

The self in action – electrophysiological evidence for predictive processing of  
self-initiated sounds and its relation to the sense of agency

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von Dipl.-Psych. Jana Timm

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Dekanin: Prof. Dr. Andrea Robitzki

Gutachter: Prof. Dr. Erich Schröger

Prof. Dr. Marc Schönwiesner

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## **Bibliographische Darstellung**

Jana Timm

**The self in action – electrophysiological evidence for predictive processing of self-initiated sounds and its relation to the sense of agency**

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Stimuli caused by our own voluntary actions receive a special treatment in the brain. In auditory processing, the N1 and/or P2 components of the auditory event-related brain potential (ERP) to self-initiated sounds are attenuated compared to passive sound exposure, which has been interpreted as an indicator of a predictive internal forward mechanism. Such a predictive mechanism enables differentiating the sensory consequences of one's own actions from other sensory input and allows the mind to attribute actions to agents and particularly to the self, usually called the "sense of agency". However, the notion that N1 and/or P2 attenuation effects to self-initiated sounds reflect internal forward model predictions is still controversial. Furthermore, little is known about the relationship between N1 and/or P2 attenuation effects and the sense of agency. Thus, the aim of the present thesis was to further investigate the nature of the N1 and/or P2 attenuation effect to self-initiated sounds and to examine its specific relationship to the sense of agency. The present thesis provides evidence that N1 and/or P2 attenuation effects to self-initiated sounds are mainly determined by movement intention and predictive internal motor signals involved in movement planning and rules out non-predictive explanations of these effects. Importantly, it is shown that sensory attenuation effects in audition are directly related to the feeling of agency, but occur independent of agency judgments. Taken together, the present thesis supports the assumptions of internal forward model theories.



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# 1 Introduction

*“Prediction allows us to direct our behavior towards the future, while remaining well-grounded and guided by the information pertaining to the present and the past.”* (Bubic, von Cramon, & Schubotz, 2010, p. 11).

As stated above predictive processing reflects one of the fundamental functions of the human brain. Within this predictive framework it has been proposed that the brain’s primary goal is to infer the causes of its sensory input, in order to allow it to successfully predict and interact with the external world (Bar, 2009; Friston, 2005; Hawkins & Blakeslee, 2004). Thus, the “predictive brain” is thought to play an important role in human information processing such as perception (Akatsuka, Wasaka, Nakata, Kida, & Kakigi, 2007; Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010; Baldeweg, 2006), action (Blakemore, Goodbody, & Wolpert, 1998; Wolpert & Flanagan, 2001) and cognitive control (Alexander & Brown, 2011). Generating predictions is highly beneficial because it allows organisms to save processing resources and to prepare appropriate reactions (Bubic et al., 2010). In addition, predictions lead to faster recognition and interpretation of external events by limiting the repertoire of potential responses to those events (Bar, 2007). Furthermore, predictive processing enables us to construct a stable and coherent representation of the external world (Kveraga, Ghuman, & Bar, 2007). Various brain areas have been associated with predictions such as primary sensory cortices, lateral and medial parietal and temporal areas, orbitofrontal, medial frontal and dorsolateral prefrontal cortex, premotor cortex, insula, cerebellum, basal ganglia, amygdala and thalamus (see Bar, 2009; Bubic et al., 2010 for reviews).

In addition to this universal predictive account, specific systems such as the motor system (Wolpert & Flanagan, 2001) and the cerebellum (Knolle, Schröger, Baess, & Kotz, 2012; Knolle, Schröger, & Kotz, 2012) have been emphasized to play a crucial role in predictive processing. Specifically, it has been proposed that the central nervous system (CNS) contains internal models, which mimic aspects of our own body and the external world to generate predictions about the future states of the body or the environment (Wolpert, Ghahramani, & Jordan, 1995). It is well known that sensory predictions generated by internal forward models provide perceptual stability in the context of all self-produced actions such as limb movements, touch or speech (Kveraga et al., 2007). Furthermore, they seem to form the basis

for the successful differentiation between sensory consequences produced by our own actions and other external events, which is normally associated with an experience of being the agents of our actions (Blakemore, Wolpert, & Frith, 2002; Frith, Blakemore, & Wolpert, 2000). But what are the precise neural mechanisms and theoretical implementations behind all this? How can assumptions of predictive internal processing of the acting self be studied experimentally? And how are action-driven predictions in auditory information processing related to a sense of self in action?

The present chapter will provide answers to all these questions. In the first section a model of predictive processing for the self in action will be introduced. To this end the basic assumptions of the efference copy and corollary discharge mechanism will be briefly explained, which have been implemented in internal models of motor control. The basic ideas of forward and inverse models will be described and the proposed connection of forward models to the sense of agency, that is the experience of causing our own actions and their sensory consequences, will be discussed. The second section will provide an overview of empirical evidence for predictive processing of the acting self. The main focus will be set on how action-driven predictions are proposed to influence the perception of sensory stimulation of the acting self across different sensory modalities. A third section will explicitly concentrate on electrophysiological effects of action-driven predictions on the processing of self-initiated sounds and its relation to the sense of agency. The last section will outline the specific research questions of the present thesis.

### **1.1 The self in action: A model of predictive processing**

Humans are agents. That is, they have the capacity to change the external world through their own goal-directed behavior. This capacity usually involves an experience of being the agent of the action and its sensory consequences (Moore & Obhi, 2012). If we, for example, clap our hands we will automatically feel that we ourselves caused the noise that goes along with it and not somebody or something else. But how can we differentiate between the sensory consequences of our own actions and the sensory consequences caused by external sources? How do we actually attribute actions and their sensory consequences to the self? As noted above the neurocognitive literature proposes that this is provided by an internal forward mechanism, which depends on predictive information arising from self-performed actions.

### 1.1.1 Efference copy and corollary discharge mechanism

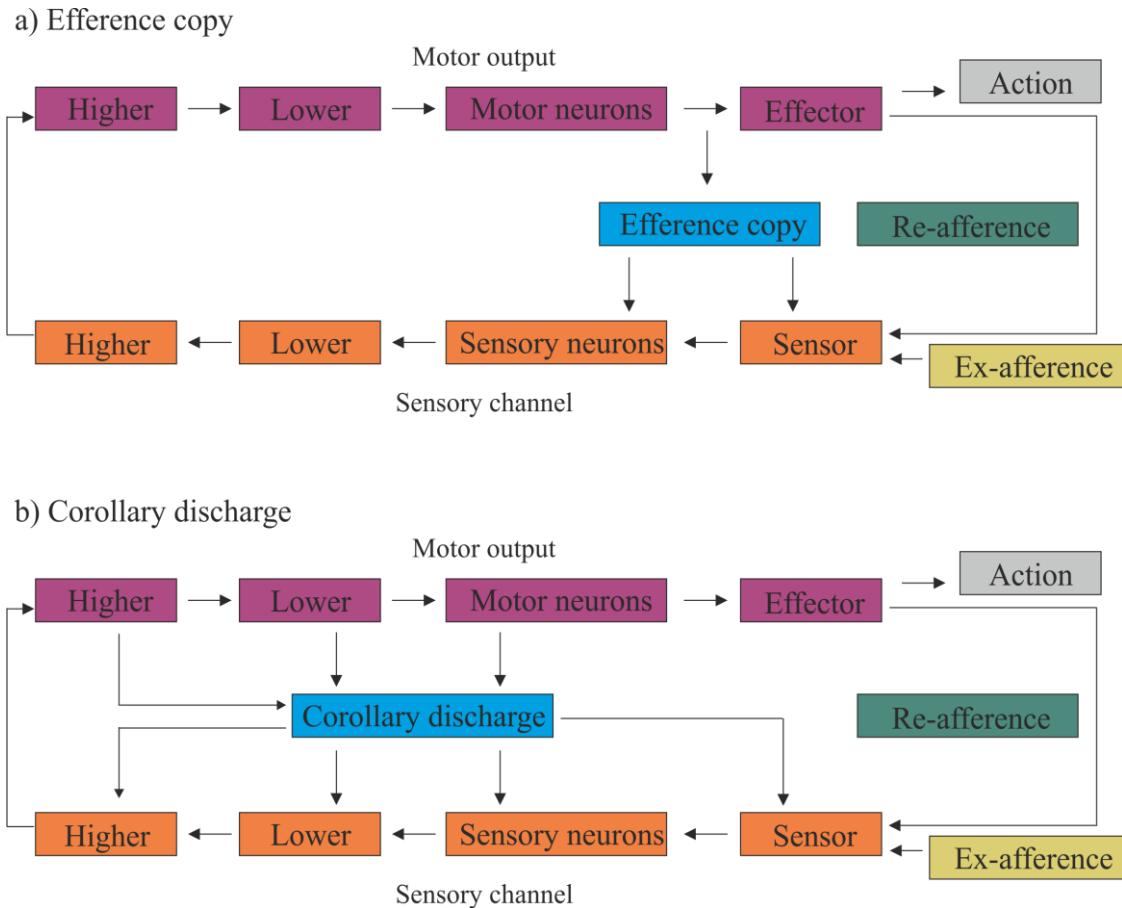
The idea that perceptual representations are related to motor representations has been already formulated within the ideomotor principle by William James (James, 1890). This assumption was supported by findings in the field of motor control, proposing a direct influence of motor activity on sensory processing based on neural signals that are fed back to the CNS (Mach, 1906), an idea that was already present in the thinking of Bell, Purkyne and von Helmholtz (Bridgeman, 2007).

All this effort influenced the seminal work on sensorimotor integration of von Holst and Mittelstaedt (1950), who discussed a fundamental distinction concerning the origin of sensory input. In their work they first described how self-produced stimuli and externally-produced stimuli are discriminated through the interaction between sensory feedback signals following an action and an efference copy of the motor command (von Holst & Mittelstaedt, 1950). Specifically, they proposed that the correct attribution of sensory input to self-produced actions depends on the differentiation between ex-afference (stimuli produced by external factors) and re-afference (stimuli produced by muscular activity). According to the authors, “re-afference is the necessary afferent reflexion caused by every motor impulse” while “ex-afference is independent of motor impulses” (von Holst & Mittelstaedt, 1950, p. 89). They suggested that the CNS mimics efferent motor commands, that is, whenever a movement is performed an efference copy signal is sent to sensory structures. Receiving an efference copy allows the system to prepare for sensory consequences associated with the movement (von Holst & Mittelstaedt, 1950). Such a predictive mechanism is, for example, reflected in the phenomena that the world around us stays stable while we move our eyes compared to when the eyeball is moved passively. However, the term “efference copy” implies an actual copy of the current efference that directly targets the muscles, thus it is thought to take place close to the motor output (see Figure 1a).

As less specific conception of motor-to-sensory circuits was suggested by Robert Sperry (1950), who proposed that a corollary discharge (CD) from an action command modulates the visual perception of movements. Similar to the ideas of von Holst and Mittelstaedt (1950), Sperry also assumed an anticipatory adjustment mechanism of central origin: “...that the kinetic component may arise centrally as part of the excitation pattern of the overt movement.

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Thus, any displacement of the visual image on the retina may have a corollary discharge into the visual centers to compensate for the retinal displacement.” (Sperry, 1950, p. 488). However, CD circuits are thought to originate in all levels of the motor pathway and can influence the sensory processing stream at different levels in various sensory systems (see Figure 1b), which is mainly supported by animal neurophysiology studies (Crapse & Sommer, 2008a, 2008b).



**Figure 1: Illustration of efference copy and corollary discharge mechanism**

The proposed efference copy (von Holst & Mittelstaedt, 1950) and corollary discharge (Sperry, 1950) mechanisms are depicted. The sensorimotor circuit comprises a motor pathway (shown in purple) and a sensory pathway (shown in orange). a) The motor system sends an exact copy of the motor command to the sensory pathway. b) The corollary discharge is less specific. CD signals can originate in all levels of the motor pathway and influence the sensory processing stream at different levels. Adapted from Crapse & Sommer (2008a).

Although addressing somewhat different issues and introducing a slightly different terminology, both the conception of efference copy (von Holst & Mittelstaedt, 1950) and corollary discharge (Sperry, 1950) were the first to demonstrate how the system predicts self-generated sensory signals and motivated the initial development of internal models.<sup>1</sup>

### 1.1.2 Theory of motor control: Internal forward and inverse models

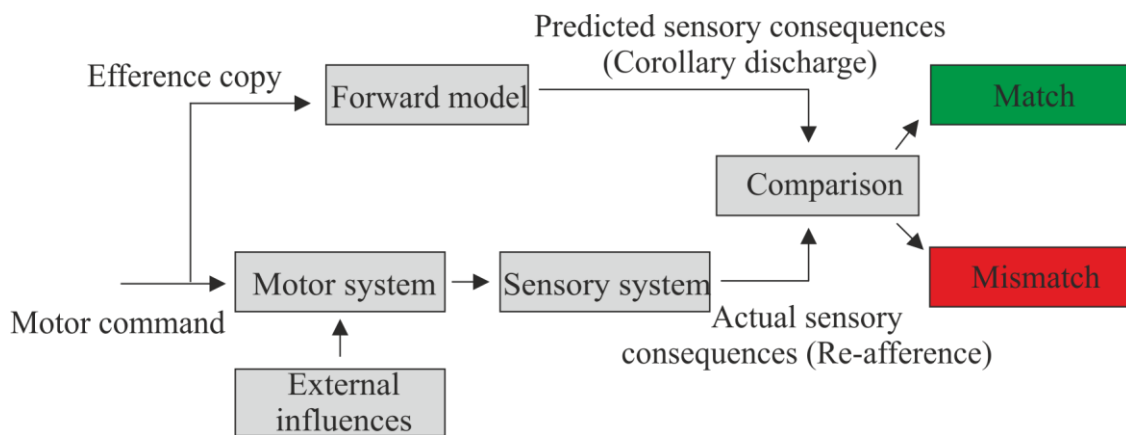
The main assumption of the motor control theory is that the CNS contains transformations, or internal models, which mimic aspects of our own body and the external world to generate predictions about the future states of the body or the environment (Wolpert et al., 1995). Originally, the internal model approach has been developed in the motor domain to explain the release of motor commands acting on the musculoskeletal system (Kawato, Furukawa, & Suzuki, 1987; Wolpert & Miall, 1996). However, it has been proposed that internal models mediate predictions across different sensory domains (Wolpert, Doya, & Kawato, 2003). In general, it has been inferred that the existence of both internal forward and inverse models are required to explain skilled motor behavior (Wolpert & Miall, 1996).

It is assumed that whenever a movement is executed a motor command is generated by the CNS. An efference copy triggered by the motor command is implemented in the forward model. Given the actual state of the system, the forward model estimates the desired state of the system and the associated sensory consequences (corollary discharge). Inverse models, on the other hand, generate appropriate motor commands to achieve the desired state (Wolpert & Flanagan, 2001; Wolpert et al., 1995; Wolpert & Ghahramani, 2000). Thus, based on efferent information the forward model generates predictions about the sensory consequences of our actions. Those internal forward predictions can be used in several ways (Wolpert & Miall, 1996). Predictions are needed to anticipate and compensate for the sensory effects of movements (Sperry, 1950; von Holst & Mittelstaedt, 1950). In addition, predictions are important to integrate sensory and motor information in order to estimate the actual state of the system (Wolpert, 1997). Furthermore, predictions can also be used to adjust motor commands online overcoming feedback delays (Miall, Weir, Wolpert, & Stein, 1993).

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<sup>1</sup> In the present thesis it will be referred to the efference copy as an exact copy of the motor command that is implemented in a predictive forward model while the corollary discharge reflects the representations of the expected sensory consequences in sensory cortices.

Importantly, forward model predictions also make it possible to cancel out re-afference, that is, the stimulation inherently resulting from the action due to movements of our own body. That is, based on efferent information of the motor command sensory consequences of self-generated movements can be correctly predicted. Thus, the comparison of the predicted and actual sensory feedback will result in little or no sensory discrepancy. Contrary, externally-generated sensory consequences are not associated with internally-generated efferent information resulting in higher sensory discrepancy. Importantly, such a mechanism enables our system to cancel out the sensory consequences of our own actions and thereby distinguish sensory consequences of one's own actions from other sensory input (Frith et al., 2000, see Figure 2). There exists evidence that predictions provided by internal forward models are used by various cognitive subsystems beyond those directly involved in the control of the given effector (Davidson & Wolpert, 2005). Such a predictive internal forward mechanism is, for example, reflected in the phenomena that we cannot tickle ourselves (Blakemore, Wolpert, & Frith, 2000). Detailed experimental evidence for internal forward predictions of different cognitive systems will be provided in section 1.2.



**Figure 2: Illustration of predictive internal forward mechanism of motor control**

Based on the efference copy of the motor command a forward model is formulated. The forward model predicts the sensory consequences (corollary discharge) of our own actions. These predictions are compared with the actual sensory consequences, which can result either in a match in case of accurate predictions or a mismatch, signaling a prediction error. Adapted from Bubic et al. (2010).



