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The "sense of agency" and its underlying cognitive and neural mechanisms

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ABSTRACT

The sense of agency is a central aspect of human self-consciousness and refers to the experience of oneself as the agent of one's own actions. Several different cognitive theories on the sense of agency have been proposed implying divergent empirical approaches and results, especially with respect to neural correlates. A multifactorial and multilevel model of the sense of agency may provide the most constructive framework for integrating divergent theories and findings, meeting the complex nature of this intriguing phenomenon.

1. Introduction

In our everyday life we often perform goal-directed actions which we normally do not reflect upon such as grasping a glass of water when we are thirsty. Actions or certain movements may happen because an intention-to-act generated a corresponding motor program in order to reach the intentional goal. But how do we know that we ourselves are the ones grasping the glass of water? An executed movement is associated with certain expected consequences, for example, feeling the arm move in a certain way or perceiving the glass in our hand. Such proprioceptive or visual reafferences as well as corresponding motor signals may not only help to adjust a given motor program but may also contribute to the feeling that we are the agents, that is, initiators and executors of our grasping the glass of water. This experience of oneself as the agent of one's own actions—and not of others' actions—has been described as "the sense of agency" (Gallagher, 2000) and is a central feature of the different phenomenal experiences constituting self-consciousness (as defined by Newen & Vogeley, 2003; Gallagher, 2000). Besides the endeavor to elucidate the functional basis of the sense of agency there is also a substantial interest in exploring dysfunctions of it. Disturbances might have a profound impact on an individual's functioning in society as observed, for instance, in the pathological condition of schizophrenia. To date, a comprehensive and integrative understanding of the sense of agency, also in relation to other cognitive processes, and its underlying mechanisms is missing. With the present paper we focused on current concepts as well as empirical findings related to the sense of agency and discuss open questions in the field.

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2. The sense of agency: Definition and concepts

The sense of agency has been defined as "the sense that I am the one who is causing or generating an action. For example, the sense that I am the one who is causing something to move, or that I am the one who is generating a certain

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thought in my stream of consciousness" (Gallagher, 2000, p. 15). As such, one can distinguish actions that are self-generated from those generated by others giving rise to the experience of a self-other distinction in the domain of action and thus contributing to the subjective phenomenon of self-consciousness (Gallagher, 2000; Georgieff & Jeannerod, 1998; Pacherie & Jeannerod, 2004). Thereby the sense of agency is different from the sense of ownership, defined as "sense that I am the one who is undergoing an experience [...] that my body is moving regardless of whether the movement is voluntary or involuntary" (Gallagher, 2000, p. 15). Passive limb movements (i.e., when my arm is moved by someone else), for example, illustrate the difference between ownership and agency. Although in normal experiences of voluntary actions both senses usually coincide and are indistinguishable (Tsakiris, Schütz-Bosbach, & Gallagher, 2007), they have often been confused in experimental situations. That is, some agency studies that employed self-recognition tasks were confounded by measuring a sense of ownership rather than of agency (also not considering that both senses may be more basic than self-recognition).

Recent conceptual developments distinguished between different levels of the sense of agency (Synofzik, Vosgerau, & Newen, 2007). According to Synofzik and colleagues, the sense of agency comprises an implicit level of "feeling of agency" as opposed to an explicit level of "judgment of agency" (also compare to Georgieff & Jeannerod, 1998). The first level is thought to be characterized by lower-level, pre-reflective, sensorimotor processes and the second level by higher-order, reflective or belief-like processes (i.e., the awareness or attribution of who has caused an action; Georgieff & Jeannerod, 1998). The introduction of a lower-level feeling of agency represented an important conceptual step given that we usually do not reflect upon our own actions (as we normally would not reflect on typing these letters). It is in accordance with Gallagher's notion of a basic form of self-consciousness, the content of which is not informed by conceptual thought or reflective processing (Gallagher, 2000; Legrand, Brozzoli, Rossetti, & Farnè, 2007). Synofzik et al. (2007) suggest a two-step model: the feeling of agency must be conceptually processed for a judgment on or an attribution of agency to occur. Although Synofzik and colleagues (2007) do not use terms such as "conscious" vs. "unconscious" or "preconscious", sensorimotor processes sought to be characteristic for the feeling level may run outside of consciousness (but may be available to awareness, see Blakemore, Wolpert, & Frith, 2002).[1] This is supported by empirical evidence that, for example, minor "violations" of intended actions or action consequences do not necessarily enter awareness (e.g., brief [<250 ms] temporal delays in sensory feedback; Blakemore & Sirigu, 2003; Fourneret & Jeannerod, 1998; Slachevsky et al., 2001), while neural signatures of such violations can be observed (David et al., 2007a; Chapter 4). Importantly, though, eempirical investigations often focused on judgments or attributions of agency, involving subjective reports and errors through misidentification (David et al., 2007a; Fourneret & Jeannerod, 1998; Frith, Perry, & Lumer, 1999; Shoemaker, 1968; Chapter 3, Table 1). By contrast, multivariate approaches that include implicit measures (e.g., kinematics, eye movements, motor potentials, brain activity, etc.) may also tap into the feeling level of agency.

