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Sense of agency as synecdoche: Multiple neurobiological mechanisms may underlie the phenomenon summarized as sense of agency

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ABSTRACT

Functional magnetic resonance imaging (fMRI) studies on the sense of agency (SoA) have yielded heterogeneous findings identifying regional brain activity during tasks that probed SoA. In this review, we argue that the reason behind this between-study heterogeneity is a “synecdochic” way the field conceptualizes and studies SoA. Typically, a single feature is experimentally manipulated and then this is interpreted as covering all aspects of SoA. The purpose of this paper is to give an overview of the fMRI studies of SoA and attempt to provide meaningful categories whereby the heterogeneous findings may be classified. This classification is based on a separation of the experimental paradigms (Feedback Manipulations of ongoing movements, Action-Effect, and Sensory Attenuation) and type of report employed (implicit, explicit reports of graded or dichotic nature, and whether these concern self-other distinctions or sense of control). We only find that Feedback Manipulation and Action-Effect share common activation in supplementary motor area, insula and cerebellum in positive SoA and inferior frontal gyrus in the negative SoA, but observe large networks related to SoA only in Feedback Manipulation studies. To illustrate the advantages of this approach, we discuss the findings from an fMRI study which we conducted, within this framework.

1. Introduction

The sense of agency (SoA) is an important psychological construct that describes the feeling of being in control of one’s own movements, actions, and consequences of these in the external world (Haggard, 2017). SoA is a frequently used term within different disciplines. In this review, we will refer to its use in experimental psychology and cognitive neuroscience, where the term either

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describes the phenomenological experience of being the agent of a movement or action (Frith, 2005; Gallagher, 2000; Jeannerod, 2003; Pacherie, 2007) or the ability to determine who is the agent of a movement or an action (Christensen & Grünbaum, 2018; Gallagher, 2000; Grünbaum & Christensen, 2020; Jeannerod, 2003). The literature on SoA is quite extensive. Many aspects of this notion have been the topic of scientific discussions, ranging from the question of which model best describes the phenomenological experience (David, Newen, & Vogeley, 2008; Synofzik, Vosgerau, & Newen, 2008; Wegner, 2002) to more recent discussions on the relation between implicit and explicit measures of SoA (Imaizumi & Tanno, 2019; Schwarz et al., 2019a, 2019b; Wen, 2019). However, one discussion which has not been in focus yet is the diversity in the experimental designs employed to study SoA and how this frames our understanding of what constitutes the neuronal network underlying the psychological construct of SoA, when SoA is studied using fMRI.

To operationalize work on SoA, Christensen and Grünbaum (Christensen & Grünbaum, 2017, 2018; Grünbaum & Christensen, 2020) have identified two dimensions of SoA that often are conflated but can help classify the studies on SoA into meaningful categories. The first dimension focuses on whether SoA can be assigned a functional role or not, and the second on the breadth of the SoA definition. Along the first dimension, SoA can be described as either an *ability* to determine the agent of an action or a *phenomenological experience* of being in control of one's movements/actions. Within this dimension, the phenomenological experience is independent of the ability. In fact, the contrast ability vs phenomenological experience does not map onto the discussion of Feeling of Agency (FoA) and Judgment of Agency (JoA) (Bayne & Pacherie, 2007; see discussion by Grünbaum (2015)), in which it is argued that JoA follows from a FoA, and therefore cannot be separated as independent aspects of SoA. The contrast ability vs phenomenological experience maps onto the discussion of whether SoA can be considered a cognitive function or a non-cognitive phenomenological experience similar to the discussion in philosophy of consciousness (Block, 2011; Cohen & Dennett, 2011; Overgaard & Grünbaum, 2012). Whether SoA falls within either of two depends on the researchers' choice of definitions of SoA or experimental manipulations such as the question asked to the participants (see Christensen & Grünbaum, 2017 exemplifying these choices made in the literature). For example, with questions like "Were 'you' or 'another' the agent of the action?" researchers study SoA as an ability. While with questions like: "To what extent did you feel in control of the action?" researchers study SoA as a phenomenological experience. The answer to either question can be dichotomous or graded.

In the second dimension, the focus is on the breadth of the definition of SoA, meaning whether is it tightly related to the movement or is it broad enough to include the consequences of the movement/action in the surrounding environment. *Narrow SoA* refers to the former, and *Broad SoA* refers to the latter realization of SoA, respectively. Christensen & Grünbaum proposed this dimension to identify the experimental categories within which most SoA studies could be classified: 1) Feedback Manipulation, 2) Action-Effect, and 3) Sensory Attenuation studies (Christensen & Grünbaum, 2017, 2018; Grünbaum & Christensen, 2020). The first category, Feedback Manipulation, includes those studies where the sensory feedback accompanying the movement, which participants perform, is modified in some trials to disrupt the agentic experience. Typically, this is done by introducing a sensorimotor mismatch. Participants make a movement such as drawing a line on a computer screen and the visual feedback of the line (or movement) is manipulated in such a way that resembles the movement in a distorted fashion either spatially or temporally. Feedback Manipulation studies can cover both narrow or broad SoA depending on how the feedback is manipulated. The second category, Action-Effect, draws upon a broad definition of SoA, focusing on the consequences of the action in the external world. Participants perform an action followed by an outcome, like pressing a button followed by a tone. Manipulations in these types of experiments include various temporal delays between the action and the outcome (Sato & Yasuda, 2005), changes in the nature of the outcome (e.g., different types of tones (e.g., Wolpe, Haggard, Siebner, & Rowe, 2013)) or the probability of different effects (Moore & Haggard, 2008). The third category, the Sensory Attenuation studies consider that the sensory consequences of voluntarily performed movements are perceived less pronounced, compared with identical externally performed ones (e.g., Blakemore, Wolpert, & Frith, 1998). The sensory consequences of the attenuation studies can either be narrowly tied to the body and the movement (e.g. the experience of touch to the body being less ticklish when done by oneself than by another) or broad to include consequences in the external world (e.g. the sound of a tone, that is perceived less intense when caused by one's action compared to another one's action).

In the literature of SoA, the neuroimaging findings indicate the involvement of a broad cortical network including the parietal lobe, insula and areas within the frontal and prefrontal cortex (Braun et al., 2018; David et al., 2008; Haggard, 2017; Sperduti, Delaveau, Fossati, & Nadel, 2011). While previous reviews have attempted to summarize these findings, the considerable variation in the exact activation sites within this broad cortical network makes it difficult to observe a clear association between the psychological construct of SoA and the neural structures supporting it. Current reviews treat the construct of agency broadly. They do not distinguish the inter-study-differences which can rise due to the definitions of SoA, experimental approaches and behavioral outcome measures. However, these distinctions may be important to gain a finer-grained attribution of the neural correlates supporting SoA. For instance, in a recent review on the effect of delay on SoA, the author used a similar argumentation to emphasize how the experimental protocol can lead to different delay effects on SoA (Wen, 2019). Evidence suggests that SoA is differentially modulated when the manipulations target the movement or the outcome of an action (David, Skoruppa, Gulberti, Schultz, & Engel, 2016), and temporal delays, compared with spatial distortions, have a more pronounced effect on SoA (Ratcliffe & Newport, 2017). Furthermore, it is still disputable whether implicit and explicit measures of SoA reflect the same process (Imaizumi & Tanno, 2019; Schwarz et al., 2019a, 2019b; Wen, 2019).

In this paper, we review the existing fMRI studies on SoA, classify the brain regions reported to be active according to the experimental procedures employed, and raise the question of whether the different experimental protocols (Feedback Manipulation, Action-Effect and Sensory Attenuation) explain SoA as a homogeneous psychological phenomenon. The motivation for this review was our Feedback Manipulation, fMRI study on SoA, where we used the influential "Alien Hand" paradigm (Nielsen, 1963) in a modified version using computer-manipulated feedback. We present our study here as an example of how the framework introduced in this review can help interpret fMRI activations concerning SoA and how one can use our summary report activity to place their results in a broader context.