### 1.1.3 Functions of internal forward models and the sense of agency

As it has been pointed out so far, internal forward predictions seem to play a crucial role in various cognitive systems enabling the discrimination of sensory consequences due to our own actions and the actions of others. Thus, it has been argued that forward model predictions allow the mind to attribute actions to agents, and particularly to the self (Blakemore et al., 2002; Frith et al., 2000). This so-called sense of agency is normally understood as the experience that we are the cause of our actions and their sensory consequences. Importantly, the sense of agency does not have to be a complex or reflective cognition. It is thought to be a minimal awareness of initiating and performing a voluntary movement or causing a certain effect in the world (Gallagher, 2000), which is already present in infants (Rochat & Hespos, 1997; Rochat, 1995). However, it has been postulated that depending on such a pre-reflective experience of agency more reflective agency attributions are possible. Those reflective agency attributions enable us to reflectively realize and to report that we are causing our movements and their sensory effects (Gallagher, 2000).

The predictive account of agency assumes that agency originates in neural processes responsible for the motor aspects of intentional actions (Haggard, 2005). That is, the sense of agency is generated by or at least linked to the motor commands sent to the muscles and the accompanying efference copy that is internally processed within predictive internal forward models (Tsakiris & Haggard, 2005; Wolpert & Flanagan, 2001). The sense of agency is thought to be affected by the match or mismatch between predictions made by forward models and actual sensory consequences. If predicted and actual sensory consequences match, we experience a coherent sense of action processing. If the comparison process indicated a mismatch the experience of agency is reduced or even absent (Blakemore et al., 2002; Frith et al., 2000; Haggard, 2005). Thus, according to the predictive account the sense of agency depends on internal pre-motor signals, that is, pre-motor brain activity produces a specific conscious experience of intention (Haggard, 2005). In line with this, it has been proposed that dysfunctions in internal forward mechanisms might underlie at least some of the symptoms of complex disorders such as schizophrenia, which is characterized by the loss of self (Feinberg, 1978; Frith et al., 2000). Patients with delusions of control, for example, experience their own actions as being made by an external agent rather than by their own will - an experience that can

easily be explained by a dysfunction in the predictive mechanisms allowing awareness of action (Frith, 2005).

However, the predictive explanation of motor intention and agency experience is still controversial. For example, the inferential account of agency downplays the specific contributions of the motor system (Wegner, 2002). In his seminal work Wegner states that “The will is a feeling” (Wegner, 2004, p. 1). Wegner (2002) proposes that movement intention and the corresponding sense of agency arise from interpreting our thoughts as the cause of our actions, irrespective of whether or not this inference is appropriate. According to Wegner (2002, 2003) we experience agency when a thought 1) appears prior to an action, 2) is consistent with the action and 3) is not accompanied by other plausible causes of the action. Thus, Wegner suggests that the sense of agency is determined by the conceptual match between preview information and subsequent sensory consequences. Accordingly, internally-generated efferent information of the motor system does not play a crucial role in generating the sense of agency (Wegner, 2002, 2003, 2004).

In accordance with the ideas of the inferential account it has been shown that participants reported an enhanced sense of agency when conscious thoughts occurred prior to their actions than when observed actions or their sensory consequences were followed by these thoughts (Wegner, Sparrow, & Winerman, 2004; Wegner & Wheatley, 1999). Additionally, an enhanced sense of agency was reported, when prior thoughts were consistent with actions or their sensory consequences but not when they were inconsistent with them (Wegner et al., 2004). However, when participants performed actions but other potential causes of actions were provided, participants tended to believe that the actions were caused by someone else (Wegner, Fuller, & Sparrow, 2003). In contrast, Sato and Yasuda (2005) found that the sense of agency decreased when the discrepancy between predicted (i.e. intended) and actual sensory consequences increased, which suggests the involvement of predictive internal pre-motor signals. Furthermore, also in favor of a predictive explanation, various studies showed that when participants are asked to estimate the time at which they initiate a movement, they consistently report it to have started several hundred milliseconds before it actually did (Haggard & Eimer, 1999; Haggard & Magno, 1999; Lau, Rogers, Haggard, & Passingham, 2004; Libet, Gleason, Wright, & Pearl, 1983; Sirigu et al., 2004). For example, in a classic study Libet and colleagues (1983) revealed that the indicated time at which participants became aware of having the “urge” to move preceded the production of the movement by

around 200 ms. These findings suggest that awareness of initiating a movement depends on the predicted sensory consequences of the movement, which are available before the sensory feedback from the movement (Blakemore et al., 2002). In line with this, a parietal-premotor network has been suggested, assuming that internal pre-motor signals are emitted through forward modeling within premotor and parietal cortex, and that these signals form the basis of movement intention and the sense of agency (Desmurget & Sirigu, 2009). This assumption is supported by findings showing that cortical electrical stimulation of parietal brain regions can generate feelings of intending to move and even the conviction of having executed the movement (Desmurget et al., 2009). Thus, according to the predictive account, both movement intention and the corresponding sense of agency result from brain processes for predictive motor control and not from retrospective inference (Haggard, 2005).

Importantly, further conceptual refinements on the sense of agency distinguish two different levels of agency representations (Gallagher, 2006; Synofzik, Vosgerau, & Newen, 2008). On a primary perceptual level we experience a feeling of agency, which represents a non-conceptual, low-level feeling of being the agent of an action. It has been proposed that it mainly depends on the automatic processing of sensorimotor signals generated by the acting self. The feeling of agency can be affected by the match or mismatch between predictions made by forward models and actual sensory consequences. In case of a match we experience a rather diffuse sense of coherent, harmonious ongoing flow of action processing. In case of a mismatch we experience an action as strange, peculiar and not fully done by us (Synofzik et al., 2008). On a second level judgments of agency are formed. On this level the non-conceptual feeling of agency is further processed. Judgments of agency reflect the belief of being the agent of an action, based on explicit conceptual and interpretative processes. If, for example, a mismatch is detected leading to a pre-reflective feeling of not being the agent of an action and its sensory effects, a specific belief is formed on the reflective level about the source of authorship. This belief formation represents an interpretative mechanism looking for the best explanation of the cause of the action. According to the authors, the way in which the agency belief formations are performed depends on how we rationalize our actions, that is, the way of giving a (more or less) plausible explanation for our experiences (Synofzik et al., 2008). It has been suggested that one's personal background belief, e.g. a narrative self-structure, might be important for explicit agency attributions (Gallagher, 2004; Stephens & Graham, 2000). Thus, this two-step account of agency proposes that the sense of agency

represents a combination of predictive and inferential processes. However, to which extent the feeling of agency and judgments of agency contribute to the overall sense of agency depends on the specific context and task requirements (Synofzik et al., 2008). The authors suggest that in unambiguous situations the feeling of agency might be strong enough and the formation of agency beliefs does not need to be further instantiated. Recent findings seem to support the assumptions of such a two-step explanation of the sense of agency (e.g. Desantis, Roussel, & Waszak, 2011; Haering & Kiesel, 2012; Moore & Haggard, 2008; Moore, Lagnado, Deal, & Haggard, 2009; Sato, 2009).

### 1.2 Empirical evidence for predictive processing of the acting self

*“...when your own behavior is involved, your predictions not only precede sensations, they determine sensation.”* (Hawkins & Blakeslee, 2004, p. 158).

As stated by Hawkins and Blakeslee (2004), the generation of predictions strongly influences the way in which we perceive the world. But how do internal forward predictions based on predictive pre-motor signals of the acting self actually contribute to self-recognition? How do internal forward predictions modulate action effects, influencing time-awareness of voluntary actions and their sensory consequences and the perception of sensory stimulation? And to which extent is all this associated with the experience of agency? This section will provide empirical evidence for predictive processing of the acting self and how it modulates perception.

#### 1.2.1 Self-recognition in action

As indicated above, internal efferent signals form the basis for functions of internal forward models. They allow us to differentiate between sensory consequences of our own actions and sensory consequences caused by external sources and to recognize us as the agent of an action. Interestingly, it has been proposed that predictive signals involved in our voluntary actions might also mainly contribute to self-recognition (Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005). Self-recognition involves deciding whether a visual image shows our own body or not and is assumed to represent a specific cognitive process typically involved in conscious experience (Tsakiris et al., 2005). Thus, self-recognition depends on the ability to correctly

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recognize motor intentions, actions and their sensory consequences. When this ability is disturbed phenomena such as the “anarchic hand syndrome” (Hari et al., 1998) or schizophrenia (Daprati et al., 1997) are often reported.

However, to which extent does self-recognition depend on internal efferent signals of the acting self? Voluntary actions always involve an inseparable combination of efferent and sensory information, which makes it difficult to determine experimentally the specific contribution of efferent signals to the representations of our own actions (Tsakiris et al., 2005). To study the influence of internal efferent information experimentally, participants usually perform a self-generated movement while they are looking at their own hand or someone’s else hand, which is either performing the same or a different movement compared to their own movement. In the following, participants are asked to judge whether they see their own hand or not. Results show that for unambiguous movements (e.g. different movements) judgments mainly depend on internal efferent signals. However, for ambiguous movements (e.g. same movements) sensory signals such as proprioception are used (Daprati et al., 1997; Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999; van den Bos & Jeannerod, 2002). Thus, these studies provide evidence that efferent as well as sensory signals seem to constitute the core of self-recognition. However, a main limitation of these experimental designs is that both efferent and sensory information are always present to the participants what makes it difficult to quantify the specific contribution of internal efferent information on self-recognition (Tsakiris & Haggard, 2005).

Thus, in a variation of this paradigm, Tsakiris and colleagues (2005) investigated the crucial role of internal efferent signals by selectively manipulating efferent information. In their experiment participants experienced a passive movement of their right hand. At the same time the participants saw a moving hand on the computer screen, which was always moved passively. This right hand could either be the own hand or the hand of the experimenter. In one condition the movement was caused by the left hand of the participants, that is, both efferent and sensory information were available. In another condition the experimenter caused the movement, that is, only sensory information was available. Participants judged whether the right hand they saw was theirs or not. It was found that the performance was significantly better when passive displacements of the right hand were self-generated by the participants’ left hand. Thus, self-recognition was more accurate when participants themselves were

authors of the action, that is, when internal efferent signals were available. These results show that self-recognition, in the sense of attributing sensory events to our own actions, seems to mainly depend on efferent signals and a sense of agency. This is consistent with findings on action recognition and prediction, showing an authorship effect in recognizing and predicting actions only for self-performed actions but not for other agents (Knoblich & Flach, 2003). Taken together, internal efferent signals have a highly predictive power, which allows the correct detection of appropriate sensory signals, thereby enabling the recognition of the self in action (Tsakiris, Schütz-Bosbach, & Gallagher, 2007).

### **1.2.2 Time-awareness of actions and sensory effects**

Internal forward predictions are furthermore known to directly modulate the temporal perception of actions and their sensory consequences in the acting self (Haggard, 2005). It has been proposed that for voluntary actions the match of predicted and actual sensory consequences leads to an efferent binding process. This efferent binding is thought to be a specific mental process with conscious consequences, which binds together intentions, actions and external sensory consequences in case of a detected match (Haggard, Aschersleben, Gehrke, & Prinz, 2002). Thus, intentional processes of the active agent, which precede the action itself are assumed to determine the perceived time of actions and sensory consequences (Tsakiris & Haggard, 2005).

Empirical evidence for this assumption was first provided by Haggard, Clark, and Kalogeras (2002), investigating the perceived time of voluntary actions and their sensory consequences. Four critical conditions were introduced. In two baseline conditions participants were asked to judge either the time of voluntary actions (button press) or the time of sensory stimulation (short sound). In two operant conditions participants performed a voluntary button press in each trial, which caused a short sound after 250 ms. In specific blocks, participants were either asked to judge the time of the voluntary button press or the time of the subsequent sound. Then the perceived times of actions and sensory consequences in the operant conditions were compared with the perceived times in the baseline conditions (Haggard, Clark, et al., 2002). The results showed that the perceived times of voluntary actions and their sensory consequences were attracted together. That is, participants perceived voluntary actions to occur later in time and their sensory consequences to occur earlier in time when these events occurred together (operant conditions) compared to when they occurred in

isolation (baseline conditions). Importantly, this effect seems to be specific to intentional actions because for involuntary button presses, induced by transcranial magnetic stimulation (TMS) over the primary motor cortex, a reverse binding effect was observed such that the perceived time interval between actions and sensory consequences increased (Haggard, Clark, et al., 2002). Thus, the authors called this phenomenon “intentional binding effect”, suggesting that it depends on predictive efferent signals of intentional actions, indicating the experience of agency (Engbert, Wohlschläger, & Haggard, 2008; Engbert & Wohlschläger, 2007; Haggard, Aschersleben, et al., 2002; Haggard, Clark, et al., 2002; Haggard & Clark, 2003; Moore & Haggard, 2008; Tsakiris & Haggard, 2003; Walsh & Haggard, 2013).

Interestingly, voluntary actions seem not only to attract sensory stimuli that follow, but also those that directly precede our voluntary actions (Haggard, Aschersleben, et al., 2002). That is, it seems that all sensory events that occur in the process of motor preparation are linked to the actual voluntary action, which supports the assumptions of an underlying predictive mechanism of the sense of agency (indicated by an intentional binding effect). Further evidence for the assumption that the sense of agency depends on predictive internal signals involved in movement preparation was provided by Haggard and Clark (2003), who studied how the disruption of an intention to act affects intentional binding. In this experiment, participants made intentional button presses, which caused a sound. On some trials TMS was applied over primary motor cortex which interrupted the preparation for intentional actions and induced an involuntary movement followed by a sound. The authors reported a significantly weaker binding effect when intentions were interrupted. The results show that efferent signals involved in voluntary movements are crucial for intentional binding. The mere co-occurrence of action and sensory consequences is not sufficient. Thus, these findings are in favor of a predictive explanation of agency experience and argue against contributions of retrospective inference (Haggard & Clark, 2003). The predictive interpretation is further supported by a finding of Engbert and Wohlschläger (2007) who manipulated the probability of the outcome (sound) for voluntary movements to investigate how this affects intentional binding. That is, in one condition the outcome probability was high (80 %) whereas in another condition the outcome probability was low (20 %). Results revealed a stronger intentional binding effect for the high probability condition, such that actions were perceived later in time when voluntary button presses were followed by a sound with high probability. However, for passive movements no differences between the conditions were observed. Importantly, in the

high probability condition intentional binding occurred irrespective of whether the voluntary button press was followed by a sound or not. Consequently, predicting the outcome of the movement was sufficient, emphasizing the influence of predictive processing in intentional binding (Engbert & Wohlschläger, 2007). Interestingly, intentional binding effects are also found in other sensory modalities suggesting a general binding mechanism based on predictive internal efferent signals (Engbert et al., 2008; Tsakiris & Haggard, 2003). For example, Engbert and colleagues (2008) found comparable binding effects for auditory, visual and somatic consequences of voluntary movements. That is, the perceived time intervals between voluntary actions and subsequent sensory consequences were shorter than those between comparable involuntary movements and the same effects (Engbert et al., 2008). Taken together, all these studies provide converging evidence that predictive models have a crucial role in constructing a conscious experience of the acting self.

However, there exists evidence that not only predictive mechanisms of the acting self but also retrospective inference contribute to the intentional binding effect as an implicit measure of the sense of agency (Moore & Obhi, 2012). For example, in the experiment of Moore and Haggard (2008), participants performed voluntary button presses. Each button press caused a sound. In one condition the outcome was predictable (i.e. button presses caused a sound in 75 % of the trials). In another condition the outcome was unpredictable (i.e. button presses caused a sound in only 50 % of the trials). The respective contributions of predictive and retrospective inferential processes to the sense of agency (indicated by intentional binding) were isolated. The contribution of predictive processes was confirmed by an increase in intentional binding on trials where the button presses did not cause a sound in the 75 % vs. 50 % conditions. This increased binding effect could only be due to the increased outcome probability. The contribution of retrospective inference processes were confirmed by an increased intentional binding on trials where button presses did cause a sound compared to trials where they did not cause a sound in the 50 % condition. In this condition the outcome was unpredictable, that is, predictive contributions were strongly reduced. Thus, the increased binding effect for trials where the button press caused a sound can only be explained by the presence of the sound, that is, the sound retrospectively initiated the shift of the perceived time of the voluntary movement (Moore & Haggard, 2008; Moore & Obhi, 2012). The assumption that both predictive and retrospective inference processes contribute to the intentional binding effect is supported by further studies (Desantis et al., 2011; Haering & Kiesel, 2012; Moore et al., 2009). The findings are in line with the proposed two-step



explanation of agency (Gallagher, 2006; Synofzik et al., 2008) such that the sense of agency is based on both predictive sensorimotor processes (Blakemore et al., 2002; Frith et al., 2000) and interpretative processes (Wegner, 2002) that need to be optimally integrated.