For the sake of simplicity, we will use "sense of agency" as a superordinate term throughout this article unless either the feeling or judgment level is specifically addressed.

3. Cognitive theories of agency, empirical indicators and related processes

3.1. Comparator Model

The predominant account on explaining the sense of agency of our own actions has been the "central monitoring theory" or "comparator model" as a theory of motor learning and motor control (Blakemore, Frith, & Wolpert, 2001; Blakemore, Wolpert, & Frith, 1998; Frith, 1992; Kawato, 1999; von Holst & Mittelstaedt, 1950; Wolpert, Ghahramani, & Jordan, 1995). Accordingly, two types of internal models are implemented in the central motor system: so-called inverse and forward models. Although the primary role of these internal motor models is considered the control and optimization of motor behavior, relevance for action awareness has also been discussed (Blakemore & Frith, 2003; Blakemore et al., 2002; de Vignemont & Fourneret, 2004; Frith, 1992; Synofzik et al., 2007). Thereby, the sense of agency particularly hinges on the forward model, which uses an efference copy, that is, a copy of a motor command predicting respective sensory consequences. Accordingly, congruence of the predicted with the actual outcome, then, supposedly would lead to the attribution of the sense of agency to oneself, whereas incongruence would indicate another agent as the cause of an action (Fig. 1). It seems like we are not necessarily aware of this comparison and its results as long as the desired state is successfully achieved (Blakemore & Frith, 2003; Fourneret & Jeannerod, 1998; Slachevsky et al., 2001). In fact, a large body of evidence suggests that the sense of agency, especially the judgment of agency, strongly depends on the degree of congruence versus incongruence between predicted and actual sensory outcome (e.g., Fourneret & Jeannerod, 1998; Sato & Yasuda, 2005; for a critical discussion of the use of the comparator model for thoughts see Vosgerau & Newen, 2007).

Many experimental investigations of the sense of agency have drawn on this theory by manipulating the sensory, particularly visual, consequences of subjects' actions (Table 1). A classical experiment was conducted by Nielsen

[1] The functional role of consciousness is different from the functional role of a representation and its content. Synofzik et al.(s) (2007) account rather focuses on the content of representations given by the feeling or judgment of agency. In principle, both the feeling as well as the judgment of agency could be both conscious and unconscious.

Table 1
Overview and taxonomy of current experiments on the sense of agency

Experiments	Task	Feedback to movement		Manipulated signals			Assessment of agency			Movements	
		Emb.	Disemb.	Eff.	Reaff.		Expl. (Judgment)		Impl	Volunt.	React.
					Prop.	V./A./T.	Each trial	Post-exp. debriefing			
Behavioral studies with healthy subjects											
Nielsen (1963)	Line drawing with spatially manipulated visual feedback (“alien” hand)	x				x	x			x	x
Fourneret & Jeannerod (1998)	Computerized line drawing with spatially manipulated visual feedback		x			x	x				x
Blakemore et al. (1998)	Self-controlled tickling with temporally and spatially delayed feedback		x			x			x		x
Haggard et al. (2002)	Judging onset of voluntary key presses inducing a finger twitch or tone		x	x			x			x	
Farrer et al. (2003a, 2003b)	Recognition of one’s own limb from a spatially deviating alien hand	x		x		x	x				x
MacDonald & Paus (2003)	Detection of temporal delays in active/passive finger movements displayed as virtual hand	x		x		x	x				x
Q6 Knoblich & Kircher (2004)	Drawing task with varying visual feedback velocity		x			x	x				x
Wegner et al. (2004)	Inducing a feeling control over others’ movements by prior instructions	x						x	x		
Tsakiris et al. (2005)	Self-/other-generated movements with manipulated visual feedback (own or other’s hand)	x		x		x	x				x
Sato & Yasuda (2005)	Button presses with associated tones (congruent/incongruent)		x			x	x			x	x
Aarts et al. (2005)	Self-/other-generated events under priming		x				x				x
Q7 Synofzik et al. (2006)	Pointing movements with spatially manipulated visual feedback		x			x	x			x	x
Q8 Tsakiris et al. (2006)	Rubber hand illusion with active/passive finger movements, tactile stimulation & temporally delayed visual feedback	x		x		x	x				x
Behavioral studies with patients (with Schizophrenia if not otherwise specified)											
Daprati et al. (1997)	Recognition of own or other’s hand performing movements	x				x	x				x
Sirigu et al. (1999)	see Daprati et al. (1997), with apraxic patients	x				x	x				x
Knoblich et al. (2004)	Drawing task Knoblich & Kircher (2004)		x			x	x				x
Farrer et al. (2003a, 2003b)	Recognition of own limb position from a spatially deviating alien hand in a deafferent patient	x			x	x	x				x
Fourneret et al. (2001)	see Fourneret & Jeannerod (1998)		x			x		x			x
Q9 Franck et al. (2002)	see Fourneret & Jeannerod (1998), with deafferent patient		x		x	x	x				x
Haggard et al. (2003)	Judging onset of key press action or action consequence (tone)		x			x			x		
Slachevsky et al. (2001)	see Fourneret & Jeannerod (1998); with patients with lesions in PFC		x			x	x				x