If SoA is a psychological construct that draws upon one common neural mechanism, we expect one brain area or a network of interconnected brain areas to be reported in all SoA studies regardless of the experimental paradigm, modality and report type used. On the other hand, if the experimental paradigm, sensory modality and report type, have a strong impact on the fMRI results, we expected that all Feedback Manipulation studies would have a different activation pattern associated with SoA compared with Action-Effect and Sensory Attenuation studies.

2. Presentation of the existing neuroimaging studies on SoA

2.1. Studies selection

We searched for literature in the database Web of Sciences on the 13th of April 2021 covering all years registered in the database using the keyword: i) "fMRI" plus "sense of agency", ii) "agency" plus "fMRI", iii) "agency" plus "magnetic resonance imaging" and iv) "agency" plus "MRI". This search revealed 706 papers, 496 of which were unique entries. From these we selected 134, based on their relevance with the notion of SoA according to their title and abstract. In addition to these papers, we also included three fMRI studies, that did not appear in our search (Kontaris, Wiggett, & Downing, 2009; Matsuzawa, Matsuo, Sugio, Kato, & Nakai, 2005; Schnell et al., 2007), which were previously included in other review studies on SoA (David et al., 2008; Miele, Wager, Mitchell, & Metcalfe, 2011; Sperduti et al., 2011). The 32 papers included in our review were selected based on the following criteria:

- Studies that used MRI technique, that report their findings in Montreal Neurological Institute (MNI) or Talairach (TAL) stereotaxic coordinates.
- Reported group results for healthy participants
- Studies of SoA using a task that required participants to make a movement (active or passive). Therefore, we excluded studies in which participants observed or thought of performing a movement (motor imagery).
- Included contrasts that compared active trials among them or active trials with passive trials. This means we excluded those studies that studied agency by comparing active movement with baseline activity.

If any of the found papers in the search did not report the above-mentioned criteria, they were excluded from the review.

We then classified the studies in the categories proposed by Christensen & Grünbaum (Christensen & Grünbaum, 2017, 2018; Grünbaum & Christensen, 2020): A) Feedback Manipulation, B) Action-Effect and C) Sensory Attenuation (Table 1). Due to the low (one) number of Sensory Attenuation studies compared with Feedback Manipulation and Action-Effect studies, the classical study of Blakemore et al., 1998 is mentioned here, but results from the study will not be presented in the overview.

We further organized the results reported (Farrer et al., 2008, Spaniel et al., 2016; Di Plinio, Perrucci, Aleman, & Ebisch, 2020 were reported in supplementary material) based on the measure of agency (explicit/implicit, dichotic/graded, perceive incongruence or not, delay detection, self/other or experience of control) and contrasts employed (see also Supplementary Table S1) in two groups: Positive agency (containing variations of *Being the agent* or *Experiencing being in control*) and Negative agency (encompassing variations of *Not Being the agent* or *Not experiencing being in control)*. To do so, we considered for the group *Positive agency* the findings from both types of studies where: 1) participants explicitly reported that they were the agent or in control of the movement/action, 2) participants explicitly reported congruency between a movement and the feedback and 3) it is assumed to be because there was no experimentally introduced manipulation. Similarly, we included a division of findings related to *Negative agency* for areas found across both types of studies where: 1) participants explicitly reported not being the agent or not in control of the movement/action, 2) participants explicitly reported incongruence between a movement and the feedback and 3) there were discrepancies introduced between the movement and the feedback. These results are also summarized in Fig. 1, and Tables 2 and 3 (see also Supplementary Table S2A and S2B). In some studies, SoA was studied broadly without, for example, comparing positive SoA with diminished SoA. Therefore, the results from these studies are included in both Positive and Negative SoA tables.

The 32 neuroimaging studies of SoA employed different reports to measure SoA, both explicit and implicit (See Tables 1 and 2 and Supplementary Table S2A & S2B). SoA was measured implicitly in eight Feedback Manipulation (Di Plinio et al., 2020; Jardri et al., 2011; Kontaris et al., 2009; Macuga & Frey, 2011; Nahab et al., 2011; Schnell et al., 2007; Spaniel et al., 2016; Tsakiris, Longo, & Haggard, 2010) and three Action-Effect studies (Kikuchi et al., 2019; Matsuzawa et al., 2005; Yomogida et al., 2010). Some studies used explicit reports (graded or dichotic), to measure the self/other dimension of SoA (Feedback Manipulation: Balslev, Nielsen, Lund, Law, & Paulson, 2006; David et al., 2007; Farrer & Frith, 2002; Farrer et al., 2008; Ohata et al., 2020; Action-Effect: Fukushima, Goto, Maeda, Kato, & Umeda, 2013; Renes et al., 2015, 2016; Spengler, von Cramon, & Brass, 2009) or the experience of control (Feedback Manipulation: Miele et al., 2011; Action-Effect: Chambon, Wenke, Fleming, Prinz, & Haggard, 2013, de Bezenac, Sluming, Gouws, & Corcoran, 2016). Other studies used explicit judgments of temporal delay as a report type (Feedback Manipulation: Farrer et al., 2008; Leube et al., 2003; Uhlmann et al., 2020; van Kemenade et al., 2019; Action effect: Kühn, Brass, & Haggard, 2013; Seghezzi & Zapparoli, 2020; delay detection: Straube et al., 2017; van Kemenade, Arikan, Kircher, & Straube, 2017) and one used judgments about the contingency between the movement and the feedback (Sasaki, Okamoto, Kochiyama, Kitada, & Sadato, 2018). It is important to note that only one Action-Effect study employed a dichotic explicit self/other report, only one Feedback Manipulation study used graded explicit self/other report, and one Feedback Manipulation study used explicit graded control report, and none of the studies used a dichotic control question. Therefore, we cannot make conclusive assumptions regarding the effect of dichotic or graded type of explicit reports on the activity reported. Likewise, because only one Feedback Manipulation study used a question related to the experience of

Table 1
Classification of the 32 fMRI studies included in this review. The studies are organized initially based on the experimental paradigm employed (Experiment) in Feedback Manipulation and Action-Effect. Thereafter, they are grouped based on the type of report acquired (Report). The symbols in the Report Column and the Symbol column are used later on to organize the regions reported in each study in the Tables 2 and 3. Additional information is provided for the strength of the scanner, whether the coordinates of the reported results are in Talairach (TAL) or Montreal Neurological Institute (MNI) space and the number of participants. H = healthy, FES = patients with first-episode schizophrenia-spectrum disorders, SCZ = schizophrenia.

Experiment	Report	Article	Symbol	Tesla	Cor	N
Feedback Manipulation	Dichotic self/other (Ds)	Balslev et al., 2006	A	3 T	MNI	16
		David et al., 2007	B	1.5 T	MNI	19
		Farrer & Frith, 2002	C	2 T	MNI	12
		Farrer et al., 2008	D1	1.5 T	MNI	18
	Graded control (Gc)	Miele et al., 2011	F	1.5 T	MNI	11
	Graded self-other (Gs)	Ohata et al., 2020	E	3 T	MNI	18
	Perceive delay (del)	Farrer et al., 2008	D2	1.5 T	MNI	15
		Leube et al., 2003	G	1.5 T	MNI	18
		Uhlmann et al., 2020	H	3 T	MNI	24
		van Kemenade et al., 2019	I	3 T	MNI	23
	Graded contingency	Sasaki et al., 2018	J	3 T	MNI	24
	No report (im)	Di Plinio et al., 2020	K	3 T	MNI	39
		Jardri et al., 2011	L	1.5 T	TAL	15H,15SCZ
		Kontaris et al., 2009	M	3 T	TAL	11
		Macuga & Frey, 2011	N	3 T	MNI	14
		Nahab et al., 2011	O	3 T	TAL	20
		Schnell et al., 2007	Q	1.5 T	TAL	15
		Spaniel et al., 2016	R	3 T	TAL	35H, 35FES
		Tsakiris et al., 2010	S	1.5 T	MNI	20
Action-Effect	Dichotic self-other (Ds)	Fukushima et al., 2013	T	3 T	MNI	17
	Graded self-other (Gs)	Renes et al., 2016	W	3 T		31H, 31SCZ
		Renes, Van Haren, Aarts, & Vink, 2015	X	3 T	MNI	23
		Spengler et al., 2009	BB	3 T	TAL	18
	Graded control (Gc)	Chambon et al., 2013	Y	3 T	MNI	28
		de Bezenac et al., 2016	AA	3 T	MNI	24
	Delay detection (delay)	Straube et al., 2017	CC	3 T	MNI	21
		van Kemenade et al., 2017	DD	3 T	MNI	21
	Duration of delay (del)	Kühn et al., 2013	EE	3 T	MNI	17
		Seghezzi & Zapparoli, 2020	FF	1.5 T	MNI	25
	No report (im)	Kikuchi et al., 2019	GG	3 T	MNI	26/28
		Matsuzawa et al., 2005	HH	3 T	TAL	6
		Yomogida et al., 2010	II	1.5 T	MNI	24