Although a recent account (Desantis, Hughes, & Waszak, 2012; Hughes, Desantis, & Waszak, 2012) doubts the predictive nature of the intentional binding effect, it seems that the modulation of the perceived times of voluntary actions and sensory consequences is mainly influenced by intentional processes of the active agent (Desantis et al., 2011; Engbert & Wohlschläger, 2007; Haering & Kiesel, 2012; Wohlschläger, Engbert, & Haggard, 2003). Interestingly, patients with schizophrenia show a stronger intentional binding effect compared to controls (Haggard, Martin, Taylor-Clarke, Jeannerod, & Franck, 2003; Moore et al., 2011; Voss et al., 2010). This finding is surprising because symptoms of schizophrenia usually are characterized by a loss of the self (Feinberg, 1978; Frith et al., 2000), which should be manifested in form of significantly weaker binding effects for schizophrenic patients compared to controls (Moore & Obhi, 2012). It has been suggested that schizophrenics may tend to misattribute their actions to external events based on impaired intentional processes preceding the action itself (Frith, 2005). This assumption is in line with findings of Voss and colleagues (2010). Using the probability design of Moore and Haggard (2008), they reported stronger inferential contributions and no predictive contributions on intentional binding in patients with schizophrenia. Importantly, the magnitude of the predictive deficit correlated with the severity of certain positive symptoms (Moore & Obhi, 2012). The authors concluded that due to aberrant predictive sensorimotor signals, the experience of agency might be mainly determined by external agency cues in schizophrenic patients (Voss et al., 2010).

Moreover, another phenomena of modulated time-awareness associated with voluntary actions and their sensory effects has been reported recently (Stetson, Cui, Montague, & Eagleman, 2006). Stetson and colleagues (2006) revealed a temporal order illusion of actions and sensory consequences. In their study, they introduced a fixed delay between motor actions (button presses) and their sensory consequences (flashes). After participants had adapted to this delay, they perceived unexpected flashes presented at shorter delays as occurring before the motor action. The authors suggested that this recalibration of motor-sensory timing results from the participants' prior expectations about little or no delay between actions and sensory consequences, which is crucial for determining causality

(Stetson et al., 2006). Similar illusions have been found in other sensory modalities (Heron, Hanson, & Whitaker, 2009; Sugano, Keetels, & Vroomen, 2010) and with more complex stimuli (Keetels & Vroomen, 2012; Yamamoto & Kawabata, 2011), suggesting a universal mechanism (Heron et al., 2009). Importantly, illusory reversals in the temporal order of a button and a subsequent stimulus occurred only when participants moved their finger actively, but not when the button was moved with a motor to tap the finger of the participants (Stetson et al., 2006). Thus, comparable to the intentional binding effect, the temporal order illusion seems to depend on intentional processes of the active agent, which precede the action itself (Walsh & Haggard, 2013). It has been suggested that the sense of agency is strongly related to the concept of causality, which can only be established when an action precede the sensory consequences (Hume, 1888, 1900). Thus, it can be assumed that temporal order judgments should also be linked to the sense of agency. However, up to now it has not been tested experimentally how the temporal order illusion is related to the sense of agency.

### 1.2.3 Perception of sensory stimulation

Internal forward predictions do not only modulate time-awareness of voluntary actions and their sensory consequences in the acting self, they also directly modulate the perception of sensory stimulation. There exists converging evidence that sensory consequences caused by our own actions are attenuated both in terms of their phenomenology and their cortical brain responses. It is assumed that this sensory attenuation represents the workings of internal forward predictions such that when a match between predicted and actual sensory consequences is detected sensory consequences are attenuated (Wolpert & Ghahramani, 2000). Thus, action-driven predictions enable us to distinguish self-generated from externally-generated sensory events (Blakemore et al., 2002; Frith et al., 2000). It has been proposed that sensory response attenuation reflects the key concept in models of motor-sensory integration because it highlights the way that perception of sensory events is modulated by the voluntary nature of the movement (Tsakiris & Haggard, 2005). As an indicator of internal predictive forward modeling in the acting self, sensory attenuation has been widely studied in cognitive neuroscience across various sensory modalities (e.g. Baess, Horváth, Jacobsen, & Schröger, 2011; Blakemore, Wolpert, et al., 2000; Ford, Gray, Faustman, Roach, & Mathalon, 2007; Gentsch & Schütz-Bosbach, 2011; Schafer & Marcus, 1973; Weiskrantz, Elliott, & Darlington, 1971; Weiss, Herwig, & Schütz-Bosbach, 2011).

### 1.2.3.1 Sensory attenuation in terms of its phenomenology

One of the most popular examples for attenuation of sensory re-afference is the phenomena that we cannot tickle ourselves (Weiskrantz et al., 1971). Specifically, it has been shown that participants judged self-generated tactile stimulation as being less ticklish than externally-generated ones. The authors argued that only in case of self-generated movements privileged access to internally-generated efferent information was possible. Thus, sensory attenuation is mainly based on efference copy signals produced with self-generated movements (Weiskrantz et al., 1971). These results were confirmed by other studies investigating more systematically the influence of predictability and the presence of sensory consequences (Blakemore, Frith, & Wolpert, 1999; Claxton, 1975). For example, Blakemore and colleagues (1999) studied how temporal delays between self-generated movements and sensory stimulation as well as the degrees of trajectory perturbations affected the perceptual attenuation of ticklishness. They reported that ticklishness to self-generated stimulation systematically increased with increasing discrepancy of predicted and actual sensory feedback in time and space. The authors concluded that the forward model generates fairly specific predictions about the timing and the spatial location of sensory events caused by voluntary movements (Blakemore, Frith, et al., 1999). These findings are supported by force escalation studies (e.g. Shergill, Bays, Frith, & Wolpert, 2003). For example, Shergill and colleagues (2003) showed that when participants were instructed to apply the same force on the other participant that had just been exerted on them, they consistently overestimated the force required. This illustrates that self-generated forces are perceived as weaker than externally-generated forces of the same magnitude. The authors concluded that force escalation can be interpreted as a byproduct of predictive sensory attenuation (Shergill et al., 2003). Interestingly, schizophrenic patients with passivity symptoms did neither report reduced ticklishness when the stimulation was self-produced (Blakemore, Smith, Steel, Johnstone, & Frith, 2000) nor did they show the normal attenuation of self-applied force (Shergill, Samson, Bays, Frith, & Wolpert, 2005), suggesting a defect related to forward model predictions (Frith, 2005). Another interesting phenomenon of predictive processing for self-generated movements comes from pain research. It has been shown that when a painful stimulus was self-inflicted, participants reported significantly less pain and a greater ability to tolerate the pain compared to when the same stimulus was applied by another person (e.g. Braid & Cahusac, 2006; Wang, Wang, & Luo, 2011). These findings

demonstrate the relevance of profound knowledge of the function of internal forward predictions in the acting self in clinical contexts.

In the experiments described so far, the perception of sensory consequences of self-generated movements was always compared to the perception of sensory consequences caused by external sources (Blakemore, Frith, et al., 1999; Braid & Cahunac, 2006; Claxton, 1975; Shergill et al., 2003; Wang et al., 2011; Weiskrantz et al., 1971). Thus, these studies provide converging evidence for the assumption that the match between predicted and actual sensory feedback attenuates self-generated sensory consequences. However, it remains unclear whether this sensory attenuation effect is attributed to the experience of agency of the acting self or if this attribution reflects a post-hoc construction. This question was addressed by Tsakiris and Haggard (2003). In their experiment participants pressed a button with their left index finger. This button press triggered the TMS, which was applied over primary motor cortex of the participant, producing a muscle twitch of the right index finger 270 ms later. The TMS output was varied, that is, the intensity of the somatic effect was unpredictable for the participants. The button was pressed either voluntarily by the participant or by an involuntary movement (e.g. a motor was pressing the finger). Although, in both conditions a physically comparable movement initiated the somatic effect, only in the voluntary condition participants intentionally caused this effect. Participants judged the intensity of the TMS-induced twitches of their right index finger (Tsakiris & Haggard, 2003). Results revealed that participants judged effects induced by voluntary movements as less intense than somatic effects that were involuntarily induced, which supports previous results of sensory attenuation for self-generated movements (Blakemore, Frith, et al., 1999; Braid & Cahunac, 2006; Claxton, 1975; Shergill et al., 2003; Wang et al., 2011; Weiskrantz et al., 1971). Moreover, they show that sensory attenuation was not determined by predictability as the intensity of the somatic effects was highly unpredictable. Importantly, these results provide direct evidence that intentional action and not the mere body movement of the acting self is required for sensory response attenuation. Thus, the authors concluded that sensory attenuation depends on predictive intentional processes of the active agent and the corresponding sense of agency (Tsakiris & Haggard, 2003). This assumption is supported by other findings in the somatosensory domain (Christensen et al., 2007; Chronicle & Glover, 2003; Haggard & Magno, 1999; Haggard & Whitford, 2004; Moore, Ruge, Wenke, Rothwell, & Haggard, 2010; Voss, Bays, Rothwell, & Wolpert, 2007; Voss, Ingram, Haggard, & Wolpert, 2006; Voss, Ingram, Wolpert, & Haggard, 2008).

Phenomenological sensory attenuation effects and their relation to the sense of agency have also been investigated in auditory information processing (Couchman, Beasley, & Pfordresher, 2012; Desantis, Weiss, Schütz-Bosbach, & Waszak, 2012; Sato, 2008, 2009; Weiss et al., 2011a; Weiss, Herwig, & Schütz-Bosbach, 2011b; Weiss & Schütz-Bosbach, 2012). Weiss and colleagues (2011a), for example, compared the loudness perception of sounds that were 1) self-initiated by a button press, 2) initiated by another person, or 3) generated by a computer. In favor of a predictive explanation, they found reduced perception of loudness intensity only for self-generated sounds. Furthermore, the perception of sounds initiated by another person or generated by a computer did not differ from each other (Weiss et al., 2011a). Weiss and colleagues (2011a) concluded that sensory attenuation in terms of a reduced intensity perception depends on motor-related signals arising from movement preparation and that those signals are self-generated, forming the basis for the experience of agency. In line with this, a reduced sense of agency for increasing discrepancies between predicted and actual auditory consequences have been reported (Couchman et al., 2012; Fu et al., 2006; Sato & Yasuda, 2005). However, there exists also evidence that phenomenological sensory attenuation in audition is also modulated by retrospective inference (Desantis, Weiss, et al., 2012; Sato, 2009). For example, Desantis and colleagues (2012) investigated the influence of causal belief on sensory attenuation of self-initiated sounds via button press. Participants had to judge the loudness of sounds that they believed were either self-initiated or triggered by another person. However, in reality the sounds were always initiated by the button press of the participants. Desantis and colleagues (2012) revealed that participants only perceived the loudness of the sounds attenuated when they believed that the sounds were caused by themselves compared to when they believed that they were initiated by another person. The authors suggested that sensory attenuation and the experience of agency are also influenced by prior beliefs about the causal link between voluntary actions and sensory changes in the external world (Desantis, Weiss, et al., 2012). This assumption is consistent with findings on intentional binding studies (Desantis et al., 2011; Haering & Kiesel, 2012; Moore & Haggard, 2008; Moore et al., 2009), showing that the intentional binding effect, as an implicit measure of agency, depends on both predictive and interpretative mechanisms.

### 1.2.3.2 Sensory attenuation of cortical brain responses

Sensory attenuation of cortical brain responses due to functions of predictive internal forward models has also been intensively investigated. In the somatosensory modality attenuated neural activity in response to self-generated tactile stimulation compared to externally-generated tactile stimulation has been reported (e.g. Blakemore, Wolpert, et al., 2000; Blakemore, Wolpert, & Frith, 1998, 1999; Hesse, Nishitani, Fink, Jousmäki, & Hari, 2010). Blakemore and colleagues (1998), for example, investigated the neural basis of attenuated sensory perception to self-generated tactile stimulation. Using functional magnetic resonance imaging (fMRI) they compared neural activity in the somatosensory cortex in response to self-generated tickle and externally-generated tickle. They found decreased activity in somatosensory cortex for self-generated stimulation relative to externally-generated stimulation. Blakemore and colleagues (1998) concluded that this reduced activity in somatosensory cortex might reflect the physiological correlate of the reduced perception associated with self-generated sensory stimulation. Moreover, there exists evidence that the cerebellum is crucially involved in the comparison process of predicted and actual sensory consequences (Blakemore, Frith, & Wolpert, 2001; Blakemore, Wolpert, et al., 1999; Knolle, Schröger, Baess, et al., 2012; Knolle, Schröger, & Kotz, 2012) and that it provides the signal used for sensory attenuation in somatosensory cortex (Tsakiris & Haggard, 2005). Cortical self-generation effects have been also reported for self-generated pain, showing distinct brain activation pattern for self-induced pain compared to externally-induced pain (Helmchen, Mohr, Erdmann, Binkofski, & Büchel, 2006; Wang et al., 2011). Specifically, pain-related brain areas were inhibited in case of self-induced pain, including the primary somatosensory cortex, anterior cingulate cortex or the thalamus (Wang et al., 2011).

Consistent with the idea of a predictive internal forward mechanism, differences in the processing of self-generated sounds (e.g. speech sounds) or self-initiated sounds (e.g. via button press) compared to externally-generated sounds have been demonstrated (e.g. Baess et al., 2011; Bäss, Jacobsen, & Schröger, 2008; Curio, Neuloh, Numminen, Jousmäki, & Hari, 2000; Ford et al., 2007; Gunji, Hoshiyama, & Kakigi, 2000; Heinks-Maldonado, Mathalon, Gray, & Ford, 2005; Houde, Nagarajan, Sekihara, & Merzenich, 2002; Knolle, Schröger, & Kotz, 2012; Martikainen, Kaneko, & Hari, 2005; Schafer & Marcus, 1973). In a seminal study Schafer and Marcus (1973) investigated electrophysiological differences in response to self-initiated and externally-initiated sounds. The experiment consisted of two conditions. In the

self-initiation condition participants were asked to press a button in a self-paced interval. Each button press triggered a short sound. In the externally-initiation condition participants passively listened to an exact replay of the sounds of the self-initiation condition. Thus, the sensory stimulation of both conditions was physically identical. However, only in the self-initiation condition pre-motor signals were available, enabling forward model predictions of the sensory input. Auditory brain responses due to self-initiation (after correcting for confounding motor activity) were then compared to auditory brain responses caused by external stimulation. Schafer and Marcus (1973) found attenuated brain responses only in response to self-generated sounds but not in response to externally-generated sounds. The attenuation effect was mainly reflected in attenuated amplitudes of the N1 and P2 component of the event-related potential (ERP). In line with findings in the somatosensory modality (Blakemore, Wolpert, et al., 2000; Hesse et al., 2010) the authors concluded that this attenuation effect confirms the successful generation of auditory predictions via forward modeling for self-initiated sounds (Schafer & Marcus, 1973).

This specific N1/P2-attenuation paradigm (also called N1/P2-suppression paradigm, Schafer & Marcus, 1973) has been used in numerous studies investigating sensory attenuation effects in response to self-initiated sounds (Aliu, Houde, & Nagarajan, 2009; Baess et al., 2011; Bässl et al., 2008; Knolle, Schröger, Baess, et al., 2012; Knolle, Schröger, & Kotz, 2013, 2012; Kühn et al., 2011; Martikainen et al., 2005; McCarthy & Donchin, 1976; SanMiguel, Todd, & Schröger, 2013) and even more complex stimuli such as self-initiated vowels (Ford et al., 2007). In addition, reduced visual N1 amplitudes (i.e. greater attenuation) in response to self-initiated visual action effects have been reported using this paradigm (Gentsch, Kathmann, & Schütz-Bosbach, 2012; Gentsch & Schütz-Bosbach, 2011; Schafer & Marcus, 1973). Furthermore, attenuated sensory responses originating in auditory cortex have been observed for self-generated speech sounds in comparison to physically identical, but passively replayed speech sounds (Curio et al., 2000; Gunji et al., 2000; Heinks-Maldonado et al., 2005; Houde et al., 2002; Numminen & Curio, 1999; Numminen, Salmelin, & Hari, 1999). These findings are consistent with forward modeling effects in other species such as invertebrates (e.g. Nocke, 1972) and vertebrates (Eliades & Wang, 2003, 2008; Müller-Preuss & Ploog, 1981; Suga & Schlegel, 1972), indicating attenuated neural activity for self-generated sounds at different levels of the auditory pathway (see for reviews Crapse & Sommer, 2008a; Poulet & Hedwig, 2006). Interestingly, schizophrenic patients with positive symptoms such as auditory

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hallucinations did not show sensory attenuation effects to self-initiated or self-generated sounds in the N1/P2-attenuation paradigm (Ford, Mathalon, Kalba, Marsh, & Pfefferbaum, 2001; Ford, Mathalon, Heinks, et al., 2001; Ford, Mathalon, Kalba, Whitfield, et al., 2001; Heinks-Maldonado et al., 2007; Whitford et al., 2011). For example, Ford and colleagues (2001) revealed no N1 attenuation difference between self-generated and externally-generated speech in schizophrenic patients compared to healthy controls, who showed attenuated N1 amplitudes to self-generated speech. These observations were interpreted in terms of a failure in the speech-related predictive internal forward mechanism (Ford, Mathalon, Heinks, et al., 2001).

