
Bralslev et al. (2006)	15	fMRI	Synch. vs. asynch. feedback (S-A); Asynch. vs. synch. feedback (E-A)
David et al. (2007)	14	fMRI	Congruent vs. incongruent feedback (S-A); incongruent vs. congruent feedback (E-A)
Farrer and Frith, (2002)	12	fMRI	Self-attribution vs. other-attribution (S-A); other-attribution vs. self-attribution (E-A)
Farrer et al. (2003)	8	PET	Parametric decrease self to other visual feedback (S-A); Parametric increase self to other visual feedback (E-A)
Farrer et al. (2008)	18	fMRI	Preserved agency vs. perturbed agency (S-A); perturbed agency vs. preserved agency (E-A)
Fink et al. (1999)	10	PET	Interaction effect of visual feedback modulation on out-of-phase bimanual movements (E-A)
Kontaris et al. (2009)	11	fMRI	Compatible vs. incompatible visual feedback (S-A); incompatible vs. compatible visual feedback (E-A)
Leube et al. (2003a)	18	fMRI	Negative correlation with feedback delay length (S-A); positive correlation with feedback delay length (E-A)
Leube et al. (2003b)	6	fMRI	Self vs. other perform-observe mismatch (S-A); other vs. self perform-observe mismatch (E-A)
Matsuzawa et al. (2005)	6	fMRI	Synchronous action–effect feedback vs. rest (S-A); Asynchronous action–effect feedback vs. rest (E-A)
Nahab et al. (2010)	20	fMRI	Parametric increase during gain of feedback control (S-A); Parametric increase during loosing of feedback control (E-A)
Schnell et al. (2007)	15	fMRI	Visuo-motor congruence vs. visuo-motor incongruence (S-A); visuo-motor incongruence vs. visuo-motor congruence (E-A)
Spengler et al. (2009)	18	fMRI	Parametric increase with decreasing discrepancy of action-effect prediction (S-A); parametric increase with increasing discrepancy of action-effect prediction (E-A)
Tsakiris et al. (2010)	20	fMRI	Active movement with synch. feedback vs. passive movement synch. feedback (S-A)
Yomogida et al. (2010)	24	fMRI	Agency error vs. Sensory matching error (E-A)

*S-A* self-agency, *E-A* external-agency

comparing conditions of distorted versus real feedback (14 experiments, 112 foci).

For one study (Matsuzawa et al. 2005) contrasts between synchronous or asynchronous visual feedback and a low-level perceptive condition were included, as a direct comparison between synchronous and asynchronous conditions was not reported.

### Statistical analysis

The technique of ALE meta-analysis has been recently described (Turkeltaub et al. 2002; Laird et al. 2005). The ALE algorithm has been modified in the current version (GingerALE 2.0, <http://brainmap.org>) (Eickhoff et al. 2009). In short, all reported foci (coordinates of maximum activation) for a given study are modelled as the peaks of 3D Gaussian probability distribution. A “modelled activation” (MA) map is computed, representing a summary of the results of that specific study. ALE scores are then calculated on a voxel-by-voxel basis by taking the union of these individual MA maps. This revised analysis tests for convergence between studies (random-effects) rather than foci (fixed-effects). Each coordinate of maximum activation was modelled by a 3D Gaussian distribution (all were based on MNI space). Statistical significance was assessed using the analytic solution implemented in the new version