control (i.e., the phenomenological content of the experience of SoA), we cannot make a complete split of studies according to the suggestions made by Christensen and Grünbaum (Christensen & Grünbaum, 2017, 2018) into the ability versus the phenomenological dimension of SoA. However, based on the report types, there were some interesting points we will address.

It is beyond the purposes of this paper to perform a full activation likelihood estimation *meta*-analysis (Eickhoff et al., 2009) of the data from these studies to find the activation peaks and subsequently perform *meta*-analyses for each of the categories separately. For a *meta*-analysis on SoA, we refer the interested reader to existing *meta*-analyses that typically pool the data reported in studies belonging to either one of the two experimental categories. (Miele et al., 2011: SoA, action monitoring and metacognition of agency; Zito, Wiest, & Aybek, 2020: SoA during motor control; Seghezzi, Giannini, & Zapparoli, 2019: SoA and Self-consciousness; Seghezzi, Zirone, Paulesu, & Zapparoli, 2019: intentionality and SoA; Sperduti et al., 2011: self-versus external SoA). Here we summarize findings regarding common activations when found in three or more neuroimaging studies within one experimental category (Feedback Manipulation or Action-Effect) (Table 2 & 3, Supplementary Table S2A & S2B) and then compare the findings between the two types of studies. We illustrate these classifications in Fig. 1. We then searched for common and distinct activity based on the type of report employed.

2.2. *What is common in these fMRI studies of SoA*

First, we compared the findings from the Feedback Manipulation and Action-Effect studies to find the areas commonly reported in both types of studies. Assuming that both categories are equally suited to study SoA, the activity reported in these regions cannot be simply explained based on the differences in the experimental design. We then focused on the areas exclusively reported in at least three studies within each experimental category. This allowed us to link activated regions with the specificities of the experimental design. Finally, we pooled the activation results from both types of experimental designs to find any additional region that has been reported in at least three of the studies regardless of the experimental design. This means for example that a region might be reported in two Feedback Manipulation and one Action-Effect study. While, we cannot say anything conclusive for the role of these latter regions in SoA, we report them here because we think future studies on SoA might use our classification and summary activity report to clarify the possible role these regions play in the SoA. This was done first for activity associated with positive and then with negative agency.

Table 2
Areas associated with positive agency. The areas displayed, are those that show activation in at least three of the reviewed studies when participants were the agent of the observed movement/action (see also Supplementary Table S1 for the contrasts used from each study). In the first column, Studies Assigned, we color-coded the rows based on the number of studies reporting these regions active as follows. Light green: at least three Feedback Manipulation studies (FM) and Light blue: at least three Action-Effect studies (AE). In the Report types column, we replace the code from each study with a code indicating whether sense of agency was studied implicitly (im) or using explicit reports (graded (G) and dichotic (D)). Explicit reports can concern a question related to self/other distinction (Gs, Ds) or experience of control (Gc, Dc). Other studies used explicit judgments of temporal delay (del) as the report type. In the comparison column we summarize the most interesting findings based on the number of studies reporting these regions according to the following color-code. Dark green: at least three Feedback Manipulation studies and in addition one or two Action-Effect studies. Dark blue: at least three Action-Effect studies and in addition one or two Feedback Manipulation studies. Orange: both three or more Feedback Manipulation and three or more Action-Effect studies. Yellow: three studies when combining both Feedback Manipulation and Action-Effect studies. Red: three or more Feedback Manipulation studies, but no activation in any Action-Effect studies. The arrows indicate whether the regions reported were related with increased or decreased activity in relation to positive sense of agency. A full table of activation found in all studies associated with positive agency is presented as Supplementary Table S2A.

Positive Agency	Studies assigned		Report types	
	FM	AE	FM	AE
Frontal Lobe				
L medial frontal gyrus	L, ↑Q, ↑R		im, im, im	
L middle frontal gyrus	↓K, ↓R	Y	im, im	Gc
R middle frontal gyrus	↑K, ↓R	Y	im, im	Gc
L supplementary motor area	B, D1, ↑K	EE, ↑AA, HH	Ds, Ds, im	IB, Gc, im
L inferior frontal gyrus	E, L, ↓R		Gs, im, im	
L precentral gyrus	E, L, ↑Q, ↓R	T, ↑AA	Gs, im, im, im	Ds, Gc
Parietal lobe				
R postcentral gyrus	L,Q, S		im, im, im	
B inferior parietal lobule	E, L, ↑R	X (left), W	Gs, im, im	Gs, Gs
L precuneus	B, ↑R	T	Ds, im	Ds
R precuneus	F, ↑K, S		Gc, im, im	
Occipital lobe				
R lingual gyrus (middle occipital)	D1, ↓R	↑BB	Ds, im	Gs

(*continued on next page*)

2.2.1. *Positive agency: similarities between feedback manipulation and action-effect studies*

The only regions associated with positive agency, which were reported in at least three Feedback Manipulation and at least three Action-Effect studies, are the left supplementary motor area, right insula and bilateral cerebellum (areas marked in orange in Table 2, Fig. 1). The supplementary motor area was found active in studies using a variety of report types. The cerebellum was found active only in Feedback Manipulation studies that used implicit reports while in the majority of Action-Effect (3 out of 4) that used explicit reports. Right insula activation was found in five out of six studies using explicit reports.

Additionally, left precentral gyrus, right anterior cingulate cortex, left posterior cingulate gyrus, bilateral inferior parietal lobule, and left insula, were reported in three or more Feedback Manipulation studies and at least one Action-Effect study in relation to positive agency (areas marked in dark green in Table 2) in studies using various report types. These regions seem to be important for positive agency, nevertheless further research is needed to clarify whether their involvement goes beyond the experimental design.

Finally, when we pooled Feedback Manipulation and Action-Effect studies, we noticed activity in bilateral middle frontal gyrus, left precuneus, right lingual gyrus, left anterior cingulate cortex, right posterior cingulate cortex and left putamen in at least three studies employing different types of reports across both categories (areas marked in yellow in Table 2).

Table 2 (*continued*)

Temporal lobe				
R superior temporal gyrus	B, E, ↑K, L, ↑Q		Ds, Gc, im, im, im	
Limbic lobe				
L anterior cingulate cortex	D1, L	↑AA	Ds, im	Gc
R anterior cingulate cortex	D1, L, ↑R	↑AA	Gs, im, im	Gc
L posterior cingulate cortex	D1, L, ↑Q ↑R	↑AA	Gs, im, im, im	Gc
R posterior cingulate cortex	D1, L	↑AA, T	Gs, im	Gc, Ds
Basal ganglia				
L putamen	B	↑AA, Y	Ds	Gc, Gc
Insular cortex				
L insula	B, C, S (pos)	↑AA	Ds, Ds, im	Gc
R insula	C, E, ↑N	↑AA, T, X	Ds, Gs, im	Gc, Ds, Gs
Other				
R Cerebellum	K, L, ↑Q, S	↑AA, X, HH	im, im, im, im	Gc, Gs, im
L Cerebellum	K, L, ↑N, ↑Q, S	↑AA, T, X	im, im, im, im, im	Gc, Ds, Gs

2.2.2. Positive agency: discrepancies between feedback manipulation studies and action-effect studies

Left medial frontal gyrus, left inferior frontal gyrus, right postcentral gyrus, right precuneus and right superior temporal gyrus are the areas linked with positive agency exclusively in Feedback Manipulation studies. Only left medial frontal gyrus and right postcentral gyrus were found active exclusively in Feedback Manipulation studies that used an implicit agency report. We did not find any area exclusively reported in three or more Action-Effect studies.