Importantly, it has been shown that sensory attenuation effects reported in the N1/P2-attenuation paradigm (Schafer & Marcus, 1973) seem to mainly depend on intentional actions of the active agent and that they cannot be explained by the mere predictability of the sensory effects (Blakemore, Rees, & Frith, 1998). In a positron emission tomography (PET) study, Blakemore and colleagues (1998) systematically manipulated the effects of predictability and self-initiation of sounds. To this end, participants performed button presses in self-paced intervals. In one condition each button press caused a sound, that is, the occurrence of the sounds was predictable. In another condition sounds were presented randomly, unrelated to the button presses, that is, the sounds were unpredictable in their occurrence. Neural responses of both conditions were compared in response to predictable or unpredictable sounds, respectively, when no intentional movements were performed. The results showed different activation patterns for effects of sound predictability and for self-initiated compared to externally-initiated sounds. The authors concluded that stimulus predictability and the recognition of sensory consequences initiated by one's own intentional actions appear to be functionally distinct processes and are carried out in different cortical areas, supporting the assumptions of an internal forward model mechanism in the acting self (Blakemore, Rees, et al., 1998).



### **1.3 Specific insight: Sensory attenuation of brain responses to self-initiated sounds – an indicator of predictive processing and the sense of agency?**

As it has been pointed out so far, sensory attenuation of cortical brain activity in response to self-generated sounds (e.g. speech) or self-initiated sounds (e.g. via button press) relative to externally-generated sounds has been interpreted in terms of a predictive internal forward mechanism (Wolpert et al., 1995). This predictive mechanism, in turn, allows the correct differentiation between self-generated sensory consequences and sensory input caused by external sources, thereby enabling the attribution of actions to the active agent (Blakemore et al., 2002; Frith et al., 2000). Specifically, it is assumed that in case of self-generated sounds (Curio et al., 2000; Gunji et al., 2000; Heinks-Maldonado et al., 2005; Houde et al., 2002; Numminen & Curio, 1999; Numminen et al., 1999) and self-initiated sounds (Aliu et al., 2009; Baess et al., 2011; Bäss et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; Knolle et al., 2013; Knolle, Schröger, & Kotz, 2012; Kühn et al., 2011; Martikainen et al., 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973) auditory forward predictions are generated, which cancel out auditory re-afference. This cancellation of auditory re-afference is thought to be reflected in an attenuated auditory N1 and/or P2 component of the ERP.

The assumption that the function of an internal forward mechanism supports predictions of self-generated speech sounds seems plausible. That is, we have extensive experience with the control of and the sensory stimulation produced by our own speech production system (Horváth, Maess, Baess, & Tóth, 2012). Thus, speech-related N1 and/or P2 attenuation effects seem to indicate the workings of an internal forward model of motor control (Curio et al., 2000; Gunji et al., 2000; Heinks-Maldonado et al., 2005; Houde et al., 2002; Numminen & Curio, 1999; Numminen et al., 1999). However, sensory processing of self-initiated sounds via button press differs in various ways from self-generated speech sounds. First, the initiated auditory stimulation is not an unavoidable consequence of the movement. Second, the auditory stimulation is not isomorphic with the action. Third, the link between the movement and the auditory stimulation is an arbitrary association that needs to be learned. Thus, the notion that attenuated N1 and/or P2 responses to such “instrumental actions”, such as self-initiated sounds via button press reflect predictive auditory processing is still controversial

(Horváth et al., 2012; Horváth, 2013a, 2013b; Makeig, Müller, & Rockstroh, 1996; SanMiguel et al., 2013; Synofzik et al., 2008; Tsakiris & Haggard, 2005).

For example, it has been suggested that the attenuation effect of the auditory N1 and/or P2 to self-initiated sounds does not reflect auditory internal forward predictions but rather a dynamic change in the distribution of attentional resources (Horváth et al., 2012; Hughes et al., 2012; Makeig et al., 1996). It is well known that especially the amplitude of the auditory N1 increases when attention is selectively directed to a sound sequence (Hillyard, Hink, Schwent, & Picton, 1973; Hillyard, 1981). Thus, it has been argued that attenuation effects to self-initiated sounds might be explained by the fact that performing a voluntary movement (button press) draws away attention from the task-irrelevant auditory processing (sounds) for a short period of time, which would result in attenuated auditory responses for sounds close to the button press (Horváth et al., 2012). Accordingly, sensory attenuation effects would merely reflect attentional differences between self-initiated and externally-initiated sounds and not sensory predictions resulting from a forward model of the motor command. In line with this, it has been reported that focused attention differed between self-initiated and externally-initiated sounds, resulting in involuntary attention shifts to externally-initiated sounds, reflected in an enlarged P3a component of the ERP to externally-initiated sounds compared to self-initiated sounds (Baess et al., 2011). Interestingly, for self-generated speech sounds reduced N1 amplitudes have been also reported when attention was selectively focused on the sounds, supporting the notion that attenuation effects to self-generated speech sounds are independent of attention effects (Kudo et al., 2004). Furthermore, it has been proposed that at least parts of the sensory attenuation effect may be the basis for the initial formation of contingent associations between motor and sensory events (Horváth et al., 2012; Tsakiris & Haggard, 2005). Thus, attenuated N1 and/or P2 responses to self-initiated sounds would be rather unspecific: any sound in the temporal vicinity of the motor act would receive attenuated processing, not indicating a specific motor-sensory prediction. Motor-sensory prediction would only be formed in a later step, once contingency can be extrapolated from repeated pairing. This notion is supported by recent findings showing that auditory input seems to be attenuated for a short period after the motor act, even if there is no contingency between button press and sound (Horváth et al., 2012; Horváth, 2013a, 2013b). Additionally, it has been suggested that, in contrast to the P2 attenuation effect, the N1 attenuation effect reflects no stimulus-specific response in auditory cortex but rather mainly represents a reduction of an unspecific component of the auditory N1 outside the auditory cortex (SanMiguel et al., 2013).

However, these findings are contradicted by previous magnetoencephalogram (MEG) studies, which specifically measured the activity of sources in auditory cortex in response to self-initiated and externally-initiated sounds, reporting an attenuated N1 and/or P2 response to self-initiated sounds (Aliu et al., 2009; Horváth et al., 2012; Martikainen et al., 2005). Furthermore, it has been shown that sensory attenuation to self-initiated sounds is largest when predicted and actual sensory consequences match precisely (Bäss et al., 2008). That is, the sensory consequences seem to be specific to the predicted sensory consequences. This specific prediction, in turn, can only be mediated by sensory-specific cortices representing the specific physical qualities of the predicted consequences. Thus, these findings support the idea that sensory attenuation in response to self-initiated sounds results from an internal forward model which predicts the sensory consequences of intentional movements of the acting self, leading to response attenuation in sensory cortices in case of a match. These findings for self-initiated sounds are consistent with effects of self-generated speech sounds (Fu et al., 2006; Heinks-Maldonado et al., 2005; Heinks-Maldonado, Nagarajan, & Houde, 2006; Hirano et al., 1997; Houde et al., 2002), suggesting shared representations of all auditory predictions.

Taken together, the assumption that cortical sensory attenuation effects to self-initiated sounds, reflected in reduced N1 and/or P2 amplitudes, depend on internal forward model predictions are supported by numerous studies (Aliu et al., 2009; Baess et al., 2011; Bäss et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; Knolle et al., 2013; Knolle, Schröger, & Kotz, 2012; Kühn et al., 2011; Martikainen et al., 2005; McCarthy & Donchin, 1976). However, less complex and non-predictive explanations such as attentional influences or mere temporal contiguity between motor action and sound have been proposed recently to explain auditory attenuation effects of instrumental actions (Horváth et al., 2012; Horváth, 2013a, 2013b; Hughes et al., 2012; Makeig et al., 1996; SanMiguel et al., 2013; Tsakiris & Haggard, 2005). Thus, the underlying neural mechanisms involved in N1 and/or P2 attenuation effects to self-initiated sounds and its interpretation in functional terms requires further research.

Moreover, very little is known about the specific relationship between N1 and/or P2 attenuation to self-initiated sounds and the sense of agency. As it has been pointed out, the sense of agency seems to be mainly driven by a match between experienced motor intentions

in pre-motor areas of the active agent (Christensen et al., 2007; Desmurget & Sirigu, 2009; Desmurget et al., 2009; Haggard & Magno, 1999; Haggard & Whitford, 2004; Moore et al., 2010; Voss et al., 2007, 2006, 2008) and the achieved goals, but can also be influenced by retrospective inferences (Gallagher, 2006; Synofzik et al., 2008). There exists converging evidence that phenomenological sensory attenuation effects indicate a sense of agency, that is, only when participants recognized themselves as the agent of the movement, sensory attenuation effects for self-initiated sounds were reported (Desantis, Weiss, et al., 2012; Sato, 2008, 2009; Weiss et al., 2011a, 2011b; Weiss & Schütz-Bosbach, 2012). However, up to now it is not clear how sensory attenuation effects of cortical brain responses to self-initiated sounds are related to the sense of agency (Gentsch et al., 2012; Gentsch & Schütz-Bosbach, 2011; Kühn et al., 2011). Proposing that internal forward mechanisms apply to instrumental actions such as self-initiated sounds via button press, movement intentions, which are thought to form the basis for agency experience, should automatically activate the predicted sensory consequences based on predictive signals of the motor command (Desmurget & Sirigu, 2009; Haggard, 2005). Thus, if the attenuation effect of the N1 and/or P2 component to self-initiated sounds indeed reflects a match of predicted and actual sensory consequences, a direct relationship to the sense of agency can be assumed. This assumption is supported by previous results interpreting a lack of N1 and/or P2 attenuation as an indicator of agency disruptions (Ford et al., 2007).

### 1.4 Research questions

The primary aim of the present thesis is to further investigate the effects of action-driven predictions on the processing of self-initiated sounds and its relation to the sense of agency. More specifically, the nature of the N1 and/or P2 attenuation effect to self-initiated sounds, usually taken as a physiological correlate of action-driven predictions, and its specific relationship to the sense of agency is examined. To this end, four experiments were conducted.

In the first experiment, it was investigated to which extent the N1 attenuation effect<sup>2</sup> to self-initiated sounds can be explained by a differential allocation of attention to self-initiated and externally-initiated sounds. To test this, the allocation of attention to the sounds was varied

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<sup>2</sup> In this experiment the N1 attenuation effect will be called N1-suppression effect.

over several levels and its influence on the N1 attenuation effect was determined. That is, attention was either directed to the sounds or was directed away from the sounds towards the own motor behavior or visual stimulation. It was hypothesized that if attention causes the N1 attenuation effect, then manipulating attention should affect the effect for self-initiated sounds. In contrast, if the N1 attenuation effect reflects the workings of an internal predictive forward model, the attenuation effect to self-initiated sounds was expected to be unaffected by an attentional difference.

The second experiment focused on the specific relationship between N1 and/or P2 attenuation effects to self-initiated sounds and the feeling of agency. Specifically, it was investigated whether attenuation effects of the auditory N1 and/or P2 component to self-initiated sounds can be explained by brain activity involved in movement planning (where conscious motor intention and the corresponding feeling of agency are thought to arise) rather than movement execution. Therefore, ERPs in response to a sound initiated by a button press were recorded. Sounds were initiated either by voluntary finger movements made by the participants, or by similar, but involuntary, movements induced by stimulating primary motor cortex with transcranial magnetic stimulation (TMS). It was hypothesized that predictive signals involved in the processing of self-initiated sounds are sent during movement planning rather than movement execution. Consequently, an attenuation of the N1 and/or P2 response was expected only for voluntary movements, but not for involuntary movements, because no predictive signals should be available to the predictive forward model during involuntary movements.

The last two experiments were conducted to examine the relation between N1 and/or P2 attenuation effects to self-initiated sounds and explicit judgments of agency. The idea was to apply a “judgment of agency illusion” to manipulate judgements of agency during self-initiation of sounds in an appropriate way and to study corresponding N1 and/or P2 attenuation effects in conditions where agency was perceived or not. More specifically, due to an induced perceptual illusion, participants either judged that they were the agent of the sound or not, although actually they did always self-initiate the sound, that is, predictive signals were always available to the internal forward model.

## Introduction

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Thus, the third experiment addressed the question whether such an illusory perception of agency for self-initiated sounds can be created experimentally. To this end, a recently reported temporal order illusion of intentional actions and their subsequent sensory effects (Stetson et al., 2006) was used and its association to judgments of agency was tested. That is, the probability of time intervals between voluntary button presses and sounds was manipulated, such that trials with identical delays between button press and sound prompted different perceptions of temporal order. Participants were asked to rate their sense of agency in these different conditions. Assuming a strong association between temporal order- and agency judgments, it was hypothesized that participants would report no experience of agency in trials in which button press and sound are perceived in reversed order.

In the fourth experiment the relationship between N1 and/or P2 attenuation effects to self-initiated sounds and agency judgments was directly tested, making use of the “judgment of agency illusion” demonstrated in the third experiment. To this end, ERPs in response to sounds initiated by button presses were recorded. In one condition, participants perceived agency over the production of the sounds, whereas, in another condition, participants experienced an illusory lack of agency. Importantly, the action-effect sequence was physically identical in both conditions, only the judgment of agency differed between conditions. Based on the hypothesis that predictive sensorimotor signals contribute to both sensory attenuation and agency judgments, it was expected to find attenuated auditory N1 and/or P2 components only when participants perceived agency but not when participants experienced an illusory lack of agency over the production of the sound.

## 2 Methods

To answer the specified research questions of the present thesis (see section 1.4) electrical activity from the human scalp will be recorded. Electroencephalography (EEG) has become a valid method to study predictive internal forward mechanisms in auditory information processing (Bäss et al., 2008; Martikainen et al., 2005) as it enables with a high temporal resolution the precise analysis of different time courses of different stimulus types (Luck, 2005). The neurophysiological principles of this method will be described briefly. Within this framework the prevalent paradigm to study electrophysiological differences between self-initiated and externally-initiated auditory stimuli will be explained in more detail (N1/P2-attenuation paradigm, see section 1.2.3.2). Furthermore, in one reported experiment of the present thesis we will take advantage of a combined method of EEG and transcranial magnetic stimulation (TMS), inducing movements by stimulating primary motor cortex with TMS. Thus, a very fundamental overview over the neurophysiological principles of this method and its combination with EEG will be provided. In addition, diverse behavioural measurements (e.g. reaction times, hit rates, error rates) will be used in some of the conducted experiments to quantify task performance. Whenever appropriate, behavioural measurements will be explained in detail in the particular experiments.

### 2.1 Electroencephalography (EEG)

In 1929, Hans Berger was the first who recorded electrical brain activity non-invasively from the human scalp (Berger, 1929). Since that time EEG provides a powerful tool in clinical research and cognitive neuroscience to study human cognitive processes. The EEG technique provides several advantages compared to other physiological measurements. It characterizes a non-invasive measurement with a high temporal resolution and low financial costs, which explains the extensive use of this method in human brain research over the last decades (Luck, 2005).

#### 2.1.1 Event-related potentials (ERPs)

The EEG is recorded from multiple electrodes placed on the scalp, according to a specified international 10-20 electrode system (Chatrian, Lettich, & Nelson, 1985). Cortical EEG

signals reflect the sum of electrical activity of post-synaptic potentials in the brain. However, the EEG contains a conglomeration of different neural sources, which makes it difficult to extract neural processes associated with specific sensory, cognitive or motor events (Luck, 2005). To isolate those event-related neural potentials (ERPs) an averaging technique is used. Specifically, epochs that are time-locked to the interesting stimulus are averaged to cancel out neural activity unrelated to the stimulus (Luck, 2005). To further increase the signal-to-noise ratio, additional analysis steps such as eye movement correction, filtering and baseline correction are normally applied. As noted before, the extracted ERPs represent neural activity associated with specific cognitive processes. They are sensitive to experimental manipulations and can be categorized according to their specific polarity, latency and topographical distribution over the scalp. In auditory processing several ERP components have been described in response to an auditory stimulus (Luck, 2005). However, in the next section we only focus on the auditory ERP components that are specifically related to self-initiation and to the research questions of the present thesis (see Figure 3).