(*continued on next page*)

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Table 1 (*continued*)

Experiments	Task	Feedback to movement		Manipulated signals			Assessment of agency			Movements	
		Emb.	Disemb.	Eff.	Reaff.		Expl. (Judgment)		Impl	Volunt.	React.
					Prop.	V./A./T.	Each trial	Post-exp. debriefing			
David et al. (2007a, 2007b)	Detection of temporally and spatially delayed visual cursor feedback to joystick movements; with subjects with autism spectrum disorders		x			x	x	x			x
Balslev et al. (2007)	Recognition of finger movements by visual cursor feedback (w/delay or not); with deafferent patient		x		x	x	x				x
Neuroimaging studies with healthy subjects											
Blakemore et al. (1998)[e]	Button presses/no button presses coupled with un-/predicted tones		x	x	x	x			x	x[b]	
Blakemore et al. (1998)	Self- or externally produced tactile (tickling) stimulations		x[c]	x	x	x			x		x
Fink et al. (1999)[e]	In/out-of-phase bimanual movements with mirror reflection (or not)	x		x		x		x			x
Chaminade & Decety (2002)[e]	Controlling a circle (leading, following or observing another circle)		x	x		x			x	x	x
Farrer & Frith (2002)	Self- or other-controlled joystick movements	x				x			x		x
Farrer et al. (2003a, 2003b)[e]	Joystick movements with spatially deviating visual feedback (varied)	x				x	x[a]				x
Leube et al. (2003)	Perform/observe hand movements of own or other hand	x		x		x			x		x
Leube et al. (2003)	Continuous hand movements filmed & played back with temporal delay	x				x	x			x[d]	
Ramnani & Miall (2004)	Conditional motor task (button presses associated with certain outcomes, i.e., shapes); different agents (subject, 3rd person, PC)		x						x		x
David et al. (2006)	Virtual ball-tossing game		x			x		x			x
David et al. (2007a, 2007b)	Detection of temporally and spatially delayed visual cursor feedback to joystick movements		x			x	x	x	x		x
Schnell et al. (2007)	Computer racing game with temporal incongruence in visual feedback		x			x	x				x
Ogawa & Inui (2007)	Visual tracking task via mouse with transient cursor or target occlusions		x			x			x	x	
Farrer et al. (2007)	Manual pg removal task with delayed visual feedback	x		x			x				x
Neuroimaging studies with patients (Schizophrenia)											
Spence et al. (1997)[e]	Cued joystick movements without visual feedback						x		x	x	
Farrer et al. (2004)[e]	Random joystick movements with spatial deviations in visual feedback	x				x	x[a]			x	

Note. This table aims to give an overview over current empirical studies and to demonstrate their diversity. It does not claim to be exhaustive.
Abbreviations. Emb., embodied (e.g., displayed is the subject's hand); Disemb., disembodied (meant in the anatomical sense, e.g., a virtual hand would also count as disembodied). Eff., efferent (central motor signals; e.g., an active vs. passive movement); Reaff., reafferent (feedback signals arising from movement; e.g. sight or feeling of moving arm, sight of joystick-driven cursor movement, etc.). Prop., proprioceptive (e.g., internal signals about the position of the body from muscles and joints); V./A./T., visual, auditory, tactile (i.e., external signals). Exp., explicit (e.g., a judgment is made on each trial, e.g., whether a movement was self-generated or not); Impl., implicit (e.g., no judgment is made, just fMRI signal, etc.). Volunt., voluntary (e.g., freely chosen, self-paced movements), React., reactive (e.g., cued, time constraint movements).
[a] After each condition block.
[b] Self-paced button presses.
[c] Touch with a foam or no feedback.
[d] Continuous hand movements (open hand, close hand) at .5 Hz.
[e] PET study.