2.2.3. Negative agency: similarities between feedback manipulation and action-effect studies

Left inferior frontal gyrus was the only region linked with negative agency in both three Feedback Manipulation and three Action-Effect studies that employed a variety of report types (areas marked in orange in Table 3, Fig. 1).

In addition, we observed activity in right superior frontal gyrus, bilateral middle frontal gyrus (dorsolateral prefrontal cortex), right inferior frontal gyrus, left precentral gyrus, left superior/inferior parietal lobe, right inferior parietal lobule, bilateral angular gyrus, right supramarginal gyrus, bilateral precuneus, right superior temporal gyrus, right middle temporal gyrus, left anterior cingulate and left posterior cingulate cortex reported in three or more Feedback Manipulation and at least one Action-Effect study (areas marked in dark green in Table 3). We also found that activity in bilateral supplementary motor areas, left cerebellum and right anterior insula was present in three or more Action-Effect and at least one Feedback Manipulation study (areas marked in dark blue in Table 3). Regarding the agency reports employed, left precuneus was the only region found active exclusively with explicit reports and left angular gyrus primarily (seven out of eight studies) in studies with explicit reports.

Finally, in addition to the areas previously reported, when we pooled Feedback Manipulation and Action-Effect studies we noticed activation in right temporoparietal junction, right anterior cingulate cortex, right posterior cingulate cortex, left putamen, bilateral caudate nucleus, left anterior insula, bilateral cerebellum and bilateral thalamus in at least three studies (areas marked in yellow in Table 3).

2.2.4. Negative agency: discrepancies between feedback manipulation studies and action-effect studies

Bilateral medial frontal gyrus, left supramarginal gyrus, left superior temporal gyrus, and left middle temporal gyrus were exclusively reported in three or more Feedback Manipulation studies in relation to negative agency (areas marked in red in Table 3). From these regions, left medial frontal gyrus and left superior temporal gyrus were found active only in studies that used implicit agency reports. No regions were found exclusively reported in three or more Action-Effect studies.

Table 3

Areas associated with negative agency. The areas displayed, are those that show activation in at least three of the reviewed studies during diminished sense of agency (see also Table 1). In the first column, Studies Assigned, we color-coded the rows based on the number of studies reporting these regions active as follows. Light green: at least three Feedback Manipulation studies (FM) and Light blue: at least three Action-Effect studies (AE). In the Report types column, we replace the code from each study with a code indicating whether sense of agency was studied implicitly (im) or using explicit reports (graded (G) and dichotic (D)). Explicit reports can concern a question related to self/other distinction (Gs, Ds) or experience of control (Gc, Dc). Other studies used explicit judgments of temporal delay (del) as the report type. In the comparison column we summarize the most interesting findings based on the number of studies reporting these regions using the following color-code. Dark green: at least three Feedback Manipulation studies and in addition one or two Action-Effect studies. Dark blue: at least three Action-Effect studies and in addition one or two Feedback Manipulation studies. Orange: both three or more Feedback Manipulation studies and three or more Action-Effect studies. Yellow: three studies when combining both Feedback Manipulation studies and Action-Effect studies. Red: three or more Feedback Manipulation studies, but no activation in any Action-Effect studies. The arrows indicate whether the regions reported were related with increased or decreased activity in relation to negative sense of agency. A full table of activation found in all studies associated with negative agency is presented as Supplementary table S2B.

Negative Agency	Studies Assigned		Report types		Comparison
	FM	AE	FM	AE	
Frontal lobe					
R superior frontal gyrus	H, ↓K, M, ↑O, ↑Q	↑DD	del, im, im, im, im	Gc	
L medial frontal gyrus	L, ↑Q, ↓R,		im, im, im		
R medial frontal gyrus	L, ↑Q ↑R, H		im, im, im, del		
L Middle frontal gyrus	B, D1, D2, H, ↓K, M, ↑O, ↑Q, ↓R	↓Y	Ds, Ds, del, del, im, im, im, im, im	Gc	
R Middle frontal gyrus	B, D1, D2, ↑K, M, ↑O, ↑Q(2), S, ↓R	↑DD	Ds, Ds, del, im, im, im, im, im, im, im	Gc	
L supplementary motor area	B, ↑K	↓AA, ↓DD, HH, II	Ds, im	Gc, Gc, im, im	
R supplementary motor area	B	↓AA, GG, HH, II	Ds	Gc,im, im, im	
L Inferior frontal gyrus (PMv)	D1, E, L, M	↑BB(sul.), II, GG	D, Gs, im, im	Gs, im, im	
R Inferior frontal gyrus	M, ↑Q, S	II, GG	im, im, im	im, im	
L Precentral gyrus	B, D2, E, L	↓AA	Ds, del, Gs, im	Gc	
Parietal lobe					
L superior/inferior parietal lobe	A, E, L, ↑O, ↑Q	II	Ds, Gs, im, im, im	im	
R inferior parietal lobule	A, H, ↑K, L, ↑O, ↑Q(2), S	II	Ds, del, im, im, im, im, im, im	im	
L Ag	C, D1, D2, H, I, ↓K	↑Y, ↑DD	Ds, Ds, del, del, del, im	Gc, Gc	
R Ag	C, D1, D2, H, ↓K, ↑O, S	↑DD, II	Ds, Ds, del, del, im, im, im	Gc, im	
L SMg	B, D2, ↑Q(2),		Ds, del, im, im		
R SMg	B, E, ↑G, ↑O, ↑Q, S	↑DD	Ds, Ds, del, im, im, im	Gc	
L precuneus	B, C, H	BB	Ds, Ds, del	Gs	
R precuneus	C, H, M, ↑O, ↑Q	CC, ↑DD	Ds, del, im, im, im	Gc, Gc	
R TPJ	↑O	↑BB, GG	im	Gs, im	

(*continued on next page*)

Table 3 (*continued*)

Temporal lobe				
L superior temporal gyrus	↑K (sul.), L, M, ↓R		im, im, im, im	
R superior temporal gyrus	E, ↑G, H, ↑K (sul.), L, M, ↑O, ↓R	↑DD, GG	Gc, del, del, im, im, im,im, im	Gc, im
L middle temporal gyrus	B, I, ↑K, M, ↑Q		Ds, del, im, im, im	
R middle temporal gyrus	A, B, E, ↑G, H, I, ↑K, M, ↑O, ↑Q, S	II	Ds, Ds, Gs, del, del, del, im, im, im, im	im
Limbic lobe				
L anterior cingulate cortex	L, I, ↑Q	↓AA	im, del, im	Gc
R anterior cingulate cortex	L	↓AA, ↑DD	im	Gc, Gc
L posterior cingulate	L,↑Q, ↓R	↓AA	im, im, im	Gc
R posterior cingulate	L	↓AA, ↑DD	im	Gc, Gc
Basal ganglia				
L putamen	↓G	↓AA, CC	del	Gc, Gc
B caudate nucleus	L, I(left)	↓AA	im, del	Gc
Insular cortex				
L anterior insula	↑O, S	↓AA, CC	im, im	Gc, Gc
R anterior insula	E, ↑O	↓AA, ↓DD, II	Gc, im	Gc, Gc, im
Other				
L Cerebellum	L (dentate), S	↓AA, II, T	im, im	Gc, im, D
R Cerebellum	L (dentate)	↓AA, HH	im	Gc, im
B Thalamus	L	↓AA, ↑BB	im	Gc, Gs