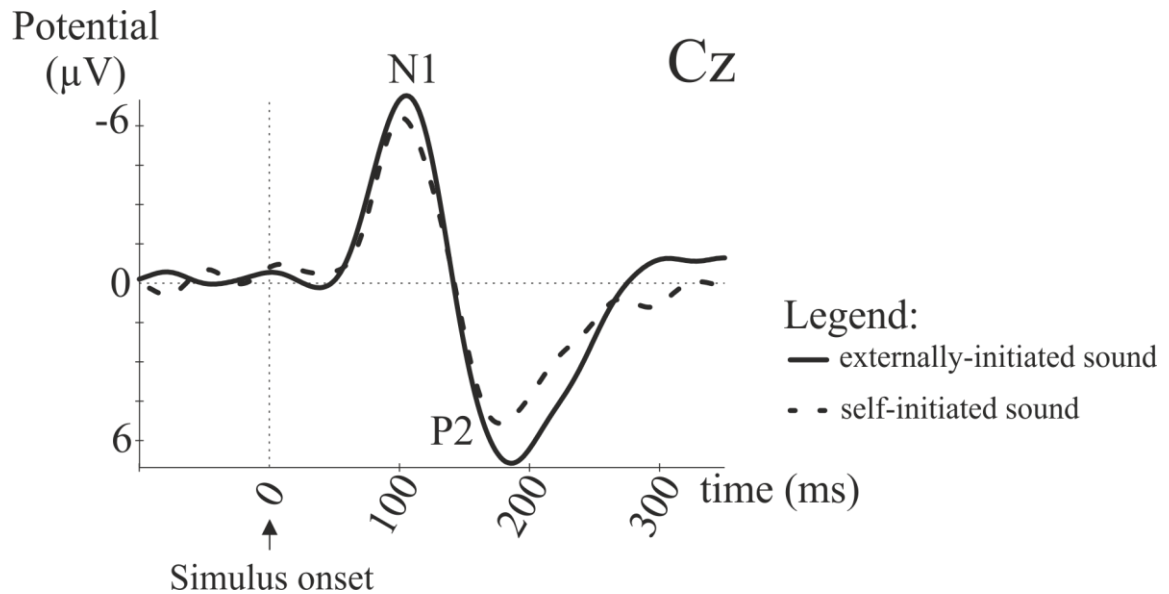
### **2.1.2 Auditory ERP components mainly affected by self-initiation: N1 and P2**

The N1 component reflects a fronto-central negativity that usually peaks at 100 ms after stimulus onset. It is well known that the auditory N1 consists of several distinct subcomponents (see for a review Näätänen & Picton, 1987). Specifically, Näätänen and Picton (1987) proposed that at least three different components contribute to the auditory N1. Component 1 and 2 describe sound processing in primary and secondary auditory cortex, respectively. Contrary, a more unspecific component (Component 3) is proposed to reflect the cortical projection of a process facilitating motor activity. Importantly, only Component 1 and 2 with sources in auditory cortex are tangentially oriented, showing a fronto-central distribution with polarity inversion at the mastoids. However, Component 3 appears slightly later in time than tangential components and shows no polarity reversal at the mastoids, as it does not originate in auditory cortex. Although N1 components do not strictly correspond to specific peaks observable in the auditory ERP, the fronto-centrally distributed N1 peak (N1b peak) is known to mostly receive contributions from Component 1 (McCallum & Curry, 1980). However, there exists evidence that also Component 3 contributes to the N1b peak (Budd, Barry, Gordon, Rennie, & Michie, 1998; Hari, Kaila, Katila, Tuomisto, & Varpula, 1982). Component 2 mainly corresponds to the so called “T complex”, which comprises a positive deflection around 100 ms (N1a peak) and a negative deflection at around 150 ms



(N1c peak) after stimulus onset, observable on anterior temporal electrodes (Wolpaw & Penry, 1975). The N1 indicates processing of auditory stimuli and is sensitive to several modulations of stimulus parameters (see for a review Näätänen & Picton, 1987). For example, it has been shown that with decreasing stimulus intensity the N1 response decreases in amplitude and increases in latency (Beagley & Knight, 1967; Harris, Mills, & Dubno, 2007; Picton, Woods, Baribeau-Braun, & Healey, 1976). Furthermore, N1 amplitude is influenced by the stimulus rate and interstimulus intervals such that N1 amplitude decreases with increasing stimulus rate and shorter interstimulus intervals (Hari et al., 1982). Importantly, the N1 component is also sensitive to attention, showing a larger N1 amplitude for attended auditory stimuli compared to unattended stimuli (Hillyard et al., 1973; Hillyard, 1981).

The P2 component denotes a more centrally distributed positivity that usually peaks at 200 ms after stimulus onset. Although the P2 co-varies with the N1 along many stimulus dimensions it has been dissociated from the N1, suggesting an independent component (see for a review Crowley & Colrain, 2004). For example, it has been demonstrated that the P2 amplitude is affected differently by increasing intensity than the N1 amplitude (Adler & Adler, 1989). Furthermore, there exists evidence that the P2 amplitude is less affected by the stimulus rate and interstimulus intervals (Kenemans, Verbaten, Roelofs, & Slangen, 1989; Roth, Ford, Stephen, & Kopell, 1976). Contrary to the N1, P2 amplitude is not increased for attended auditory stimuli compared to unattended ones (Näätänen & Picton, 1987). In general, the P2 seems to reflect a more cognitive processing than the N1 (Crowley & Colrain, 2004; Knolle, Schröger, & Kotz, 2012).



**Figure 3: Schematic illustration of auditory ERP components**

ERPs elicited in response to an auditory stimulus in the paradigm used in the present thesis. ERPs in response to externally-initiated sounds (solid black line) and self-initiated sounds (dotted black line) are depicted at the fronto-central electrode Cz, reflecting the auditory N1 and P2.

### 2.1.3 Specification of the experimental paradigm

To study internal forward predictions in auditory information processing, sensory effects in response to self-initiation are usually compared to effects in response to external sources. As noted before, a particular paradigm to study electrophysiological differences between self-initiated and externally-initiated auditory stimuli has been introduced by Schafer & Marcus (1973). In this paradigm, participants were asked to initiate sounds with finger movements via button press. That is, in this motor-auditory condition the sounds were the sensory consequences of the motor actions. The sequence of self-initiated sounds was recorded and played back passively to the participants in an auditory-only condition. Thus, the auditory stimulation of the sounds was physically identical in both conditions. To control for motor activity caused by self-initiation of a sound an additional condition was applied. In this motor-only condition button presses elicited no sounds. To isolate sound-evoked brain activity from motoric activity associated with the finger movements, the motor-only condition was subtracted from the motor-auditory condition. The resulting responses were then compared with responses in the auditory-only condition. An attenuated N1 and P2 response was reported in response to self-initiated sounds compared to passive sound exposure (Schafer &

Marcus, 1973). The so called N1/P2 attenuation effect (also called N1/P2 suppression effect) has been replicated in several studies on auditory predictive processing (Aliu et al., 2009; Baess et al., 2011; Bässl et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; Martikainen et al., 2005; McCarthy & Donchin, 1976). Based on these results, the N1/P2 attenuation effect is usually interpreted as the reflection of a successfully generated prediction. Thus, in the present thesis variations of this prevalent paradigm will be used to answer the specified research questions (see section 1.4).

## **2.2 Transcranial magnetic stimulation (TMS)**

By the end of the last century electrical stimulation of the human cortex during brain surgery was a widely used technique to study the functional role of different brain areas (Penfield, 1954). However, in 1980 Patrick Merton first demonstrated that it is also possible to stimulate the human cortex through the skull (Merton & Morton, 1980). Only 5 years later the first TMS for clinical applications was introduced by Professor Anthony Barker (Barker, Jalinous, & Freeston, 1985). TMS is still a relatively young technique, however it has developed into a powerful tool in clinical research and cognitive neuroscience to study functions and dysfunctions of the human brain non-invasively and painlessly (Ziemann, 2011).

### **2.2.1 Neurophysiology**

TMS uses an electromagnetic “figure-of-eight”- shaped coil, which is placed on the scalp of the participant. This coil produces a strong and rapid changing magnetic field orthogonally to the plane of the coil by first charging a large capacitor to a high voltage and then discharging it through the coil (Malmivuo & Plonsey, 1995). The magnetic field induces an electric pulse in the underlying nervous tissue, and thereby usually disrupts the normal pattern of activity (Taylor, Walsh, & Eimer, 2008). Thus, specific cortical areas can be either activated or inhibited, which provides a useful tool to study consequences of cortical activity on behavior (Siebner & Ziemann, 2007).

### 2.2.2 Combined method of TMS and EEG

However, it has been noted that as a stand-alone technique, the potential of TMS to gain knowledge is relatively limited. To enhance this potential, TMS has been combined with simultaneous neurocognitive measurements such as EEG (Ziemann, 2011). The combined method of TMS and EEG is normally used to expand on the measurements of direct TMS effects in the brain. Furthermore, it also retrieves information of cortical excitability at the time of application of the TMS pulse (Ziemann, 2011). Thus, over the last years the combination of TMS and EEG provided a powerful tool to study causal interactions between neural areas involved in perception and cognition (Taylor et al., 2008; Walsh & Cowey, 2000, see Figure 4).



**Figure 4: Illustration of combined method of TMS and EEG**

The picture shows the typical setup of a combined TMS-EEG experiment. The “figure-of-eight”-shaped TMS coil is placed on the head of the participant to stimulate a specific brain region. At the same time the EEG activity is recorded using TMS-compatible electrodes. Source: Ziemann (2011).

### 3 Experiments

#### 3.1 The N1-suppression effect for self-initiated sounds is independent of attention<sup>3</sup>

##### Abstract

If we initiate a sound by our own motor behavior, the N1 component of the auditory event-related brain potential (ERP) that the sound elicits is attenuated compared to the N1 elicited by the same sound when it is initiated externally. It has been suggested that this N1 suppression results from an internal predictive mechanism that is in the service of discriminating the sensory consequences of one's own actions from other sensory input. As the N1-suppression effect is becoming a popular approach to investigate predictive processing in cognitive and social neuroscience, it is important to exclude an alternative interpretation not related to prediction. According to the attentional account, the N1 suppression is due to a difference in the allocation of attention between self- and externally-initiated sounds. To test this hypothesis, we manipulated the allocation of attention to the sounds in different blocks: Attention was directed either to the sounds, to the own motor acts or to visual stimuli. If attention causes the N1-suppression effect, then manipulating attention should affect the effect for self-initiated sounds. We found N1 suppression in all conditions. The N1 per se was affected by attention, but there was no interaction between attention and self-initiation effects. This implies that self-initiation N1 effects are not caused by attention. The present results support the assumption that the N1-suppression effect for self-initiated sounds indicates the operation of an internal predictive mechanism. Furthermore, while attention had an influence on the N1a, N1b, and N1c components, the N1-suppression effect was confined to the N1b and N1c subcomponents suggesting that the major contribution to the auditory N1-suppression effect is circumscribed to late N1 components.

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<sup>3</sup> This study is based on the article: Timm, J., SanMiguel, I., Saupe, K., & Schröger, E. (2013). The N1-suppression effect for self-initiated sounds is independent of attention. *BMC Neurosciene*, 14, 2.

### 3.1.1 Introduction

It is important to differentiate sensory information resulting from one's own actions from environmental events, which are not the result of our own actions. It has been proposed that this differentiation is based on an internal forward model (Wolpert & Flanagan, 2001; Wolpert et al., 1995; Wolpert & Ghahramani, 2000), an idea that relates to the reafference principle (von Holst & Mittelstaedt, 1950) and the concept of corollary discharge (Sperry, 1950) in physiological literature. Specifically, when a movement is executed, a copy of the current motor command (efference copy) is used to make predictions of the sensory consequences of the movement (corollary discharge). This sensory prediction is then compared with the actual sensory feedback. If the two correspond, sensory responses are attenuated, thereby enabling a differentiation between the sensory consequences of one's own actions and the actions of others. Such sensory attenuation for self-generated compared to externally-generated sensations - as an index of an internal predictive mechanism - has been widely investigated in psychophysical research (Blakemore, Wolpert, et al., 2000; Weiskrantz et al., 1971).

Within this self-generation framework, the N1 suppression paradigm has become a popular approach to investigate predictive auditory sensory processing (Aliu et al., 2009; Bässl et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; McCarthy & Donchin, 1976; Schafer & Marcus, 1973). In this paradigm, participants listen to sounds that are either initiated by their own button presses, or externally initiated. The N1 component of the event-related brain potential (ERP) is attenuated for the sounds that were self-initiated compared to the externally-initiated sounds. This N1-suppression effect has been explained as the result of an underlying predictive mechanism. In the traditional blocked version of this paradigm, self-initiated sounds and externally-initiated sounds are presented in different blocks, bearing several caveats that obscure an unambiguous interpretation in terms of the predictive coding framework (Hughes et al., 2012). For example, it seems possible that the participants' arousal level differs between the active condition in which participants initiate the sound by their own motor behavior and the passive condition in which participants simply listen to the externally-initiated sounds. In a modified so-called mixed N1 suppression paradigm self-initiated and externally-initiated sounds are presented within the same block. Thus, sustained arousal differences between self- and externally-initiated sounds are eliminated. Studies using this paradigm also yielded (an even larger) N1-suppression effect for self-initiated sounds (Baess

et al., 2011; Horváth et al., 2012). This demonstrates that the N1-suppression effect seems to occur selectively for self-initiated sounds and seems not to be caused by different arousal levels in active and passive conditions of the blocked design.

Although sustained differences in arousal are well controlled in this mixed design, it is obvious that transient arousal effects cannot be controlled for. Even more important, the improved paradigm has not been designed for excluding attentional influences on the N1-suppression effect. In fact, an enlarged P3a to externally-initiated sounds compared to the P3a for self-initiated sounds reported for the mixed design (Baess et al., 2011) suggests that externally-initiated sounds received more attention. As the N1 is known to increase with attention (Alho & Vorobyev, 2007; Hillyard et al., 1973; Hillyard, 1981; Horváth & Winkler, 2010; Nobre, 2010), it seems well possible that differences in the N1 between self- and externally-initiated sounds were in fact caused by a difference in attention directed to self- and externally-initiated sounds. The cognitive psychologist's silver bullet to test for an attentional confound on an effect of interest (here, the N1-suppression effect) is to vary the allocation of attention over several levels and determine its influence on the effect (cf. Logan, 1978, 1979). Therefore, we measured the N1-suppression effect with the mixed design<sup>4</sup> and manipulated the allocation of attention between blocks comprising three different attention conditions: While participants are performing the self-initiation task, attention is directed either to the sounds, the motor acts or to visual stimuli. Less attention should be directed to the sounds when participants attend to the motor act or to the visual stimuli than when they attend to the sounds. If the N1-suppression effect critically depends on an attentional difference, no (or a reduced) N1 suppression should occur when equating attention to externally and self-initiated sounds. In contrast, if N1 suppression for self-initiated sounds reflects a genuine suppression effect rather than an attentional difference, we expect comparable N1 suppression in all three attention conditions, supporting the assumption of an underlying genuine internal predictive mechanism.

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<sup>4</sup> As the recording of neural responses to motor activity without sounds in separate experimental blocks and subtracting these responses from the motor responses of the active condition could lead to biased estimates of sensory processing (Horváth et al., 2012; Hughes et al., 2012), we used a variant of the mixed N1 suppression paradigm, in which 50 % of the button presses trigger a sound while the other 50 % do not. With this, the representation of the motor command (efference copy) should be fully eliminated.

Moreover, in order to focus on effects that truly reflect attenuation of sensory responses due to a match of incoming stimulation with predicted stimulation in sensory cortex, we will make a more detailed analysis of the auditory N1, separating suppression effects for the N1a, N1b, and N1c components (Näätänen & Picton, 1987; Woods, 1995). It is well known that sensory and non-sensory (unspecific) components contribute to the auditory N1 (Näätänen & Picton, 1987). Importantly, only sensory components with sources in auditory cortex are tangentially oriented, showing a fronto-central distribution with polarity inversion at the mastoids. Contrary, the unspecific component, which reflects the orienting response, appears slightly later in time than tangential components and shows no polarity reversal at the mastoids, as it does not originate in auditory cortex. If the N1-suppression effect truly reflects attenuation of sensory responses that match internal sensory predictions, then sensory-specific components generated in auditory cortex should be attenuated. If on the contrary the N1-suppression effect mostly reflects differences in the orienting response generated by self- and externally-initiated sounds then the unspecific N1 component should be most affected. Finally, by comparing the N1-suppression effects due to self-initiation and the N1-attention effects, we can determine whether the predictive modeling (putatively) underlying the N1 suppression resembles attention effects. Indeed, previous research has reported attention in time effects that share characteristics of attention to other feature effects (Lange, 2011; Nobre, 2010).

### **3.1.2 Materials and Methods**

#### **3.1.2.1 Participants**

Fifteen healthy volunteers (7 male, 1 left-handed) participated in the experiment. Two male participants had to be excluded from the analysis due to low signal-to-noise ratio. Mean age of the remaining thirteen participants was 22.92 years (range: 19 to 29 years). All participants reported normal hearing and normal or corrected-to-normal vision. None were taking any medication affecting the central nervous system. All participants received either course credit or payment for their participation. The experiment was undertaken with the understanding and written consent of each subject. The experimental protocol conformed to the Declaration of Helsinki and the ethics guidelines of the German Association of Psychology (ethics board of the Deutsche Gesellschaft für Psychologie, DGPs: <http://www.dgps.de/dgps/aufgaben/ethikrl2004.pdf>) and did thus not require any additional ethics approval.