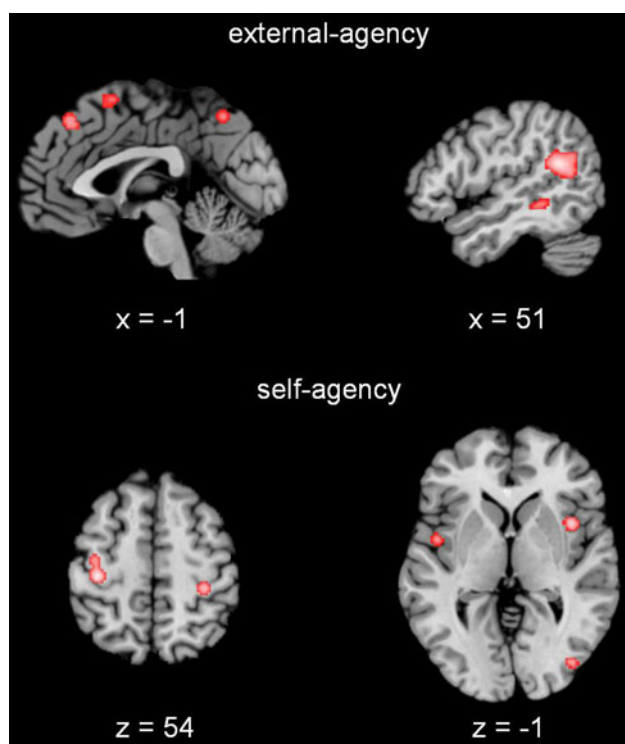
of GingerALE. A *p* threshold corrected for multiple comparisons using the false discovery rate (FDR) was fixed to 0.05 (Genovese et al. 2002; Laird et al. 2005). Each ALE map was overlaid onto an anatomical template generated by spatially normalizing the International Consortium for Brain Mapping (ICBM) template to the MNI space. A minimum cluster size of 200 mm<sup>3</sup> was applied.

### Results

The meta-analysis for self- and external-agency revealed a dissociable profile of activations. For external-agency activations were found in the superior temporal gyrus (STG), inferior parietal lobe (IPL), precuneus, pre-SMA, and dorsomedial prefrontal cortex (dMPFC). For self-agency we found activations in bilateral insula, bilateral primary somatosensory cortex and left pre-motor cortex (Fig. 1). Table 2 reports coordinates of activations maxima.

### Discussion

In the present study we conducted a quantitative meta-analysis of 15 neuroimaging studies to investigate different neural correlates of self- and external-agency. We found a



**Fig. 1** Results from the activation likelihood estimation for external- and self-agency meta-analyses. All activations are significant at  $p < 0.05$  corrected for multiple comparisons using the false discovery rate (FDR)

clear dissociation between areas activated in the two conditions. For external-agency attribution activations in a set of brain areas, reported in previous studies, such as TPJ precuneus, dMPFC and pre-SMA, were found. For self-agency we found activation in premotor and primary somatosensory cortex, the most interesting result being that insula was clearly more involved in this condition.

In the following we will briefly discuss the role of areas activated in external-agency attribution and later we will focus on the possible role of insula in self-agency.

Activations in areas surrounding TPJ are consistent with previous studies (Brass et al. 2009; Nahab et al. 2010; Schnell et al. 2007; Spengler et al. 2009; Yomogida et al. 2010). Interestingly this activity is more present in external-agency condition. It must be remembered that the external attribution of agency was experimentally induced in the experiments reported by manipulating the sensorimotor congruency between actual movements and the respective visual feedback. More than a specific mismatch detection mechanism between sensory signals (Tsakiris et al. 2008), we suggest that activity in TPJ could represent a general mismatch detection mechanism including the detection of a visuo-motor discrepancy. Indeed this is coherent with the absence of activation in self-agency

**Table 2** Peaks of activation for external- and self-agency

Region	Brodmann area	MNI coordinates		
		x	y	z
External-agency				
R STG	BA 39	52	-50	18
L IPL	BA 40	-50	-56	44
Medial FG	BA 6	6	8	60
R MFG	BA 6	44	16	46
SFG	BA 8	2	38	46
L MTG	BA 37	-46	-60	8
R MFG	BA 6	32	0	60
R SG	BA 40	58	-56	36
R SFG	BA 6	22	4	66
Precuneus	BA 7	-4	-64	50
R pre CG	BA 6	40	6	36
Self-agency				
L post CG	BA 3	-36	-24	56
R insula	BA 13	40	10	0
R post CG	BA 3	34	-32	54
L insula	BA 13	-46	-2	-4
L pre CG	BA 6	-58	2	30