2.3. Summary

In summary, we found that Feedback Manipulation and Action-Effect studies report activity in a broad network related to positive or negative SoA (Fig. 1; see also Tables 2 and 3). For example, studies in both the Feedback Manipulation and Action-Effect categories agree on the involvement of supplementary motor area, insula and cerebellum for positive SoA, while left inferior frontal gyrus for negative SoA. This finding could indicate that these areas are highly relevant for positive and negative SoA, respectively. Nevertheless, this is not strictly true. Within each category, we see that for *both positive and negative SoA,* a similar network of brain regions is reported. Specifically, in Feedback Manipulation studies, this network includes the same frontal, parietal, temporal and medial regions. In Action-Effect studies, the left supplementary motor area, cerebellum and right insula. One possible explanation for this result is that these areas could be responsible for monitoring the ongoing actions, and that activity in these areas does not explicitly map onto negative or positive SoA. The fact that these areas are reported consistently within each experimental category for both negative and positive SoA indicates that the activity in these regions is driven by the specificities of the experimental protocol and argues against conceptualizing SoA as a homogeneous psychological phenomenon. In the following section we will describe an fMRI study we conducted ourselves and see how the findings fit with previous studies that we have now organized in separate categories.

3. Presentation of our fMRI study

In this experiment we studied broad SoA with a Feedback Manipulation protocol after collecting explicit dichotic reports from the participants. We analyzed the data from 10 healthy right-handed participants with no neurological or psychiatric history. We provide a

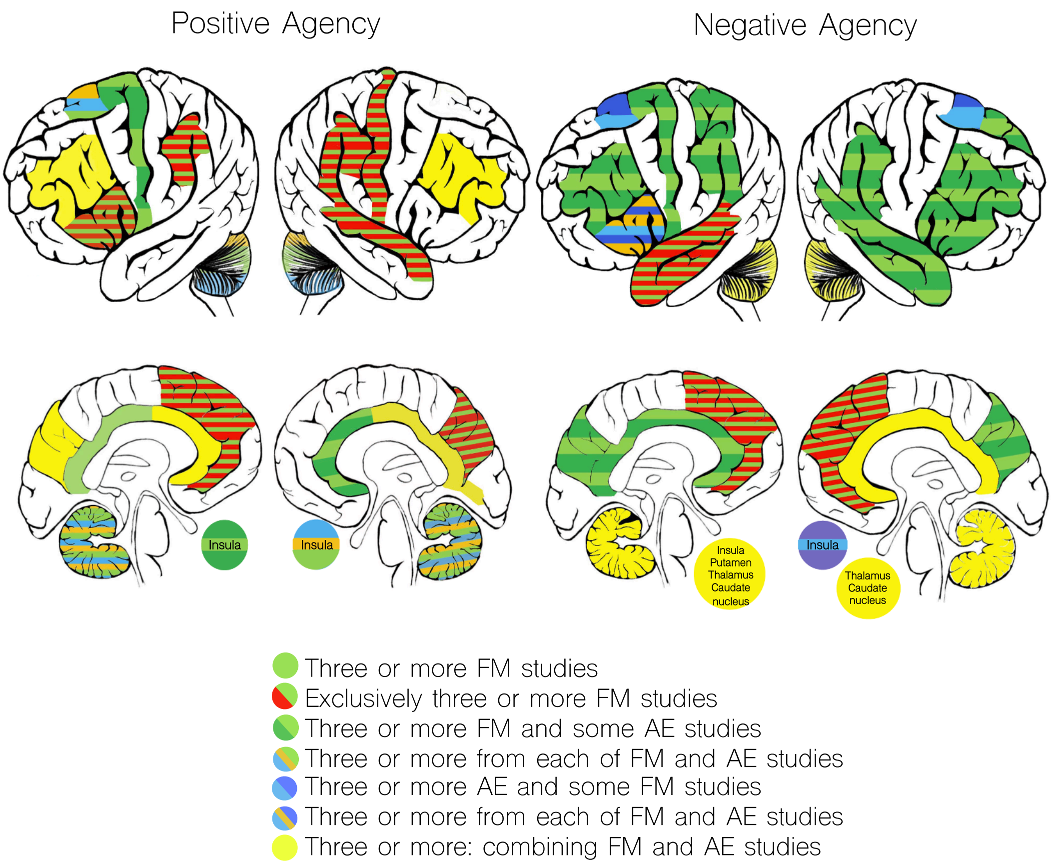

Fig. 1. Sense of Agency related brain activity. Being the agent (left): Here we summarize the activity reported in the 32 fMRI studies of sense of agency (SoA) reviewed in the current paper, when agency is explicitly reported or implicitly assumed due to congruent feedback. Not being the agent (right). Here we summarize the activity when absence of SoA is explicitly reported or implicitly assumed due to incongruent feedback. We highlight the activity over the brain regions reported active with color-coding as displayed in the figure, based on the number of Feedback Manipulation (FM) and Action-Effect studies (AE) report these regions to be active. See also Tables 2 and 3.

detailed description of this study (including participants' details, data acquisition and data analysis protocol) in the Supplementary Material.

3.1. Methods

3.1.1. Experimental paradigm

At the beginning of each trial a red circle with a smaller blue circle on top of it appeared on the bottom of the screen (Fig. 2). After 1500 ms, the red circle disappeared from the bottom of the screen and reappeared in the top position of the screen and participants received written instructions to initiate their movement. They had to use a stylus pen to move the blue circle towards the red circle in a straight line, after the instruction to move had been presented. The movement had to be performed fast and precise (upper limit of a total of 1500 ms). Once the participants finished their movement, they used a computer mouse to explicitly report if they felt they were the agent of the observed movement ("Was it you, who controlled?", "Yes" or "No", i.e., a dichotic Yes/No judgment of agency). We used the percentage of positive answers to this question to estimate the subjective agency fractions. The duration of each trial was approximately 6000 ms, as a jitter in time was introduced in the onsets of each trial to randomize the inter-stimulus intervals.

The main experiment consisted of 180 trials. There were three types of trials: self-movement (SM), computer-manipulated (CM) and pause (P) trials. These determined the type of feedback participants received while making their movement (SM or CM) or resting (P). The trials were presented in a pseudo-random order. In 18 SM trials the cursor (blue circle) moved congruent with participants' movement; in 18P trials participants were instructed not to move and just follow with their eyes the blue circle moving; and in 144 CM trials the cursor moved in a trajectory that deviated a few angles to the left or to the right of the hypothetical direct straight line (middle axis) they were instructed to draw. CM trials were further split in three levels: minimum, medium and maximum angle, based on the size of the trajectory's angle deviation (see supplementary material for further details). We ran the main experiment during the functional scanning session. The whole functional scanning lasted 21 min.