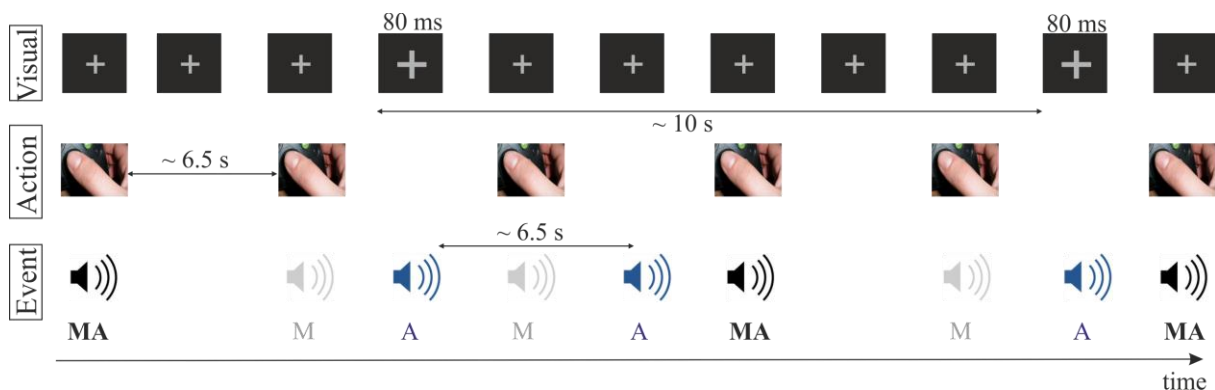


### 3.1.2.2 Experimental conditions

Participants were asked to fixate on a grey cross constantly displayed on the center of a black screen. Small extensions of the fixation cross (from a visual angle of  $0.69^\circ$  to  $0.74^\circ$  with a distance to the monitor of 100 cm) were presented for 80 ms duration using a variable stimulus onset asynchrony (SOA) of 5-15 s. These extended fixation crosses were not predictable for the participants. Using a mixed experimental design self-initiated and externally-initiated sounds were presented in the same block (Figure 5). Participants were instructed to press a button with their left or right thumb (depending on handedness) with self-paced intervals of 5-8 s (mean: 6.5 s). In 50 % of the trials button presses initiated a 50 ms sine tone of 1000 Hz (including 10-ms rise and 10-ms fall times) which was presented immediately after the button press through headphones (Sennheiser HD 25-1) (motor-auditory condition in the blocked design, MA). The intensity of the sounds was adjusted to a comfortable loudness by the participant with soft foam earplugs inserted to attenuate any other sounds. In the remaining 50 % of the trials button presses were not followed by any sound (motor-only condition in the blocked design, M). For the participants it was not predictable whether the button press would initiate a sound or not. Additionally, externally-initiated sounds (with the same physical parameters as the self-initiated sounds) were presented randomly between button presses (auditory-only condition in the blocked design, A). Externally-initiated sounds were unpredictable in their occurrence. The SOA between two externally-initiated sounds ranged randomly between 5-8 s. All sounds were generated with MATLAB (<http://www.mathworks.com>). To avoid a possible overlap with preceding self-initiated sounds, externally-initiated sounds were always presented at least 1 s after the occurrence of a button press. When the SOA between a preceding externally-initiated sound and a button press (initiating a sound or not) was smaller than 1 s both trials were excluded, but the respective number of trials were added at the end of the block to avoid loss of data. In addition to the self-initiation task the allocation of attention was manipulated block-wise. Three attention conditions were included (*Attention Sound*, *Attention Motor*, *Attention Visual*). In the *Attention Sound (AS)* condition participants were instructed to count all sounds they could hear, including self-initiated and externally-initiated ones. In the *Attention Motor (AM)* condition participants counted all button presses they made. In the *Attention Visual (AV)* condition they were asked to count all extended fixation crosses they saw on the screen. Thus,

## Experiments

less attention should be directed to the sounds when participants attend to the motor act or to the visual stimuli than when they attend to the sounds.



**Figure 5: Schematic illustration of the experimental mixed design**

Participants were asked to fixate on a grey cross constantly displayed on the center of a black screen. Small extensions of the fixation cross (from a visual angle of  $0.69^\circ$  to  $0.74^\circ$ ) were presented for 80 ms duration. The extended fixation crosses were unpredictable in their occurrence using a variable SOA of 5-15 s. Additionally, participants pressed a button approximately every 6.5 s. (range 5-8 s). With a probability of 50 % button presses were followed by a sound immediately (MA, black). In the remaining 50 % button presses were not followed by any sound (M, grey). It was not predictable if the button press would initiate a sound or not. Additionally, externally-produced sounds (with the same physical parameters as the self-initiated ones) occurred randomly between button presses (A, blue). Externally-produced sounds were unpredictable in their occurrence with a variable SOA between 5-8 s (mean of 6.5 s).

### 3.1.2.3 Experimental procedure

During EEG recordings, participants were seated in a sound-attenuated and electrically shielded chamber. Auditory stimulation was run via MATLAB using the Cogent2000 toolbox ([http://www.vislab.ucl.ac.uk/cogent\\_2000.php](http://www.vislab.ucl.ac.uk/cogent_2000.php)). Participants were instructed to press the button once every 5-8 s (mean: 6.5 s). They were informed that a button press would be followed by a sound or silence. Participants were informed about the occurrence of the externally-initiated sounds. However, they were not provided with further information about them. To get used to the self-initiation task participants received several training blocks before the experiment. In these training blocks visual feedback of the button press SOA was given after each button press. In the main experiment visual feedback about the mean button press interval and the responses that were too slow or too fast were only shown at the end of

each block. To avoid data loss, a block was repeated whenever participants pressed the button more than 5 times too slow or too fast within one block. In addition to the self-initiation task, participants had to count either all the sounds they could hear (*AS*), all the button presses they made (*AM*) or all the extended fixation crosses they saw (*AV*). Participants were always informed before the beginning of each block about the respective task. After each block they reported the number of counted events. To make sure participants attended to the particular events effectively the block was repeated whenever they miscounted more than  $\pm 2$ . Meta-blocks, including all three attention conditions, were repeated eight times. Thus, the EEG experiment consisted of twenty-four experimental blocks. In the meta-blocks the attention conditions (*AS*, *AM*, *AV*) were pseudo-randomized.

Each block consisted on average of twelve (range: ten to fourteen) self-initiated sounds (*MA*) and silent button presses (*M*), respectively. This variation was included to make the counting task less predictable for the participants. A comparable number of externally-initiated sounds (*A*) was presented depending on the mean SOA of the self-paced button presses. In total a mean of 96 trials were analysed for each event (*MA*, *A*, *M*) for each attention condition (*AS*, *AM*, *AV*), respectively.

### 3.1.2.4 Data recording and analysis

EEG activity was recorded continuously with Ag/AgCl electrodes from 60 standard locations (Fp1, Fp2, AF3, AFz, AF4, F7, F5, F3, F1, Fz, F2, F4, F8, FT7, FC3, FC1, FCz, FC2, FC4, FC6, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO9, PO7, PO3, POz, PO4, PO8, PO10, O1, Oz, O2) according to the international 10-20 electrode system (Chatrian et al., 1985) including the left and right mastoid (*M1*, *M2*). An additional electrode was placed at the tip of the nose (serving as offline reference). EOG was measured using the setup described by Schlögl and colleagues (2007) with one electrode at nasion and two electrodes at the outer canthi. EEG signals were sampled at 500 Hz.

Automatic eye movement correction was applied on the data according to the procedure described in (Schlögl et al., 2007), preceded by a 1 to 100 Hz offline band-pass filter. After EOG artifact correction, data were filtered with a 1-25 Hz band-pass filter (Kaiser-window,

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ripple: 0.017, length: 5653 points). For each trial, an epoch of 600 ms duration including a 200 ms pre-stimulus baseline was extracted from the continuous EEG record. Epochs with amplitude changes exceeding 75  $\mu$ V on any channel were rejected from further analysis. ERPs were averaged time-locked to stimulus onset separately for each event type, attention condition and participant. Button press errors (inter-press interval < 5000 ms or > 8000 ms) were removed from the EEG analysis.

To correct for motor activity present in responses to self-initiated sounds, the ERPs elicited by button presses followed by no sound were subtracted from the ERPs elicited to the self-initiated sounds. This motor-response-corrected ERP was then compared with the ERP of the externally-initiated sounds. In all figures and analysis, ERPs elicited by the self-initiated sounds were corrected this way. This approach has become an appropriate procedure in previous research (presenting MA and M conditions in separate blocks) to measure auditory processing activity in the presence of motor-related activity. However, presenting MA and M conditions introduces a possible confound, namely that it cannot be completely ruled out that non-motor responses, e.g. responses related to temporal expectations of the sound, might also be eliminated subtracting the ERPs elicited by button presses followed by no sound from the ERPs elicited to the self-initiated sounds. However, as the N1-suppression effect observed in the present study was virtually identical to the one reported in previous studies using no mixed design suggests that the suppression effects are not an artefact of the subtraction method of the mixed design.

Because of the multiple components with separate and potentially overlapping latencies underlying the N1 (Näätänen & Picton, 1987) we investigated three separate intervals in the N1 latency range which fit to the peaks N1a, N1b and N1c that have been described in the literature before (Budd et al., 1998; Näätänen & Picton, 1987; Wolpaw & Penry, 1975; Woods, 1995). Intervals for the N1a and N1c peaks were defined to encompass the first and second peak of the N1 at temporal electrodes. The interval for the N1b peak was defined to encompass the broader N1 peak at central and frontal electrodes. Thus, ERP effects were investigated around the grand-average peaks in the latency range of 85–150 ms (N1b time window), 60–100 ms (N1a time window) and 115–150 ms (N1c time window) after stimulus onset (see Figure 6). ERP amplitudes were calculated from the individual averages as the mean amplitude within these specified analysis time windows. A repeated measurement analysis of variance (ANOVA) with the factors *Attention* (AS, AM, AV), *Production* (self-

initiated vs. externally-initiated), *Laterality* (far left: F7, T7, P7; left: F3, C3, P3; midline: Fz, Cz, Pz; right: F4, C4, P4; far right: F8, T8, P8) and *Anterior-Posterior* (frontal: F7, F3, Fz, F4, F8; central: T7, C3, Cz, C4, T8; parietal: P7, P3, Pz, P4, P8) was computed for each N1 time window, on the mean amplitudes of the electrodes F7, T7, P7, F3, C3, P3, Fz, Cz, Pz, F4, C4, P4, F8, T8, P8. Moreover, in order to identify the sensory specific N1 component generated in auditory cortex, a further repeated measurement ANOVA with the factors *Attention* x *Production* was calculated for the mastoid signals in the latency range of 70-110 ms, since the generator for this component has a tangential orientation and results in N1 responses which are negative over frontocentral locations but are also recorded with inverted polarity on the mastoids.

For studying the scalp topographies in the interesting latency ranges, ERP voltage distributions were transformed into scalp current density (SCD) distributions, computing the second spatial derivative of the interpolated potential distribution (Perrin, Pernier, Bertrand, & Echallier, 1989, 1990). The maximum degree of the Legendre polynomials was chosen to be 50, and the order of splines ( $m$ ) was set to 4. A smoothing parameter  $\lambda$  of  $10^{-4}$  was applied. For behavioural data a one-way repeated ANOVA with the factor *Attention* was computed to compare inter-press time intervals, total number of button presses and timing errors for the self-initiation task between the attention conditions (*AS*, *AM*, *AV*). Furthermore, the counting rates of the attention task for all attention conditions were compared. The counting rates represent the total number of correctly counted events in relation to the total number of actual events of each attention condition. Greenhouse-Geisser correction was applied where appropriate. Additional pairwise comparisons (p-value alpha-adjusted using the Bonferroni correction) were conducted when appropriate to clarify the origin of significant effects. Only interactions that are relevant for the addressed question are reported.

### 3.1.3 Results

#### 3.1.3.1 Behavioral data

Table 1 summarizes the behavioural results for the self-initiation task (inter-press time intervals, total number of button presses, timing errors) and the attention task (counting rates) obtained in the three attention conditions (*AS*, *AM*, *AV*). For the self-initiation task the

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analysis revealed no main effect of *Attention* for inter-press time intervals [ $F(2,24) = 0.29$ ; *n.s.*], total number of button presses [ $F(2,24) = 2.31$ ;  $p = .120$ ] and timing errors [ $F(2,24) = 0.80$ ; *n.s.*]. However, with regard to the attention task a main effect of *Attention* was observed [ $F(2,24) = 5.22$ ;  $p < .05$ ]. Pairwise comparisons showed lower counting rates for the *AM* condition compared to the *AV* condition [ $t(12) = 4.22$ ;  $p = .001$ ]. However, the effect size of this effect is low ( $\eta^2 = 0.30$ ). No differences were obtained comparing *AS* to *AM* [ $t(12) = -1.43$ ;  $p = .176$ ] or *AS* to *AV* [ $t(12) = 1.50$ ;  $p = .158$ ]. Taken together, no fundamental differences of task demands were observed between the three attention conditions.

**Table 1: Behavioral results for all three attention conditions (*AS*, *AM*, *AV*)**

	Attention Sounds ( <i>AS</i> )	Attention Motor ( <i>AM</i> )	Attention Visual ( <i>AV</i> )
<b><i>Self-initiation task</i></b>			
Interval button presses (ms)	6233 (386)	6153 (425)	6188 (359)
Number of button presses	29.23 (2.8)	31.30 (2.5)	29.38 (2.78)
Timing errors (%)	2.33 (4.16)	2.94 (3.91)	1.06 (2.88)
<b><i>Attention task</i></b>			
Counting rates (%)	98.37 (4.59)	99.34 (3.71)	97.24 (3.59)

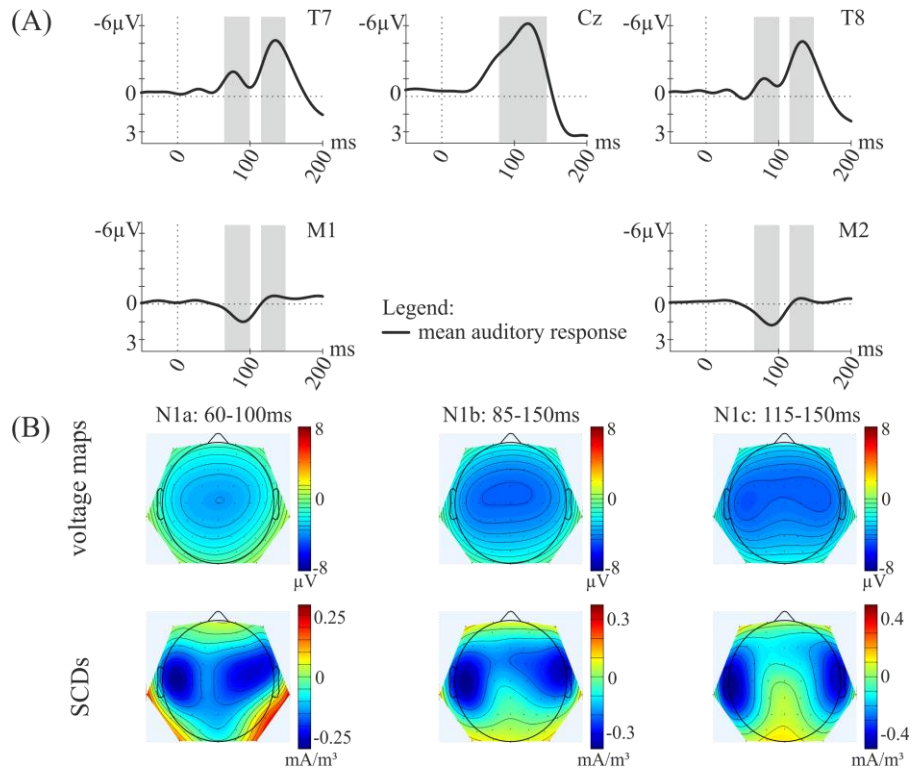
SD is given in parentheses.