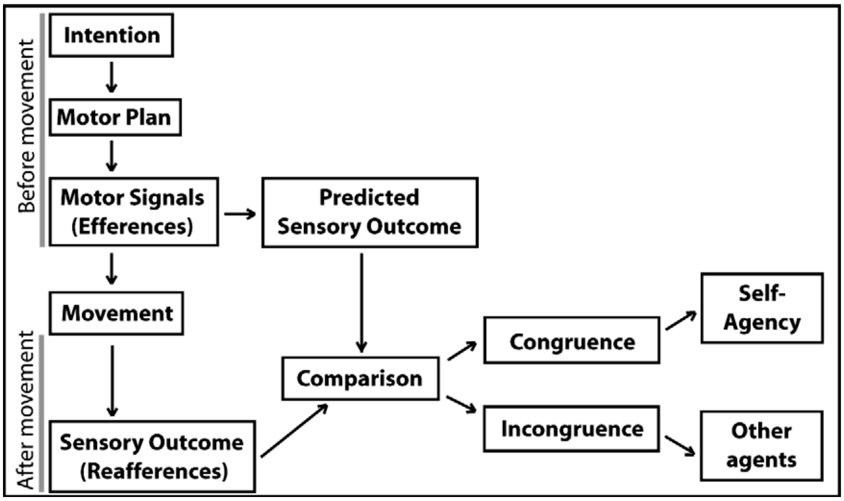

Fig. 1. Central monitoring theory or comparator model.

(1963): Subjects were asked to draw a line on a piece of paper. They could either see their own or, unbeknownst to the subject, an "alien hand" (i.e., the experimenter's hand). The alien hand's movements spatially deviated from the subject's own movement. Interestingly, subjects adjusted their own actual movement to the false visual feedback without being aware of the adjustment. Since 1963 many adaptations of this manipulation have evolved (Daprati et al., 1997; David
Q3 et al., 2007a,2007b; Farrer et al., 2003a; Farrer, Franck, Paillard, & Jeannerod, 2003b; Farrer & Frith, 2002; Fink et al., 1999; Fourneret & Jeannerod, 1998; MacDonald & Paus, 2003; Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999; Slachevsky et al., 2001). Research thereby indicated that visual signals might overrule proprioceptive or motor signals (cf. van Beers, Wolpert, & Haggard, 2002), suggesting that vision is the dominant modality. However, the sense of agency cannot be considered as being solely influenced by visual reafferences (Tsakiris & Haggrad, 2005; Tsakiris et al., 2007). Critically, only a few experiments manipulated internal signals such as proprioceptive (in deafferent patients: Balslev, Cole, & &Miall, 2007; Farrer et al., 2003b) or motor signals (e.g., active vs. passive movements: Blakemore et al., 1998; Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005; Table 1). This may be due to the notion that internal parameters of action monitoring like motor plans, motor programs or efference copies are automatic and consciousness to them limited. Nevertheless, conscious access to prior intentions and visual feedback is available (de Vignemont & Fourneret, 2004), allowing experimental manipulations. The distinction between a feeling and judgment level (chapter 2) may come into play again here with internal signals appearing to be related to the implicit and pre-reflective feeling of agency. However, if subjects are instructed to explicitly evaluate self-other agency for each trial (e.g., Balslev et al., 2007; Tsakiris et al., 2005) internal signals such as intentions as much as external signals such as visual reafferences may influence the subjects' judgments, at least to a certain degree.

The comparator model has also been associated with abnormalities of action awareness. For example, patients with schizophrenia may suffer from delusions of control, in which they experience others' actions as a consequence of their own intentions or attribute their own actions to external sources (Daprati et al., 1997; Franck et al., 2001; Frith & Done, 1989; Haggard, Martin, Taylor-Clarke, Jeannerod, & Franck, 2003). Several authors have explained such delusions as a breakdown of central monitoring mechanisms (Blakemore et al., 2002; Frith, 1992; Frith & Done, 1989; cf. Fourneret, Franck, Slachevsky, & Jeannerod, 2001; Gallagher, 2004). Other studies suggested that central monitoring is not impaired in schizophrenia because patients show normal visual-motor adaptation (Fourneret et al., 2001; Knoblich, Stottmeister, & Kircher, 2004) with errors arising on the judgment or attribution level of agency (e.g., Fourneret et al., 2001).

3.2. Simulation theory

The "simulation theory"—similar to the comparator model or central monitoring theory—also proposes a functional role
Q5 of the motor system is (also understood as opposing account, Jeannerod & Pacherie, 2004). This theory posits that in understanding or predicting other people's behavior we use our own experiences to simulate those of others (Goldman, 1989). The discovery of "mirror neurons" in the macaque brain, which discharge both during action execution and observation (i.e., including another agent; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001), lent some support to simulation theory (critically discussed in Saxe, 2005) but direct neurophysiological evidence from the human brain has yet to be delivered (Keysers & Perrett, 2004). Nonetheless, simulation theory—assuming shared representations for self and other—can not explain why we normally do not confuse our own and others' actions. This is in line with Sebanz and Frith (2004) who argued that "the mirror neuron system does not provide an explicit representation of other agents" and that "an additional mechanism must be assumed", realizing the representation of me or someone

else as the agent (as supported by Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006, or evidence from neuroimaging such as Farrer & Frith, 2002; Farrer et al., 2003a,2003b). In the literature—as opposed to the mirror neuron system—this has also been referred to as a "'Who' system" (de Vignemont & Fourneret, 2004; Georgieff & Jeannerod, 1998). The "Who"-question certainly is at the core of the ability to distinguish self from other or the development and integrity of human self-awareness. Decety and Sommerville (2003) suggested that self-awareness and agency (i.e., a Who system), in fact, are used to navigate within shared representations. To date, however, it remains debated which signals or mechanisms mainly contribute to this system and whether they need to be conscious. The comparator and predictor mechanism of the forward model may add to this issue (i.e., *congruence* between predicted and actual state might be used to register a sensory event as caused by oneself, *incongruence* to the registration of a sensory event as externally caused; previous chapter) but, clearly, can not be the only relevant mechanism (chapters 3.3. and 3.5).[2]