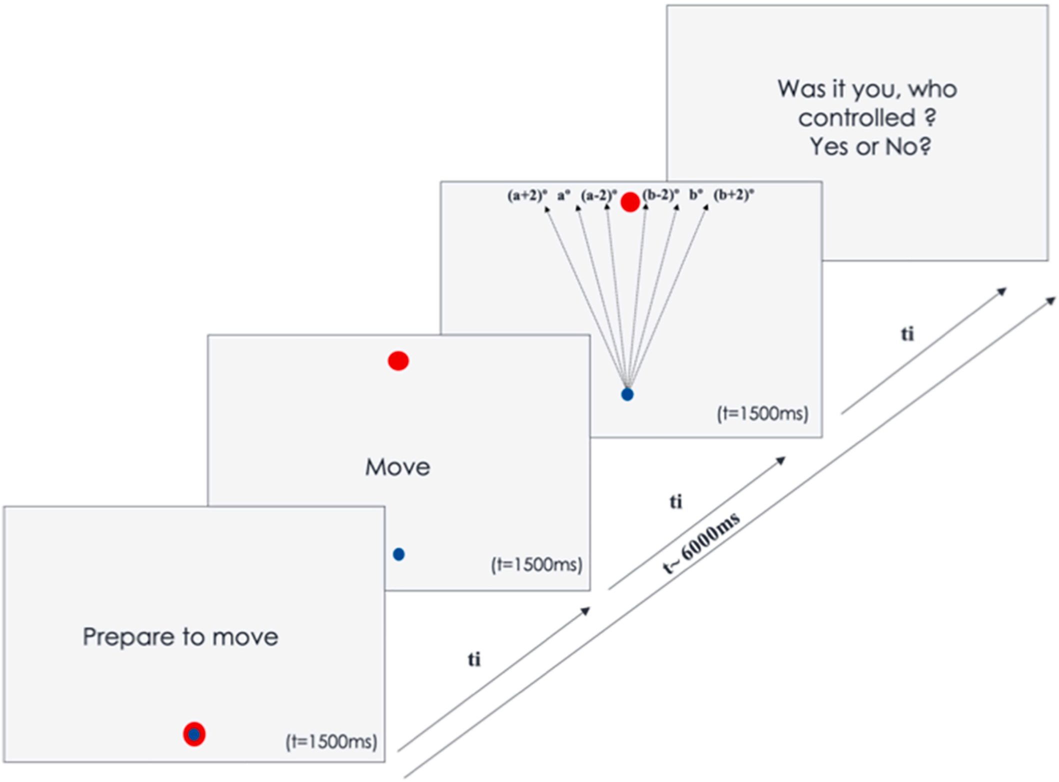

Fig. 2. Main experiment. Illustration of a computer manipulated movement trial (CM) during the main experiment. Every trial consisted of four steps. Participants were given written instructions throughout the trial. They had to use a stylus to control the movement of the blue circle from the bottom of the screen to the top, following the relocation of the red circle from the bottom to the top of the screen. These steps were preparation, movement, evaluation and back to the bottom of the screen. Every step had a duration of 1500 ms, while a jitter in time (t_i) was introduced between the steps. The third rectangular demonstrates the deviations of the movement presented on the screen, as the incongruent feedback, during the different CM trials. The angles a^o and b^o, where defined during the calibration test. See the text for further explanations. Apart from these CM trials, there were also trials where participants controlled the cursors' movement and trials where they were instructed to relax and watch the cursor move. At the end of each trial, they had to make a judgment of who was the agent of the observed movement. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. Results

A one-way ANOVA of the transformed agency yes fractions revealed a significant main-effect of perturbation size ($F(3, 27) = 37.5$, $p < 0.001$, eta2[g] = 0.733, $BF_{10} = 58.3\ 7\ {}^*10^7$). Post hoc comparisons, using Bonferroni corrections, indicated that agency score fractions were significantly different between conditions. Specifically, with the exception of SM and CM-minimum angle deviation trials, smaller perturbations led to larger proportions of positive agency judgments (see also Fig. 3). In other words, participants reported more often to be the agent of the movement when the deviations were either small or absent.

3.2.1. fMRI results

In this experiment we tested which brain areas are significant for the broad SoA. To find the regions which were active when participants experienced that they were the agent of the observed movement, we used the contrast [Agency Yes > Agency No]. Significant activity was found in: right anterior cingulate gyrus (cluster peak-t = 7.98, $p_{FWE\text{-}corr} < 0.001$, $BF_{10} = 15$, effect size = 2), right middle cingulate gyrus (cluster peak-t = 6.37, $p_{FWE\text{-}corr} < 0.001$, $BF_{10} = 5$, effect size = 1), left middle cingulate gyrus (cluster peak-t = 5.56, $p_{FWE\text{-}corr} < 0.001$, $BF_{10} = 3$, effect size = 0), left precentral gyrus (cluster peak-t = 7.57, $p_{FWE\text{-}corr} < 0.001$, $BF_{10} = 11$, effect size = 1), left postcentral gyrus (cluster peak-t = 7.18, $p_{FWE\text{-}corr} < 0.001$, $BF_{10} = 8$, effect size = 1) and left precuneus (cluster peak-t = 6.39, $p_{FWE\text{-}corr} < 0.001$, $BF_{10} = 5$, effect size = 1) (Table 4. and Fig. 4.). No significant activations were found for the contrast [Agency Yes < Agency No], $p_{uncorrected} > 0.1$.

3.3. Interim discussion

In summary, we found areas of activation in our fMRI experiment associated with positive SoA in the right anterior cingulate cortex, right middle cingulate cortex, left precentral gyrus, left postcentral gyrus and left precuneus. We used a Feedback Manipulation

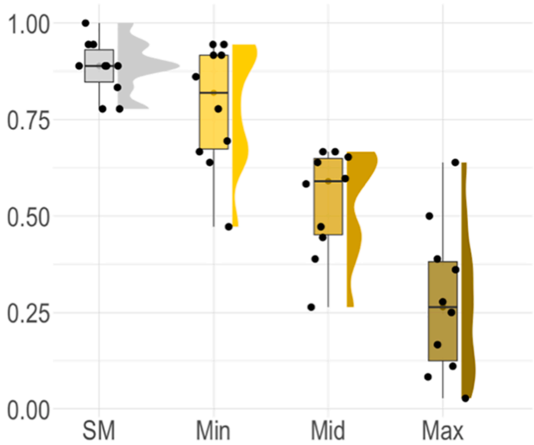

Fig. 3. Agency Fractions. Box plot and half violin plots illustrate the interquartile range and smoothed distributions of the data along with all sample points (n = 10). The fraction of Agency Yes scores correspond to the number of trials within each condition where participants reported "Yes" to the question "Was it you, who controlled?" over the total number of trials. The trial types included here are: self-generated movement (SM, in grey), during which the feedback was congruent with participants' movement and computer-manipulated movement (CM, shades of yellow), during which the blue circle moved in a trajectory that deviated a few angles from the hypothetical direct straight line they were instructed to draw. CM trials were divided based on the magnitude of the deviation in: maximum (Max), medium (Mid) and minimum (Min). The stars indicate the significance level based on post hoc pairwise comparisons using Bonferroni corrections. ***: $p < 0.001$, **: $p < 0.01$, * $p < 0.05$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4

Statistical test results of between group analysis. Statistical test results of between group analysis of the contrast [Agency Yes > Agency No], using classical and Bayesian inference, based on the participants' explicit reports on whether they felt they were the agent controlling the observed movement or not. Whole brain analysis, voxel level threshold $p < 0.001$ (uncorrected), cluster level FWE correction of $p < 0$ 0.05, with a minimum cluster consisting of > 50 voxels. Bayes factors are given for the voxels showing peak activity based on the classic inference. Next to the BF we include in parenthesis the cluster size based on the Bayesian inference. Active voxels and brain areas are given in Montreal Neurological Institute (MNI) stereotaxic coordinates (mm) in a probabilistic way. Number of participants: 10.