Only clusters exceeding  $200 \text{ mm}^3$  are reported

STG superior temporal gyrus, IPL inferior parietal lobule, Medial FG medial frontal gyrus, MFG middle frontal gyrus, SFG superior frontal gyrus, MTG middle temporal gyrus, SG supramarginal gyrus, pre CG precentral gyrus, post CG postcentral gyrus

condition in which no mismatch is present. Moreover, this interpretation is in line with results by Yomogida and colleagues (2010) who found activity in TPJ in an oddball-error detection task. It also meets the results of Decety and Lamm (2007)'s meta-analysis which led the authors to conclude that the mechanism implemented in TPJ is not domain specific but rather represents the comparison of internal predictions with external events.

Precuneus activations have been reported in social cognition studies linked to different processes such as perspective-taking (Ruby and Decety 2001; 2003), observation of social interaction (Iacoboni et al. 2004), self-referential processes (Spreng et al. 2009; van der Meer et al. 2010) and causal attribution of social events (Seidel et al. 2010). In particular precuneus activations were found for both first and third person perspective (Ruby and Decety 2001), for first person perspective only (Ruby and Decety 2003) or for external attribution of the cause of a social event (Seidel et al. 2010). These controversial findings could be due to different paradigms used in these studies and to different levels of abstraction of the underlying cognitive processes. Anyway our finding that precuneus was particularly involved in attribution of agency to others is in line with Seidel's (2010) results and suggests

that this structure could be involved in the attribution of the cause of events to an external source.

Another region activated in external-agency was the dMPFC with coordinates lying closer to BA 8 than other medial regions (BA 10 or BA 9) classically involved in self-referential processes. This area has been reported to be involved in events prediction and decision making under uncertainty (Volz et al. 2003, 2004, 2005). In most of the studies considered here the normal sensory–motor association is experimentally broken to induce “external-agency” attribution. In this condition uncertainty about the association between intentions or movements and their outcomes might emerge, recruiting the dMPFC.

Pre-SMA was also more active in external-agency condition. This motor area is known to be involved in higher motor functions such as preparation and selection of movements (Picard and Strick 1996). Recently Moore and colleagues (2010) found that temporarily disrupting pre-SMA functioning by means of transcranial magnetic stimulation abolished the “intentional binding” effect. In accordance with this finding we expected to find this area more active in the self-agency condition. One possible explanation for our results is that pre-SMA is also involved in control, monitoring and conflict resolution of actions (Garavan et al. 2003; Nachev et al. 2005; 2007; Ullsperger and von Cramon 2001). We can suppose that under action-feedback incongruence subjects implicitly try to adapt their movements to the visual feedback or on the contrary to suppress this automatic response to synchronize the action with the visual feedback. In both cases an enhanced control over movements would be required calling for a greater recruitment of pre-SMA.

As activity of pre-SMA is linked to intention (Lau et al. 2004) and motor preparation and not to motor execution itself (Cunnington et al. 2002, 2006), we suggest that activity in this region in external-agency condition is driven by an intention-feedback incongruency and not by a sensory-motor discrepancy.

Regions more active in self-agency were premotor and primary somatosensory cortex. Activations in these areas have been previously reported in studies comparing active versus passive movements (Ciccarelli et al. 2005; Francis et al. 2009; Tatsuya et al. 1999). These results could suggest a role of these structures in self-agency as only during active voluntary and not during passive movement one can experience control over its action that is a fundamental feature of agency. The most evident activation for self-agency was found in bilateral insular cortex. Insular lesions have been reported to be responsible of anosognosia for hemiparesis (Karnath and Baier 2010), patients affected by this trouble are convinced to normally control their limbs in spite of their deficits, this can be seen as a sign of dysfunction of awareness for motor control.