The relevance of simulation for the sense of agency may be probed within a population, for which simulation deficits have been convincingly proposed such as autism spectrum disorders (Dapretto et al., 2006; Oberman et al., 2005). We investigated the sense of agency in subjects with high-functioning autism or Asperger syndrome (David et al., 2007b). Subjects performed comparably to healthy control subjects without evidence for an agency impairment. However, our subjects did show deficits in perspective taking which has been explicitly linked to simulation (Gallese & Goldman, 1998; Langdon & Coltheart, 2001). This finding is in accordance with related data from Sebanz and colleagues (2005) who found that subjects within the autism spectrum did not show deficits in representing another person's action but exhibited mentalizing deficits. These clinical data support the idea that the simulation theory may not be adequate for exhaustively explaining the sense of agency (also see Sebanz & Frith, 2004).

3.3. *Intentional binding*

Haggard and colleagues proposed an eminent role of "intentional binding" for the sense of agency (Haggard, Clark, & Kalogeras, 2002; Haggard et al., 2003; Tsakiris & Haggard, 2003). Accordingly, intentions contribute substantially to action awareness; that is, in normal agency experiences an action occurred because or via an intention. Importantly, Haggard et al. refer to a special case of intention, namely an intention-in-action, which is not separate from the action itself and which includes a representation of the goal of an action (Searle, 1983). In several experiments similar to the seminal work by Libet, Wright, Feinstein, & Pearl (1979), Haggard and colleagues supported their idea of intentional binding showing that voluntary—but not involuntary or passive—movements and movement consequences are temporally bound together in conscious awareness (Haggard & Clark, 2003; Haggard et al., 2002; Tsakiris & Haggard, 2003; cf. Sato & Yasuda, 2005). That is, subjects judged the perceived onset of voluntary movements as occurring later and the sensory consequences as occurring earlier than it was actually the case (for a discussion and critique of Haggard et al.'s as well as Libet's experiments and their interpretation, e.g., see Geyer, 2004, or Consciousness and Cognition, Vol. 11(2), 2002).

It is also possible that the subjects' intention may overrule a given sensory feedback to a respective movement. That is, once an intention to act has been formed, actions and action consequences are more likely attributed to oneself even if they were externally generated (e.g., David et al., 2007a; Fourneret & Jeannerod, 1998; Jeannerod & Pacherie, 2004). Wegner discussed the tendency of subjects to naturally perceive themselves as causally effective (Wegner & Sparrow, 2004; Wegner & Wheatley, 1999). For example, Wegner and colleagues investigated the influence of action-relevant thoughts that increased the feeling of self-efficacy over movements, such as the mere perception of a given instruction or effects of priming (Aarts, Custers, & Wegner, 2005; Wegner, Sparrow, & Winerman, 2004). In contrast to Haggard and colleagues' "constructive" view on intentional binding or the assumption of internal predictive models such as the comparator, Wegner and colleagues "reconstructive" account rather assumes that subjects retrospectively attribute (or post hoc evaluate) intentions to themselves to explain that or how an action happened (for a discussion and empirical validation of the two accounts, see Haggard & Clark, 2003 and Knoblich & Sebanz, 2005).

3.4. *Related processes*

With this chapter we aim to describe cognitive processes often mentioned and discussed in relation to the sense of agency such as imitation and perspective taking, and more basic, domain-general processes such as executive functions and attention. For example, imitation and perspective taking also imply the distinction between oneself and others. Are they prerequisites for the sense of agency (Nadel, 2004) or do they emerge from it as a more fundamental process (Meltzoff & Gopnik, 1993)? Both a first-person perspective and a sense of self-agency have been proposed as key constituents of human self-consciousness (Gallagher, 2000; Metzinger, 2000; Vogeley et al., 2004). Moreover, viewpoint-specific visual-spatial cues have been discussed as indicators for the sense of agency ("knowing where the body is and what tools or environmental opportunities are available in its current orientation helps to determine what the person could have authored"; Wegner et al., 2004, p. 838). In fact, others' actions may be associated with allocentric (coding object-to-object relations in space) as op-

[2] While incongruence between predicted and actual movement consequences usually triggers an online correction of my movement (e.g., "I missed the cup so I adjust my reaching towards it"), it normally does not necessarily lead to an attribution of the action to another agent or external sources (e.g., "I missed the cup so someone else drew it back"). These different experiences may be modulated by additional factors such as knowledge ("The cup could not have moved away by itself"), environmental cues ("There was no-one else in the room to move it") and intentions ("It was my intention to grab it because I was thirsty").