K_E	$P_{(FWE-corr)}$	$P_{(unc)}$	Zm	Cluster peak t-value	BF_{10} (cluster size)	MNI coordinates(x, y, z)			Anatomical description	
63	0.000	0.000	4.24	7.98	15(32)	3	14	26	R ACC	Area 33
			3.85	6.37	5	6	14	35	R MCC	R MCC
			3.57	5.56	3	−6	5	38	L MCC	L MCC
			4.14	7.57	11	−21	−22	65	L Precentral Gyrus	Area 4a
113	0.000	0.000	4.05	7.18	8(24)	−21	−34	56	L Postcentral Gyrus	Areas 3a/4p/3b
			3.83	6.39	5(17)	−15	−46	68	L Precuneus	Areas 5L (SPL)/ 5 M (SPL)

protocol and explicit dichotic agency reports. According to our classification, activity in the right anterior cingulate cortex and left precentral gyrus comes as no surprise. These regions have been primarily linked with positive SoA in Feedback Manipulation studies (right anterior cingulate cortex: Farrer et al., 2008; Jardri et al., 2011; Spaniel et al., 2016 and left precentral gyrus: Ohata et al., 2020; Jardri et al., 2011; Schnell et al., 2007; Spaniel et al., 2016) and in a few Action-Effect studies (right anterior cingulate cortex: de Bezenac et al., 2016 and left pre central gyrus: de Bezenac et al., 2016; Fukushima et al., 2013). Activity in the middle cingulate cortex has not been previously reported in relation to positive SoA. Nevertheless, none of the previous studies separated activity in the cingulate cortex to anterior posterior and medial, only to anterior and posterior. Therefore, it may be an anatomical reporting bias. Prior to our classification, the activity in the left postcentral gyrus and left precuneus would seem at odds with those areas we summarize in Tables 2 and 3. Namely, the areas most commonly reported in studies of SoA. However, this is not strictly true when comparing our results with the regions listed in Supplementary Table S2A. In this table, we present *all the areas* found in studies of SoA. Activity in the left postcentral gyrus and left precuneus is linked with positive SoA in both Feedback Manipulation (left postcentral gyrus: David et al., 2007; Schnell et al., 2007 and left precuneus: David et al., 2007; Spaniel et al., 2016) and Action-Effect studies (left postcentral gyrus: de Bezenac et al., 2016 and left precuneus: Fukushima et al., 2013). First, we see that all the regions found in our study were reported in both Feedback Manipulation and at least one Action-Effect study. This means the involvement of these regions goes above and beyond the characteristics of the Feedback Manipulation protocol used. Additionally, the studies that report the same areas as the ones we do used both implicit and explicit self-other (graded or dichotic) reports, which implies the involvement of these regions is not limited to the online monitoring of the movement. Finally, we see that these regions are linked to both positive and negative SoA (at least in one study). The fact that the activity we report is not reported exclusively in relation to negative or positive

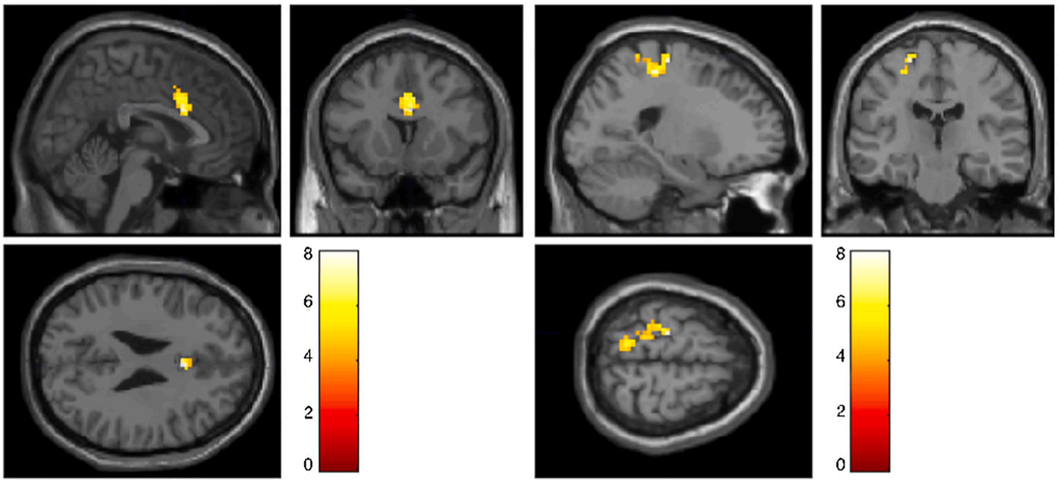

Fig. 4. Activation of the comparisons showing the regions that were significant more active in the “agency yes” compared to the “agency no” condition where participants explicitly reported they were or not the agent of the movement respectively. (Left) The cluster containing the right anterior cingulate gyrus and (right) the cluster containing the left precuneus, left precentral and left postcentral gyrus. Whole brain for the “Angles Separated” design where we specified eleven conditions, one for every combination of agency report and type of trial. The maps are superimposed on sagittal (left-top), coronal (right-top) and axial (bottom). Voxel level threshold $p < 0.001$(uncorrected). Cluster level FWE correction, $p < 0.05$, $N = 10$, color-bars represent t values.

SoA means that these areas are responsible for monitoring the action and are not specifically activated in relation to the SoA. Without the knowledge gained from the initial framework developed in this paper, we would not be able to sort out the differences that particular design elements provide to the activation maps.

3.3.1. Limitations of our study

One limitation of our study is the explicit agency report employed, which only indirectly addressed the ability dimension of SoA. By using the question “Was it you, who controlled?”, we only implicitly addressed the “You” in contrast to someone/something else. One should more explicitly study the self/other distinction by considering both the format of the question and the possible answers to it. In addition to that, the greatest limitation of our study is the low sample size, which is in general related to either high probability of false positives or low probability of measuring significant results (Button et al., 2013). Therefore, the activity measured when participants reported being the agent of the movement and the absence of activity related to the diminished SoA should be considered carefully. Nevertheless, our motivation for the current paper was to provide a framework for studying SoA. Hence, our study was primarily used as an example to illustrate the possibilities and benefits of this framework.

4. General discussion

In this paper, we reviewed 32 fMRI studies on the psychological construct SoA. We classified the results reported in those studies based on the experimental design and measure of agency employed. We followed the classification proposed by Christensen and Grunbaum, according to which there are three types of experimental designs used to study SoA: 1) Feedback Manipulation, 2) Action-effect, and 3) Sensory attenuation (Christensen & Grünbaum, 2017, 2018; Grünbaum & Christensen, 2020). Due to the low (one) number of Sensory attenuation fMRI studies, we focused on the other two. The main difference between these two types of studies is whether the manipulation is tightly related to the movement/ action participants perform (Feedback Manipulation) or the consequences of movement/action in the environment (Action-effect). The strength of classifying the studies into separate groups based on the experimental protocol is that it allows us to identify brain areas related to positive and negative SoA independently of experimental design and compare the reported areas within each group. There are two key findings of the present review: first there are regions commonly reported in both types of studies and second several regions are consistently reported in relation to both positive and negative agency within each type.

4.1. Commonalities between experimental type - elements of agency

Both Feedback Manipulation and Action-Effect studies agree on the involvement of supplementary motor area, insula and cerebellum in positive SoA and inferior frontal gyrus in the negative SoA. Both studies agree on these regions, which renders them highly relevant for SoA. The insula is involved in various processes, spanning from decision making and time perception to awareness of sensation and music perception, all of which contribute to some extent to self-awareness and subjective experiences (Craig, 2009; Gogolla, 2017). Furthermore, based upon the common co-activation the insula exhibits with the anterior cingulate cortex, it has been postulated that they form a salience network. The salience network is responsible for processing sensory stimuli, strengthening physiological awareness, and coordinating the central executive network and the default mode network to engage the relevant regions for the task in question (Menon & Uddin, 2010). In addition, the supplementary motor area and cerebellum are considered key areas for internal models of motor control. Namely, the former is responsible for providing the efference signal (Haggard & Whitford, 2004), a copy of the motor command necessary to perform a movement. At the same time, the latter uses this information to predict the sensory consequences of the movement and compare this prediction against the actual sensory information to estimate the error of performed movement (Tanaka, Ishikawa, Lee, & Kakei, 2020; Welniarz, Worbe, & Gallea, 2021; Wolpert, Miall, & Kawato, 1998). The involvement of the inferior frontal gyrus in negative agency is somewhat less clear as this area is linked to various processes spanning from language, speech and executive function, particularly inhibiting motor outputs (Dick, Garic, Graziano, & Tremblay, 2019; Liakakis, Nickel, & Seitz, 2011). Nevertheless, according to one account, inferior frontal gyrus, along with the rest of the regions responsible for inhibiting motor outputs, are activated in the presence of unexpected events (Wessel & Aron, 2017), which is highly relevant in situations of negative agency (e.g., when there is incongruency between the movement/action and the feedback). Interestingly, while all these areas commonly found in both types of studies seem to be highly relevant for SoA, they were also recently reported among the regions of a broad brain network responsible for predictive processing in language, music and action perception (Siman-Tov et al., 2019). That is, this network is not exclusively linked to SoA.