Moreover, recently a central role in the physiopathology of schizophrenia has been assigned to the insula (for a review see: Wylie and Tregellas 2010). One of the most striking symptoms of this psychiatric disorder is a disturbed representation of the self that can manifest in several forms, notably in deficits of awareness for action and misattribution of self-generated voluntary movements. Interestingly, impairment in predicting action–effect relation and morphological abnormalities in insular cortex both correlates positively with the severity of positive psychotic symptoms (Voss et al. 2010; Crespo-Facorro et al. 2000).

All these data support a central role of insula in self-agency coherently with our results. But why is insula involved in the experience of control over its own actions?

This region has been classically seen as responsible for visceral sensation and emotional processing. Moreover, due to its spread connectivity it appears to play a role in integrating multimodal signals (for a review see Augustine 1996).

Recently there has been a growing interest on the functional role of the insula as it has become evident that this structure is activated in a multiplicity of processes, for example in a recent meta-analysis over more than 800 neuroimaging studies, Kurth and coworkers (2010) evidenced insula activation over 13 different domains ranging from basic perceptual functions such as olfaction, gustation and interoception, to high-level cognitive processes such as attention, working memory and language, with a functional differentiation between the anterior–ventral part for social-emotional function, the anterior–dorsal part for cognitive functions and the mid-posterior part for sensorimotor functions. Moreover, an overlap between all processes indicating a functional integration was found in the anterior–dorsal part in a location corresponding to that in our results.

This overlap could represent integration between different functional systems and will result during self-agency in greater insula activity due to an increased match between different inputs, in this case between actions and the corresponding visual feedback, this explication firstly proposed by Farrer and Frith (2002) fits well with our results.

Anterior insula has also been implicated in time processing (Wiener et al. 2010) and particularly in subjective timing (Craig 2009a; Wittmann et al. 2010). Of particular interest for our discussion is that “intentional binding”, that is considered as an implicit measure of agency, consists of a distortion of the duration between an action and its consequences (Haggard et al. 2002). Craig (2009a) proposed that time estimation in the insula would be supported by the formation of a “global emotional moment” at each time point resulting from the sequential integration of information of increasing complexity, from interoceptive to salient environmental and motivational information, in a

posterior-to-anterior progression culminating in the dorsal–anterior insula. The passage across different “global emotional moments” could constitute the base of interval estimation.

Interestingly this model directly links time perception and self-awareness or the “sentient self” as defined by the author (Craig 2009a, b, 2010), indeed this interpretation is in line with several studies that found insula activation in self-referential processing, (for a meta-analysis see: van der Meer et al. 2010).

Our results confirm the role of insula in self-representation and strength the idea of this region as a possible neural substrate of the “embodied self”.

## Conclusions

We found, by means of a quantitative meta-analysis of 15 neuroimaging studies, a dissociation between brain regions involved in self- and external-agency attribution. Of particular interest is the involvement of insula in self-agency as this structure is seen as a possible neural correlates of the “embodied self”.

Our study shows that classical brain regions usually linked to the “sense of agency” are actually more involved in external-agency attribution than in the pure experience of “me generating an action”.

We suggest that novel theoretical frameworks and experimental protocols should emerge to clarify the functional role of the different structures reported in the present work.

Two interesting candidates are: the “intentional binding” paradigm, adapted for neuroimaging studies, or other implicit measure of agency, that could confirm a direct role of the insula in this phenomenon, and spontaneous imitation, used in our team as a paradigm allowing interactants to synchronize actions while alternating the role of imitator and model (Dumas et al. 2010). This has the advantage of avoiding confounds due to sensorimotor discrepancy, as in imitation action and visual feedback are coupled, while maintaining an exchange of control over others movements between two interacting agents leading to an experience of being in control (self-agency) or being controlled (external-agency).

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