### 3.1.3.2 Electrophysiological data

In Figure 6A the grand-average auditory response across all conditions is depicted at central, temporal and mastoid electrodes. The ERP waveform shows a negative deflection in the typical N1 latency range at Cz and a double-peaked N1 at temporal electrodes with polarity inversion at the mastoids for only the early peak. Voltage maps and scalp current densities (Figure 6B) show the corresponding distributions for this deflection over the scalp in the N1b (85-150 ms), the N1a (60-100 ms) and the N1c (115-150 ms) time window, respectively. In the following, modulations of this auditory response caused by self-initiation and attention are reported. Statistical results for all time windows are presented in Table 2. Most importantly, for all three N1 time windows no interaction of the experimental factors *Production* and *Attention* was found (N1b window:  $F(2,24) = 0.85$ ; *n.s.*; N1a window:  $F(2,24) = 6.24$ ;  $p = .536$ ; N1c window:  $F(2,24) = 0.80$ ; *n.s.*). Thus, auditory N1 effects due to self-initiation and due to the allocation of attention for each time window will be presented separately (see Additional file 1 for grand-average ERPs as well as voltage maps and scalp current densities

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(SCDs) of single attention conditions *AS*, *AM*, *AV*). Furthermore, no interaction of *Attention* x *Production* was observed for the analysis of the mastoids [ $F(2,24) = 0.72$ ; *n.s.*]. Thus, effects due to attention and self-initiation will be discussed separately as well.



**Figure 6: Illustration of the mean auditory response**

(A) Grand-average ERPs (mean of attention conditions *AS*, *AM*, *AV* as well as self-initiated and externally-initiated sounds) at temporal and central electrodes and the mastoids. Analysed time windows are marked in grey. (B) Voltage maps and scalp current densities (SCDs) during the latency ranges of the N1a (60-100 ms), N1b (85-150 ms) and N1c (115-150 ms) time window. Note that only part of the baseline is included to the graphs.

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**Table 2: Results of the ANOVA for all N1 time windows**

	N1b time window (85–150 ms)			N1a time window (60–100 ms)			N1c time window (115–150 ms)		
	<i>F</i>	<i>p</i>	$\eta^2$	<i>F</i>	<i>p</i>	$\eta^2$	<i>F</i>	<i>p</i>	$\eta^2$
Attention <sup>2</sup>	32.45	**	.730	10.57	**	.468	38.39	**	.762
Production <sup>1</sup>	18.31	**	.604	1.61	.228	.118	24.95	**	.675
Laterality <sup>3</sup>	38.46	**	.762	36.71	*	.754	10.37	**	.464
AnteriorPosterior <sup>2</sup>	6.32	*	.345	7.96	**	.339	3.80	.062	.241
Attention x Production <sup>2</sup>	0.85	.407	.066	6.24	.536	.049	0.80	.430	.063
Attention x Laterality <sup>4</sup>	9.65	**	.446	4.82	*	.287	9.93	**	.453
Attention x AnteriorPosterior <sup>3</sup>	17.83	**	.598	6.37	*	.347	9.02	**	.434
Production x Laterality <sup>3</sup>	30.85	**	.720	3.02	.076	.201	11.97	**	.499
Production x AnteriorPosterior <sup>2</sup>	4.05	.058	.253	2.90	.093	.194	3.76	.071	.239
Laterality x AnteriorPosterior <sup>4</sup>	2.03	.123	.145	4.71	*	.282	2.91	*	.196
Attention x Laterality x AnteriorPosterior <sup>5</sup>	1.69	.155	.123	1.70	.150	.124	2.53	*	.174
Production x Laterality x AnteriorPosterior <sup>4</sup>	2.85	*	.192	2.61	.051	.179	1.74	.168	.127
Attention x Production x Laterality <sup>4</sup>	1.92	.148	.138	1.12	.349	.085	1.56	.215	.115
Attention x Production x AnteriorPosterior <sup>3</sup>	0.66	.548	.052	0.53	.618	.042	0.43	.657	.034
Attention x Production x Laterality x AnteriorPosterior <sup>5</sup>	1.15	.340	.088	1.18	.324	.090	1.24	.295	.094

*F* values, *p* values and partial  $\eta^2$  for each N1 time window are reported.

<sup>1</sup> *F*(1,12).

<sup>2</sup> *F*(2,24).

<sup>3</sup> *F*(4,48).

<sup>4</sup> *F*(8,96).

<sup>5</sup> *F*(16,192).

\*\* *p* ≤ .001.

\* *p* ≤ .05.

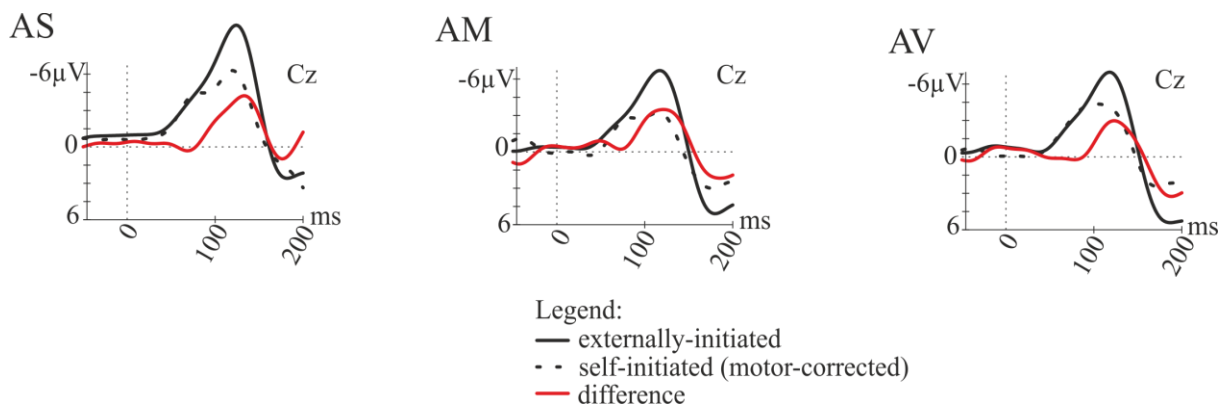
### 3.1.3.2.1 Self-initiation effects on the auditory N1

In Figure 7 grand-average ERP waveforms at Cz elicited by externally-initiated sounds and self-initiated sounds as well as the self-initiation effect (externally-initiated minus self-initiated) are shown, separately for the three attention conditions. Since comparable self-initiation effects were obtained in all attention conditions (*AS*, *AM*, *AV*) the mean of all three attention conditions was calculated and used for the further analysis. Figure 8A shows the grand-average ERP waveforms at Cz for the mean of all three attention conditions (*AS*, *AM*, *AV*) elicited by externally-initiated sounds and self-initiated sounds as well as the self-initiation effect (externally-initiated minus self-initiated). Furthermore, voltage maps and scalp current densities (SCDs) show the corresponding distribution over the scalp of the mean self-initiation effect in all three N1 time windows (Figure 8B). The analysis for the N1b time



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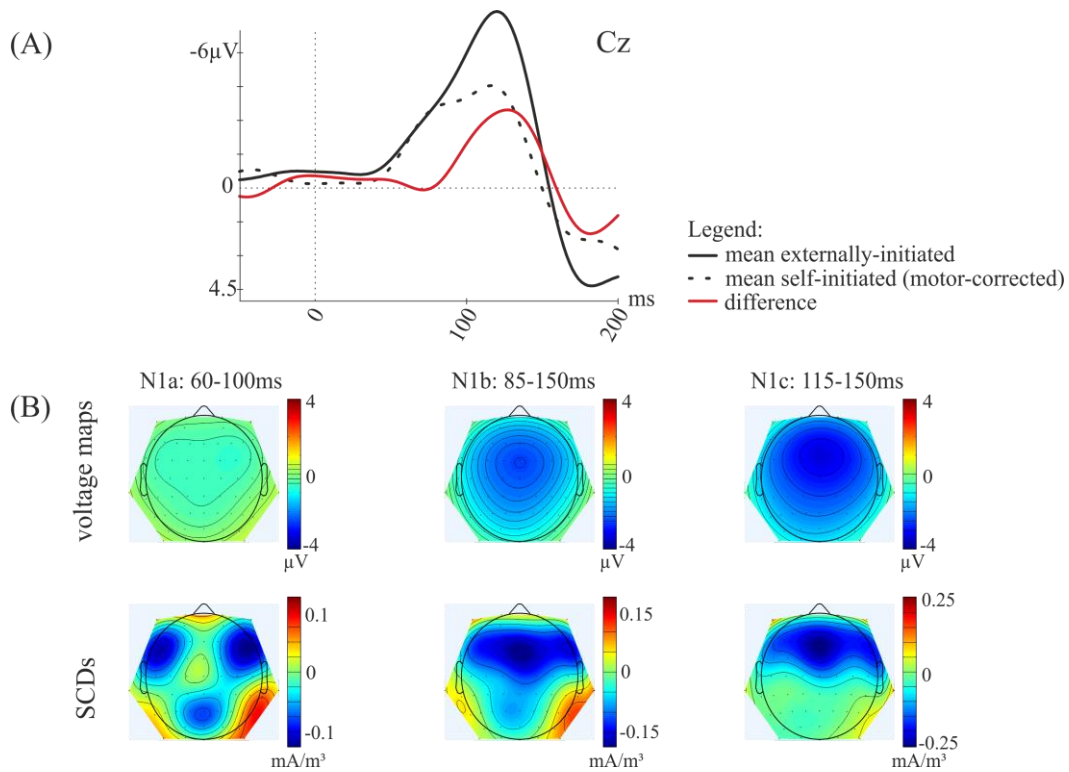
window revealed a main effect of *Production* [ $F(1,12) = 18.31$ ;  $p = .001$ ]. Also for the N1c time window a significant main effect [ $F(1,12) = 24.95$ ;  $p < .001$ ] was observed. This main effect of *Production* for both time windows was caused by lower amplitudes for self-initiated sounds compared to externally-initiated sounds. However, for the N1a time window no main effect of *Production* was found [ $F(1,12) = 1.61$ ;  $p = .228$ ], showing comparable amplitudes for self-initiated and externally-initiated sounds. Furthermore, for the N1b time window an interaction of *Production*  $\times$  *Laterality*  $\times$  *Anterior-Posterior* [ $F(8,96) = 2.85$ ;  $p = .039$ ] was obtained. Pairwise comparisons revealed lower amplitudes at frontal and central electrodes ( $p < .05$  for F3, F4, Fz, F7, F8, C3, Cz, C4) for self-initiated compared to externally-initiated sounds, indicating a fronto-central distribution of the self-initiation effect (see Figure 8B, upper panel). The SCD topography of this effect also shows a pattern pointing at a fronto-central effect (see Figure 8B, lower panel). For the N1c time window no such interaction was observed [ $F(8,96) = 1.74$ ;  $p = .168$ ]. However, the analysis revealed an interaction of *Production*  $\times$  *Laterality* [ $F(4,48) = 11.97$ ;  $p = .001$ ], showing a more central than lateral distribution of the self-initiation effect (see Figure 8B, upper panel). Again, the SCD distribution supports a fronto-central effect (see Figure 8B, lower panel). Contrary, for the N1a time window no interaction with the experimental factor *Production* was found. Additionally, at the mastoids no main effect of *Production* was obtained [ $F(1,12) = 2.98$ ;  $p = .110$ ].



**Figure 7: Illustration of the self-initiation effect for single attention conditions**

Grand-average ERPs at Cz elicited by externally-initiated sounds (black solid line), self-initiated sounds (black dotted line) and the difference waves (externally-initiated minus self-initiated, red line), separately for the single attention conditions *Attention Sounds* (AS), *Attention Motor* (AM) and *Attention Visual* (AV).

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**Figure 8: Illustration of the mean self-initiation effect**

(A) Grand-average ERPs (mean of all attention conditions *AS*, *AM*, *AV*) at Cz elicited by externally-initiated sounds (black solid line), self-initiated sounds (black dotted line), as well as the difference wave (externally-initiated minus self-initiated, red line). (B) Voltage maps and scalp current densities (SCDs) of the difference wave during the latency ranges of the N1a (60-100 ms), N1b (85-150 ms) and N1c (115-150 ms) time window.

### 3.1.3.2.2 Comparison of self-initiation effects and attention effects on the auditory N1

In the following, attention effects are outlined and then compared to the self-initiation effect. In order to simplify the comparison, we focused on effects of attending (*AS*) vs. not attending (*AM*, *AV*) to sounds, pooling the attention effects for the *AM* and *AV* conditions, which were rather similar (cf. Additional file 2). Thus, we compared effects of attending to sounds (*AS* vs.  $[\text{AM}+\text{AV}]/2$  [over all production conditions]) to effects of self-initiating the sounds (*A-MA* [over all attention conditions]). Figure 9A shows the grand-average ERP waveforms at Cz elicited when attending the sounds and when not attending the sounds as well as the attention effect (attended minus unattended) for the mean of self-initiated and externally-initiated sounds. Furthermore, voltage maps and SCDs show the corresponding distribution

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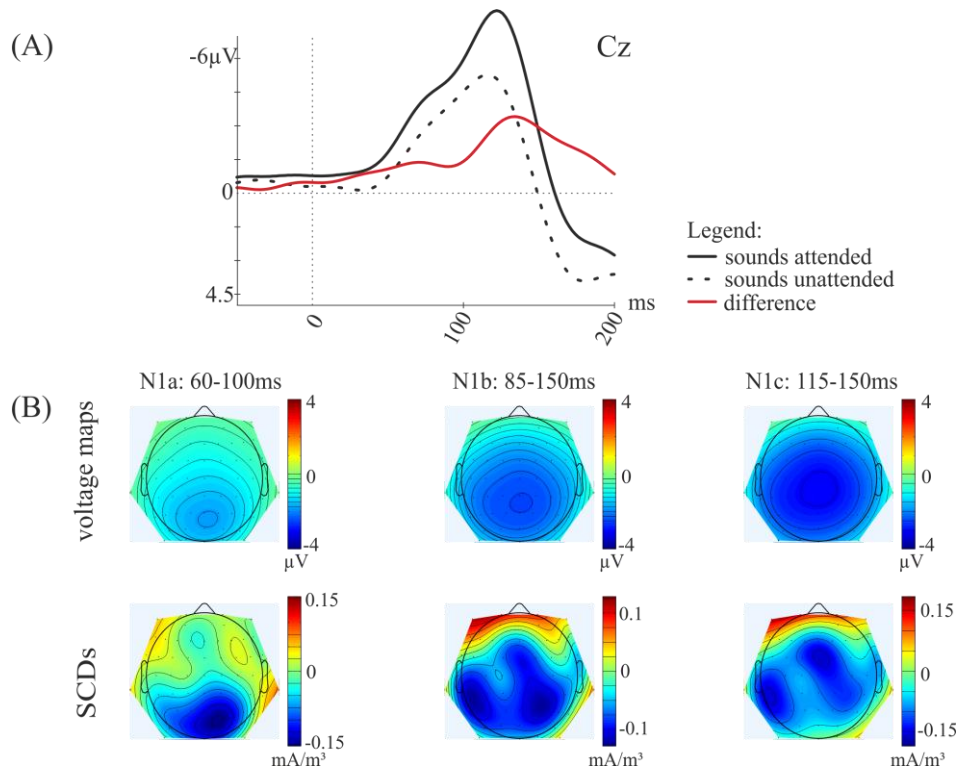
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over the scalp of the attention effect in all three N1 time windows (Figure 9B). The analysis for all N1 time windows revealed a main effect of *Attention* (N1b time window:  $F(2,24) = 32.45$ ;  $p < .001$ ; N1a time window:  $F(2,24) = 10.57$ ;  $p = .001$ ; N1c time window:  $F(2,24) = 38.39$ ;  $p < .001$ ). Pairwise comparison indicated higher activity for attending the sounds compared to not attending the sounds (N1b time window:  $t(12) = -7.87$ ;  $p < .001$ ; N1a time window:  $t(12) = -4.89$ ;  $p < .001$ ; N1c time window:  $t(12) = -8.28$ ;  $p < .001$ ). There was also a significant interaction of *Attention* x *Laterality* for the N1b time window [ $F(8,96) = 9.65$ ;  $p < .001$ ] and the N1a time window [ $F(8,96) = 4.82$ ;  $p < .01$ ]. Pairwise comparisons for the N1b time window showed higher amplitudes for attended compared to unattended sounds for all laterality levels [far left ( $t(12) = -6.29$ ;  $p < .001$ ), left ( $t(12) = -8.01$ ;  $p < .001$ ), midline ( $t(12) = -8.90$ ;  $p < .001$ ), right ( $t(12) = -7.50$ ;  $p < .001$ ), far right ( $t(12) = -4.72$ ;  $p < .001$ )]. For the N1a time window the post-hoc analysis indicated higher amplitudes for attended compared to unattended sounds for all laterality levels except the far right (F8, T8, P8) level [far left ( $t(12) = -3.23$ ;  $p < .05$ ), left ( $t(12) = -5.03$ ;  $p < .001$ ), midline ( $t(12) = -6.16$ ;  $p < .001$ ), right ( $t(12) = -6.14$ ;  $p < .001$ ), far right ( $t(12) = -2.54$ ;  $p = .130$ )]. For both time windows the attention effect shows a more parietal distribution (see Figure 9B, upper panel) compared to the self-initiation effect (see Figure 8B, upper panel).