4.2. Impact of experimental paradigm

The second key finding of our review is that many regions were consistently reported active in connection to SoA within each experimental category, both for negative and positive SoA. Action-effect studies report the supplementary motor area, cerebellum and insula in both positive and negative agency. Likewise, Feedback Manipulation studies the medial frontal gyrus, inferior frontal gyrus, precentral gyrus, inferior parietal, precuneus, superior temporal and cingulate cortex. Notably, we found some regions in the left hemisphere, namely the medial frontal gyrus, supramarginal gyrus, superior and middle temporal gyrus, exclusively reported in Feedback Manipulation studies concerning negative agency. Given that activity in these regions is predominantly found in studies measuring SoA implicitly or using a delay detection questionnaire suggests that activity in these areas is tightly linked to the experimental protocol employed. That is, Feedback Manipulation experiments focus on the "narrow SoA" closely related with the movement one performs, and the Action-Effect studies on the "broad SoA" (Christensen & Grünbaum, 2017, 2018). Indeed, our summary report indicates that the regions exclusively reported in Feedback Manipulation studies are important for the online monitoringof a movement. For instance, precuneus with the medial prefrontal cortex constitute part of the default mode network (DMN) of the brain. The DMN is most commonly related to an activation decrease during goal-directed, attention-demanding non-self-referential tasks (Raichle et al., 2001; Raichle, 2015). Part of the DMN is related to processing of self-referential stimuli (see Qin & Northoff, 2011). Whilst the DMN has been predominantly associated with decreased activity during active-goal directed actions (Buckner, Andrews-Hanna, & Schacter, 2008), recent studies support the opposite. They describe DMN as a dynamic network that continuously adjusts its topology to effectively support the brain, according to the current brain state (Lin et al., 2017). Overall, the impact of the experimental paradigm on the regions reported goes against conceptualizing SoA as a homogeneous psychological phenomenon equally measured using either experimental design.

It is important to note that in our effort to better understand how the different experimental protocols affect our SoA, we tried to be as inclusive as possible. This means for example that we collapsed the findings from Action-Effect studies measuring the effect of action selection fluency on SoA (Chambon et al., 2013) with Action-Effect studies that employed implicit measures of agency like the intentional binding effect (Kühn et al., 2013; Seghezzi & Zapparoli, 2020) and studies in which participants pressed a button and visual stimuli appeared synchronously or with a delay (Matsuzawa 2005). In the study measuring the action selection fluency, the focus is on the prospective components of agency and particularly, how this fluency affects our agency. According to the intentional binding effect, the time between a movement and the movement's outcome is perceived shorter, for voluntarily executed movements: "Press a button on the keyboard and report when you hear the resultant tone." (Haggard, Clark, & Kalogeras, 2002; Moore & Obhi, 2012). These three examples illustrate that even though our classification helped us to better organize the findings from the different types of studies, further research is needed to specify the within-group differences that may exist due to the specificities of each task.

4.3. Agency report

In some of the studies participants gave explicit agency reports and in others SoA was implicitly measured. Recent studies provide accumulative evidence that there is no direct behavioral relationship between explicit and implicit measures of agency, (Ma, Hommel, & Chen, 2019; Schwarz et al., 2019a, 2019b). Unfortunately, regarding the explicit reports based on our review it remains unclear whether explicit dichotic (Were you the agent, yes or no?) or scaled explicit reports (from X to Y how much did you feel you were the agent?) result in a distinctive brain activity pattern (See also Supplementary Tables S2A & S2B). In addition, due to the low number of studies employing a question that is related to the phenomenological perceptual experience of control in Feedback Manipulation studies, we cannot explicitly state whether there are any neural correlates related to a narrow phenomenological experience of SoA, that is unrelated to external events caused by the action.

4.4. Studying sense of agency

It has been argued before that SoA comprises an omnipresent phenomenological experience accompanying volitional movements, running in the background of any executive processes (Moore, 2016). In other words, in our everyday life SoA becomes evident only when it is absent. To consciously experience SoA, it implies that a person needs to effortfully attend their movements or actions while performing them. This rather nonexclusive -yet simple to understand- interpretation illustrates some of the common pitfalls in studies of SoA. For years now, SoA has been a synecdoche in many studies employing different experimental paradigms and report types. Studies belonging to the Feedback Manipulation and Sensory Attenuation categories, focus on the movement, while Action-Effect studies focus on the consequences of the movement in the surrounding environment. In spite of the criticism regarding the efficacy of these experimental strategies (Christensen & Grünbaum, 2017, 2018; Zaadnoordijk, Besold, & Hunnius, 2019), less focus has been given so far to the impact of these designs in the neuronal activity pattern reported. In order to optimize the experimental strategies though, it is important to scrutinize the findings from existing neuroimaging studies and look for where they converge or diverge. After comparing the findings of different studies within and between the different categories it became evident that there is a noticeable diversity in the reported results between categories that pose limitations in conceptualizing SoA as one unified psychological phenomenon. While we found a few areas commonly reported in both, we also found a number of areas exclusively in Feedback manipulation studies. Therefore, when studying SoA the characteristics of the design should be taken into consideration and explicitly discussed. Furthermore, it is interesting that despite the description of SoA being an omnipresent phenomenological experience, only relatively few of the experimental studies reviewed here have employed a question that addresses this aspect of SoA, more studies actually focus on the ability aspect of SoA. In order to determine the exact neurobiological differences between the ability and phenomenological aspect of SoA therefore requires that more studies actually study the impact of the different questions on the behavioral task employed. Based on the findings presented in the previous section (see also Fig. 1. and Supplementary Tables S2A & S2B) SoA seems less likely to constitute one homogeneous psychological phenomenon. This finding agrees with several previous papers that have put forward this idea (David, 2012; Gallagher, 2012; Pacherie, 2007; Synofzik et al., 2008).

4.5. Limitations

One limitation of our review -in particular concerning Action-effect studies- is that we included within each experimental category studies that focused on different aspects of SoA (see *Impact of Experimental paradigm*). Another limitation is that we used the MNI and Talairach coordinates reported in each study, and we did not transform the coordinates into a single coordinate system. Nevertheless, since we did not plan to run a *meta*-analysis on the reported results, we decided this was sufficient for the purpose of our study. Additionally, each study used a variety of contrasts to measure SoA (see Supplementary material) and we need to emphasize that this might have led to some simplification of the overall findings reported in this review. Finally, because -similar to our study- some of the studies we reviewed here have low sample sizes, the findings they report could be reflecting false positives and hidden effects. Therefore, the outlook we get from our review needs to be further verified.

4.6. Future direction

The classification of the fMRI studies on SoA led to some interesting findings that require further investigation. For example, it would be interesting to explicitly test the effect of the experimental protocol and particularly the difference between the narrow and broad SoA within the same experiment and participants. Furthermore, it would be interesting to study how the explicit report types, namely dichotic vs graded and narrow vs phenomenological impact the neural underpinnings of SoA.

5. Conclusion

Our review emphasizes the diversity in the studies of SoA and how this diversity poses limitations in understanding the notion of SoA. We summarized the most commonly reported areas in the studies of SoA and proposed a way to divide these findings in separate groups depending on the experimental protocol and measure of agency employed. Feedback Manipulation and Action-Effect share common activation in supplementary motor area, insula and cerebellum in positive SoA and inferior frontal gyrus in the negative SoA. But besides that, we find that left medial frontal gyrus, left inferior frontal gyrus, right postcentral gyrus, right precuneus and right superior temporal gyrus are the areas linked with positive agency exclusively in Feedback Manipulation studies. Based on the current review, SoA is less likely to constitute a homogeneous psychological phenomenon, and it requires careful consideration when interpreting the results of SoA studies, because the results seem to depend on the experimental protocols employed.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.concog.2022.103307.

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