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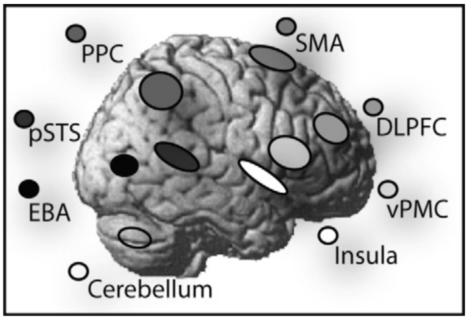

Fig. 2. Brain regions associated with the sense of agency.

posed to egocentric (subject-to-object) representations (Farrer & Frith, 2002; Jeannerod, 1999). By contrast, it has been suggested that perspective taking has evolved from an action representation system (Frith & Frith, 1999). These claims have led us to investigate the sense of agency in relation to perspective taking (David et al., 2006,2007b).[3] Partially overlapping activation patterns confirmed a kinship between visual-spatial perspective taking and agency (David et al., 2006). In contrast, and with respect to mental perspective taking ("mentalizing"), we found a behavioral dissociation between mentalizing and the sense of agency in the neurodevelopmental syndrome of high-functioning autism (David et al., 2007b; Table 1), rather lending support to the view that mentalizing evolves from or after the formation of an action representation system (Frith & Frith, 1999). In the same sample we found evidence for another dissociation, namely, between impaired attention and executive functions and an intact sense of agency (David et al., 2007b; a similar dissociation has been shown for schizophrenia; Turken, Vuilleumier, Mathalon, Swick, & Ford 2003). This is interesting as attention and executive functions such as self-monitoring are often regarded as confounding factors in agency paradigms (e.g., shifts of attention towards incongruent sensory feedback). Double dissociations between an intact sense of agency and impaired attention, executive function or mentalizing suggest some degree of orthogonality between agency and those processes.

3.5. Concluding remarks

Despite different theoretical accounts on the sense of agency, an understanding of the sense of agency must include the insight that it is not a unitary but complex cognitive phenomenon. Cues from different sources must be taken into account, such as (i) efferent or central motor signals (Blakemore et al., 1998; Tsakiris et al., 2005), (ii) reafferent feedback signals from proprioception (Farrer et al., 2003b), or, (iii) vision (Balslev et al., 2007; Fourneret & Jeannerod, 1998; Slachevsky et al., 2001), (iv) action intentions or prior action-relevant thoughts (Aarts et al., 2005; Haggard et al., 2002; Wegner & Sparrow, 2004; Wegner & Wheatley, 1999), (v) knowledge (Wegner & Sparrow, 2004), and, (vi) cues from context or environment (Wegner & Sparrow, 2004). "Often these authorship indicators converge and complement each other, sometimes they conflict, but each may be sufficient to support inferred authorship in the absence of others" (Wegner & Sparrow, 2004, p. 1203).

It can be critically asked how many experimental paradigms investigating the sense of agency—including our own studies (David et al., 2007a,2007b; cf. David et al., 2006)—actually corresponded to everyday experiences. For example, often induced effects on disembodied or extracorporeal events in the visual field were investigated (e.g., cursor movements; Chaminade & Decety, 2002; Farrer & Frith, 2002; Sato & Yasuda, 2005; more in Table 1) with probably only minor bearings on real-world situations. The ecological validity of paradigms (e.g., David et al., 2006; Hunter et al., 2003) is an important issue for any empirical research project, demonstrating the dilemma many researchers face when planning their experiments, and which needs to be considered when interpreting results and putting them into perspective.

4. Neural correlates of agency

By means of functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), several brain areas have been implicated in the sense of agency (Blakemore et al., 2001; Farrer & Frith, 2002; Farrer et al., 2003a; Fink et al., 1999; Jeannerod, 2004; Leube et al., 2003). These include brain regions known to be involved in the motor system such as the ventral premotor cortex (vPMC), the supplementary motor area (SMA and pre-SMA) and the cerebellum as well as regions such as the dorsolateral prefrontal cortex (DLPFC), the posterior parietal cortex (PPC), the posterior segment of the superior temporal sulcus (pSTS) and the insula (Fig. 2). Unfortunately, the current literature does not yet provide a consistent or clear picture with respect to the exact functions and contributions of these brain regions to the sense of agency. In a classificatory attempt, the first group of brain regions (e.g., vPMC, SMA, cerebellum) constitutes a network of sensorimotor transformations and motor control, whereas the second group of brain regions rather represents a set of heteromodal asso-

[3] The process of imitation is highly associated with the idea of simulation and a mirror neuron system and the reader may refer to chapter 3.2. for a discussion with respect to the sense of agency.

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ciation cortices implicated in various cognitive functions. This has been exemplified in relation to the PFC by Fuster (1997), Fuster (2001) who proposed the PFC's relevance for the organization of behavior in the temporal domain (for a review see Vogeley & Kupke, 2007). Accordingly, motor system-related regions may subserve "executive" functions whereas heteromodal associative regions subserve "supervisory" functions. However, the proposed classificatory, functional distinction remains speculative requiring further empirical validations.

In the following, we summarize the available evidence on the neuroscience of agency in an attempt to putting the empirical results into perspective. The presence of different neural correlates might reflect different agency indicators, sub-processes or levels of agency processing. Accordingly, some of the proposed neural correlates of agency could be linked to the theoretical accounts and mechanisms discussed in previous chapters.

4.1. Brain regions associated with the comparator model

With respect to the central monitoring theory or comparator model (chapter 3.1), the PPC represents a very likely candidate for providing reference to the agent of an action as this region seems to monitor the concordance between self-produced actions and their visual consequences, being especially involved in the detection of visual-motor incongruence (Chaminade & Decety, 2002; Farrer & Frith, 2002; Farrer et al., 2003a,2007; Fink et al., 1999). Similarly, the cerebellum has been implicated in signaling discrepancies between predicted and actual sensory consequences of movements (e.g., an associated tone; Blakemore et al., 2001). Thus, the PPC and cerebellum may well represent neural correlates of the central monitoring or comparator mechanism described earlier (Blakemore & Sirigu, 2003).[4]

Especially with respect to the PPC, there is converging evidence on this hypothesis based on findings from neuroimaging Q4 both in patients and healthy subjects (e.g., Farrer et al., 2004; Farrer & Frith, 2002; Spence et al., 1997) as well as from experiments in subjects with posterior parietal lesions (Sirigu et al., 1999) including *virtual* lesions by means of transcranial magnetic stimulation (TMS; MacDonald & Paus, 2003). These lesion data, in particular, make a strong case in favor of the PPC being crucially involved in the sense of agency. Nevertheless, the PPC has also been implicated in several other cognitive processes such as visual-spatial attention (Behrmann, Geng, & Shomstein, 2004; Constantinidis, 2006) and multimodal integration (Xing & Andersen, 2000). Recently, a region in visual association cortex called the *extrastriate body area* (EBA; Downing Q11 et al., 2001) has been reported to show greater activity during self-generated movements (Astafiev, Stanley, Shulman, & Corbetta, 2004). This finding opened the possibility that the EBA may also be involved in the sense of agency as suggested by Jeannerod (2004). Indeed, activity in the EBA could be shown to be differentially modulated by a manipulation of agency responding to the perception of visuo-motor incongruence. Furthermore, the EBA showed a similar response pattern as the PPC as well as an increased functional connectivity to the PPC underlining a close functional relationship between them (David et al., 2007a). Alternatively, spatial representations within the EBA in an allocentric reference frame (Chan, Peelen, & Downing, 2004; Saxe, Jamal, & Powell, 2006) may represent another mechanism by which the EBA contributes to the sense of agency.

4.2. Brain regions associated with the simulation theory

Different brain regions including the STS, parts of the PPC (especially the inferior parietal lobule) and the vPMC have been discussed as key nodes of the human mirror neuron system (Keysers & Perrett, 2004). They are thought to encode motor aspects of actions executed by oneself *and* others, thus, not differentiating between specific agents (Rizzolatti et al., 2001; chapter 3.2). This has been particularly demonstrated for the vPMC and the more inferior part of the PPC, whereas possible mirror functions of the pSTS irrespective of visual signals remain controversial (Keysers & Perrett, 2004). The current empirical evidence suggests that the pSTS mainly responds to the perception of biological motion or intentional actions of others (e.g., Grossman et al., 2000; Pelphrey, Morris, & McCarthy, 2004; Ramnani & Miall, 2004; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004). One study has also linked pSTS activation—similar to the PPC—to the processing of increasing visuo-motor incongruence during self-generated hand movements (Leube et al., 2003). It is unclear how the pSTS or the PPC could subserve a comparator mechanism—and thus possibly a distinction between self and other—as well as compute shared codings of ones own and others' actions at the same time. Future studies are needed to reconcile such discrepant findings; nevertheless, different parts of posterior parietal and temporal cortices may well subserve different subfunctions.

4.3. Brain Regions associated with intentional binding

The phenomenon of intentional binding (chapter 3.3) may be related to increased activation of the SMA or pre-SMA and insula. Recruitment of these regions has specifically been associated with awareness and execution of self-generated actions, action preparation and the subject's own intention-to-act (Cunnington, Windischberger, Robinson, & Moser, 2006; Farrer &

[4] On the notion of a "central monitoring mechanism" and the homunculus problem: Inputs to the central monitoring mechanism may come from "distal" sensory signals but also from "central" functional mechanisms elsewhere in the sequence of information processing. This functional aspect is not related to the ontological aspect of the implementation or realisation of such processes in the nervous system. We assume that the central monitoring mechanism is realized on basic levels of neural activity.

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Frith, 2002; Farrer et al., 2003a; Haggard & Clark, 2003; Haggard & Whitford, 2004; Lau, Rogers, & Passingham, 2006). Intriguing evidence on the relevance of the supplementary motor cortex for the experience of intentional actions comes from a neurological condition: Lesions in the SMA have been associated with the so-called anarchic hand syndrome, in which patients experience unintended actions of their own hand just as if the hand had a "will on its own" (Della Sala, Marchetti, & Spinnler, 1991).

4.4. Brain regions associated with the feeling versus judgment level of agency

We found that visual-motor incongruence was sometimes registered at the neural level (e.g., in extrastriate and posterior parietal cortices) but did not necessarily enter awareness leading to a correct judgment on the feedback as incongruent (David et al., 2007a,2007b; cf. Farrer et al., 2007). A neural response towards sensorimotor incongruences, on which subjects could not explicitly report, has also been previously discussed (e.g., for the cerebellum, Blakemore & Sirigu, 2003: "the sensory discrepancy signalled by the cerebellum is not available to awareness", p. 242). This may offer support for the distinction between the agency levels of feeling and judgment as proposed by Synofzik et al. (2007). Can the feeling-judgment distinction be mapped onto different neural correlates? Synofzik et al. (2007) describe the feeling of agency as implicit, low-level or pre-reflective and characterized by sensorimotor processes. These may run outside awareness such as the comparator mechanism (chapter 3.1; Fig. 1) but can be made available to our conscious awareness (for more information see Blakemore et al., 2002). In this sense, the feeling of agency may indeed be mapped onto brain areas implicated in the comparator—as one possible constitutive process—such as the cerebellum and the PPC (Blakemore & Sirigu, 2003) or visual association areas such as the EBA or pSTS (David et al., 2007a; Iacoboni et al., 2001; Leube et al., 2003), which are not necessarily involved in the conscious detection of a sensorimotor mismatch (David et al., 2007a). By contrast, the judgment of agency has been described by Synofzik et al. (2007) as being of reflective and attributive nature informed by conceptual thought. There is evidence that the PFC may be required at the level of conscious monitoring (Slachevsky et al., 2001) but not at the level of sensorimotor integration. Indeed, the DLPFC has been implicated in conflict monitoring and detection such as between one's own intended action and the sensory outcome (e.g., Fink et al., 1999; Schnell et al., 2007). Nonetheless, the distinction between feeling and judgment levels of agency (Synofzik et al., 2007) as well as a potential mapping of these different levels onto different neural correlates, which may or may not contribute to awareness, require further theoretical developments and empirical evaluations.

Q12

4.5. Connectivity between brain regions

Despite the recent flurry of cognitive neuroscience research on the sense of agency, only little evidence exists on how the different, proposed neural correlates are functionally connected during agency processing (see David et al., 2007a, as the hitherto only example). Although there is no generally and widely used method to calculate functional connectivity in the human brain but many different approaches exist, connectivity analyses have proven to be help- an insightful in explaining the brain-behavior relationships (see Grol et al., 2007, for a convincing demonstration of parieto-frontal connectivity during grasping). Increasing technological possibilities and improved methodologies allow us to go beyond the pin-pointing of single brain area/behavior relationships, particularly if the cognitive process under investigation is rather complex—as it is the case for the sense of agency. Connectivity analyses should guide future neuroimaging work, especially in light of increasing evidence for a disconnection pathology as suggested to underlying disorders such as schizophrenia (Federspiel et al., 2006; Liang et al., 2006).

5. Conclusion

The investigation of the sense of agency is an increasingly prominent field of research in psychology as well as cognitive neurosciences alike. Nonetheless, we still face many open questions and controversies how the distinction between one's own and others' behavior is drawn. Different understandings of the sense of agency and assumed different underlying mechanisms, in turn, lead to rather diverse operationalizations and results such as to differences in activation patterns between existing neuroimaging studies. At the current stage, a multifactorial and multilevel (Synofzik et al., 2007; Wegner & Sparrow, 2004)—but parsimonious—model appears to provide the most helpful and comprehensible framework for integrating divergent theories and findings. For example, the recent introduction of a distinction between a pre-reflective and a reflective level of agency (Synofzik et al., 2007) seemed suitable and helpful (for further theoretical developments with respect to different representational levels of agency also linking agency and responsibility, see Synofzik et al. this volume). Future experimental operationalization of the sense of agency, thus, should consider the distinction between different levels of agency and employ systematic explorations of different agency indicators and their possible interplay in order to meet the complex nature of this intriguing phenomenon.

6. Uncited reference

Q1 de Hamilton et al. (2007).

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