The SCD distribution reveals that the putative sources of this attention effect are located in more parietal areas compared to the self-initiation effect (see Figure 8B, lower panel). However, the distribution for the N1b time window shows a more widespread activity than the distribution of the N1a time window (see Figure 9B, lower panel). Furthermore, there was a significant interaction of *Attention* and *Anterior-Posterior* for the N1b [ $F(4,48) = 17.83$ ;  $p < .001$ ] and the N1a [ $F(4,48) = 6.37$ ;  $p < .01$ ] time window. Pairwise comparisons revealed higher activity for attended compared to unattended sounds for all levels of both time windows [N1b time window: frontal ( $t(12) = -5.83$ ;  $p < .001$ ), central ( $t(12) = -7.86$ ;  $p < .001$ ), parietal ( $t(12) = -8.72$ ;  $p < .001$ ); N1a time window: frontal ( $t(12) = -2.91$ ;  $p = .039$ ), central ( $t(12) = -4.37$ ;  $p < .01$ ), parietal ( $t(12) = -5.91$ ;  $p < .001$ )]. Again, this attention effect shows a parietal distribution (see Figure 9B, upper panel), which is supported by a parietal pattern of activity in the SCDs (see Figure 9B, lower panel). For the N1c time window no such interactions were found. However, the analysis revealed an interaction of *Attention* x *Laterality* x *Anterior-Posterior* [ $F(16,192) = 2.53$ ;  $p < .05$ ] for this time window, indicating a parietal and left-lateralized distribution of the attention effect, which shows a more anterior

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distribution than the N1b and the N1a time window (see Figure 9B, upper panel). This finding is also supported by the SCDs which point at a more central topography (see Figure 9B, lower panel). Finally, at the mastoids no main effect of *Attention* was found [ $F(2,24) = 1.03$ ;  $p = .374$ ].



**Figure 9: Illustration of the attention sound effect**

(A) Grand-average ERPs (mean of self-initiated and externally-initiated sounds) at Cz elicited by attending the sounds (black solid line), not attending the sounds (black dotted line), as well as the difference wave (attended minus unattended, red line). (B) Voltage maps and scalp current densities (SCDs) of the difference wave during the latency ranges of the N1a (60-100 ms), N1b (85-150 ms) and N1c (115-150 ms) time window.

### 3.1.4 Discussion

In the present study we investigated to which extent the N1-suppression effect for self-initiated sounds can be explained by a differential allocation of attention to self-initiated and externally-initiated sounds. To overcome possible limitations of the traditional blocked design self-initiated sounds and externally-initiated sounds as well as the motor control were presented within the same block. The allocation of attention was manipulated block-wise in

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three different attention conditions (*AS*, *AM*, *AV*), so that attention was directed to the sounds or was directed away from the sounds towards the own motor behavior or the visual stimulation. Moreover, we compared effects of self-initiation with attention effects to determine whether the underlying neural processes affect the same or different structures.

Horvath and colleagues (2012) have proposed that that N1 suppression might possibly be caused by split attentional resources in active conditions compared to passive conditions of the traditional blocked design (Aliu et al., 2009; Bässl et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; Martikainen et al., 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973). We found an attenuation of the auditory N1 for self-initiated compared to externally-initiated sounds that was independent from the allocation of attention. That is, the N1 suppression was the same, irrespective of whether attention was directed to the sounds, directed to the motor act or directed to the visual stimuli. Thus, the N1-suppression effect cannot be explained by attentional differences between self- and externally-initiated sounds. In other words, sensory suppression to self-initiated sounds cannot be explained by the fact that the motor act draws away attention from auditory processing. Our finding is consistent with a recent study reporting reduced N1 amplitude during self-vocalization using a selective attention task to assess the N1 component independent of the attention effect (Kudo et al., 2004).

Similar to forward modeling effects in other species (Eliades & Wang, 2003; Müller-Preuss & Ploog, 1981), it has been argued that the N1-suppression effect is a very basic and automatic phenomenon (Horváth et al., 2012). Horvath and colleagues (2012) showed that the auditory input seems to be attenuated for a short period after the motor act, even if there is no contingency between button press and sound. It seems that the sensory processing during self-initiation of sounds is merely affected by the concurrent motor act (Makeig et al., 1996). Our finding that the neural processes underlying the N1 suppression are not modulated by attention strongly supports the view that they are rather automatic. In fact, the definition of an automatic (versus a controlled) process is that it does not interfere with attention (cf. Hackley, 1993; Kahneman & Treisman, 1984).

As predicted, the allocation of attention to the sounds resulted in an increase of the auditory N1, as compared to the N1 elicited by the sounds when attention was directed to the button

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presses or to the visual stimuli. This finding is consistent with results from previous studies (Alho, Woods, & Algazi, 1994; Giard, Perrin, Pernier, & Peronnet, 1988; Hillyard, 1981; Näätänen & Picton, 1987; Woldorff & Hillyard, 1991). However, previous studies often obtained a more fronto-central distributed auditory attention effect (Alho et al., 1994; Talsma & Kok, 2001, 2002), whereas we obtained a more parietal distribution. Nevertheless, top-down controlled attention has been reported to involve temporo-parietal and superior parietal areas (Salmi, Rinne, Koistinen, Salonen, & Alho, 2009), which is consistent with the distribution of our attention effect.

Moreover, the comparison of the self-initiation effect and the attention effect revealed that partly separate N1 components (Näätänen & Picton, 1987) are affected. Whereas all N1 components (i.e. N1a, N1b, N1c) were modulated by attention, only the late part of the N1 (i.e. N1b, N1c) was suppressed by self-initiation. Thus, we conclude that the predictive modeling underlying the N1-suppression effect is not “only” attention in time (Lange, 2011; Nobre, 2010) but a mechanism that is separable from a mere attentional mechanism. In the present report, the frontocentral peak of the N1b did not coincide with the time of polarity reversal at the mastoids, which occurred slightly earlier. The N1b component is known to receive contributions from both the tangentially oriented, sensory-specific component and the unspecific component of the N1 (Näätänen & Picton, 1987). Because the unspecific component occurs later in time, its contribution tends to delay the peak of the N1b on frontocentral leads (Budd et al., 1998). Thus, the window of analysis chosen here around the peak of the N1b probably receives its largest contribution from the unspecific N1 component. There were no self-initiation effects at the mastoids on the polarity-inverted N1 deflection. This finding suggests that a large part of the N1-suppression effect may be due to the suppression of the unspecific N1 component rather than the attenuation of sensory responses in auditory cortex as stipulated from internal predictive models theory. Thus, it could be speculated that the N1-suppression effect as measured in most ERP studies may largely reflect the fact that self-initiated sounds are less arousing compared to externally-initiated sounds. However, the lack of N1 suppression on the mastoids and on fronto-central electrodes at the time of polarity reversal at the mastoids in the present experiment does not necessarily imply that sensory responses are not attenuated by self-initiation in auditory cortex at all. Indeed, previous MEG studies, which specifically measure the activity of tangentially oriented sources on auditory cortex, have found N1 suppression for self-initiated sounds (Aliu et al., 2009; Horváth et al., 2012; Martikainen et al., 2005).

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In conclusion, we could show that the N1 suppression was equally large and of equal distribution when subjects directed their attention towards the sound and when they directed their attention away from the sounds, towards the button presses or the visual stimuli. Thus, the self-initiation effect can hardly be explained by the differential amount of attention devoted to self- and externally-triggered sounds. Instead, the present results support the notion that N1 suppression for self-initiated sounds seems to reflect the activity of an internal predictive mechanism. Whereas the effects of voluntary attention affect all N1 components, the self-initiation effect seems to be confined to the N1b and N1c components. The present mixed design provides a useful tool to measure genuine self-initiation effects.





### 3.2 Motor intention determines sensory attenuation of brain responses to self-initiated sounds<sup>5</sup>

#### Abstract

One of the functions of the brain is to predict sensory consequences of our own actions. In auditory processing self-initiated sounds evoke a smaller brain response than passive sound exposure of the same sound sequence. Previous work suggests that this response attenuation reflects a predictive mechanism to differentiate the sensory consequences of one's own actions from other sensory input, which seems to form the basis for the sense of agency (recognizing oneself as the agent of the movement). The present study addresses the question whether attenuation of brain responses to self-initiated sounds can be explained by brain activity involved in movement planning rather than movement execution. We recorded event-related potentials in response to sounds initiated by button presses. In one condition, participants moved a finger to press the button voluntarily, whereas, in another condition, we initiated a similar, but involuntary, finger movement by stimulating the corresponding region of the primary motor cortex with transcranial magnetic stimulation. For involuntary movements no movement intention (and no feeling of agency) could be formed, thus no motor plans were available to the forward model. A portion of the brain response evoked by the sounds, the N1-P2 complex, was reduced in amplitude following voluntary, self-initiated, movements, but not following movements initiated by motor cortex stimulation. Our findings demonstrate that movement intention and the corresponding feeling of agency determine sensory attenuation of brain responses to self-initiated sounds. The present results support the assumptions of a predictive internal forward-model account operating prior to primary motor cortex activation.

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<sup>5</sup> This study is based on the article: Timm, J., SanMiguel, I., Keil, J., Schröger, E., & Schönwiesner, M. (under revision II). Motor intention determines sensory attenuation of brain responses to self-initiated sounds.

### 3.2.1 Introduction

Stimuli caused by our own actions receive a special treatment in the brain. This claim is supported by the finding that self-generated stimuli are perceived to be less intense than other, externally-generated, stimuli (“sensory attenuation”, (Blakemore, Wolpert, et al., 1998)). Models of motor control suggest that these effects indicate the successful prediction of the sensory consequences of our motor acts (Wolpert et al., 1995). Specifically, those models assume that whenever an action is performed, copies of our motor commands are routed as corollary discharges (CD) to sensory structures, and the sensory consequences resulting from the action are predicted via forward modeling. The comparator model proposes that predicted and received sensory feedback is then compared, leading to sensory attenuation in case of a match (Tsakiris & Haggard, 2005). This comparison has also been proposed as the basis for the sense of agency (Blakemore et al., 2002; Frith et al., 2000), because it enables differentiating the sensory consequences of one’s own actions from other sensory input.

However, the precise neural implementation of the comparison process is unknown. Animal neurophysiology studies have established that CD circuits originate in all levels of the motor pathway and can influence the sensory processing stream at different levels in various sensory systems (Crapse & Sommer, 2008a). In humans, research has been mostly focused on the somatosensory modality; that is, on the processing of voluntary movements and their direct proprioceptive and tactile consequences. These studies provide converging evidence that CD signals originate upstream from the execution of the motor command in primary motor cortex (Christensen et al., 2007; Haggard & Whitford, 2004; Voss et al., 2007). Thus, when body movements are involuntary, no sensory attenuation occurs (Chronicle & Glover, 2003; Haggard & Whitford, 2004). A similar picture emerges for the sense of agency, which seems to be driven by a match between experienced motor intentions, formed in premotor and parietal cortex, and the achieved goals (Haggard, 2005). Thus, studies focusing on voluntary movements and their proprioceptive feedback indicate that the CD signals necessary to recognize oneself as the agent of the movement, and for the movement’s feedback to be processed as self-generated, are issued during movement planning, rather than upon movement execution.

Proposing a universal predictive mechanism for sensory processing of voluntary movements (Wolpert et al., 2005) the same CD circuits might be involved in the processing of self-

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generated auditory stimuli. Several studies have shown that auditory stimuli self-generated via instrumental action (i.e. sounds which are self-initiated via button press), elicit an attenuated N1-P2 complex in the auditory event-related potential (ERP) compared to passive sound exposure (Aliu et al., 2009; Baess et al., 2011; Bäсс et al., 2008; Knolle, Schröger, & Kotz, 2012; Martikainen et al., 2005; Schafer & Marcus, 1973). The attenuation of the N1-P2 complex might reflect a match in the comparator and is also used as an indicator for agency disruptions (Ford et al., 2007). However, the presumption that the N1-P2 attenuation reflects predictive processing is still controversial (SanMiguel et al., 2013; Synofzik et al., 2008; Tsakiris & Haggard, 2005). For example, recent findings show that auditory input seems to be attenuated for a short period after the motor act, even if there is no contingency between button press and sound (Horváth et al., 2012; Horváth, 2013a, 2013b). Moreover, only little is known about the specific relationship between N1-P2 attenuation to self-initiated sounds and the sense of agency (Gentsch & Schütz-Bosbach, 2011; Kühn et al., 2011). Thus, the present study aims to shed further light on the underlying neural mechanisms engaged in the processing of self-initiated sounds and the N1-P2 attenuation.

To this end we use electroencephalography (EEG) to record ERPs from the human scalp in response to a sound initiated by a button press. Participants either move a finger to press the button, or a similar finger movement is initiated by stimulating primary motor cortex with transcranial magnetic stimulation (TMS). Thus, both voluntary and involuntary finger movements are the result of activity in the participant's motor cortex. However, TMS-evoked finger movements cannot be planned by the participant, that is, the intention to move and the corresponding feeling of agency is missing. Assuming that CD signals are sent during movement planning rather than movement execution (Chronicle & Glover, 2003; Haggard & Whitford, 2004), no CD should be available to the predictive forward model for the TMS-evoked finger movements. We expect to find an attenuated N1-P2 complex only in response to the voluntary finger movements, but not in response to the TMS-evoked movements. Thus, our study can answer the question of whether the forward-model account of the N1-P2 attenuation to self-initiated sounds is appropriate.

### 3.2.2 Materials and Methods

#### 3.2.2.1 Participants

Twenty-four healthy right-handed volunteers were recruited for the experiment. Seven participants were excluded for technical reasons (six because the TMS artifact could not be corrected and one due to a low signal-to-noise ratio of the EEG recording). The mean age of the remaining seventeen participants was 24.06 years (range: 18 to 31 years). All participants reported normal hearing and normal or corrected-to-normal vision, had no history of hearing disorder or neurological disease and took no medication affecting the central nervous system. The experimental procedures conformed to the World Medical Association's Declaration of Helsinki and were approved by the local ethics committee. All participants provided informed consent and were compensated for their participation.

#### 3.2.2.2 Procedure

During EEG recordings, participants were seated comfortably and were instructed to move as little as possible during the experiment. They were also instructed to fixate their gaze on a grey cross displayed on a black computer screen in order to reduce eye movements. Stimulus generation and acquisition of behavioural responses were controlled by a computer using MATLAB (The MathWorks, [www.mathworks.com](http://www.mathworks.com)) and the Cogent 2000 toolbox ([www.vislab.ucl.ac.uk/cogent\\_2000.php](http://www.vislab.ucl.ac.uk/cogent_2000.php)). Auditory stimuli were sine tones with a frequency of 1 kHz and a duration of 50 ms (including 10 ms squared-cosine onset and offset ramps). Sounds were presented through ER1 insert earphones (Etymotic Research, [www.etymotic.com](http://www.etymotic.com)). The intensity of the sounds was adjusted to a comfortable loudness by the participant prior to the experiment.

The experiment consisted of two main conditions ("voluntary" and "involuntary") and several control conditions. All conditions involved EEG recording and some conditions involved TMS (see respective sections below). In the voluntary condition, participants were instructed to press a piezoresistive force sensor ("button"), connected to an Arduino microcontroller board ([www.arduino.cc](http://www.arduino.cc)), with their right index and middle fingers in a self-paced interval of 2.5-4.5 s (mean 3.5 s). Each press initiated sound presentation after a 100 ms delay, inserted to avoid overlapping of the TMS artefact and the sound-evoked responses in the EEG

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recordings (see detailed explanation below). In the involuntary condition, we applied a single TMS pulse (see below) to the left primary motor cortex that elicited an involuntary finger movement of the participants, leading to a button press every 2.5-4.5 s (mean 3.5 s), which in turn elicited a sound 100 ms later. The TMS-induced movements were similar but of course not identical to the voluntary movements. In both conditions the experimenter was present in the laboratory. In the involuntary conditions the experimenter adjusted the position of the TMS coil. In the voluntary conditions the experimenter silently supervised the experiment in the background.

It is well known that each TMS pulse induces an ERP which mainly affects local cortical activity in the primary motor cortex (Siebner & Ziemann, 2007). Moreover, the abrupt electromagnetic forces in the stimulating coil produce a short click every time a single TMS pulse is delivered (Counter & Borg, 1992), which evokes auditory responses in the EEG. It has been shown that the TMS coil click can affect processing of simultaneously presented auditory stimuli (Tiitinen et al., 1999). We controlled for this possible confound by introducing an artificial temporal delay of 100 ms between button presses and sound presentation. Thus, in both voluntary and involuntary conditions the temporal delay between button press and onset of self-initiated sound was identical. In the present study TMS pulses to primary motor cortex elicited finger movements with a latency of 60-110 ms (mean latency: 85.7 ms, standard deviation: 24.38 ms), thus, the temporal delay between TMS pulses and the onset of self-initiated sounds was around 185 ms. Furthermore, in the analysis sensory attenuation effects to self-initiated sounds were only identified within conditions, that is, differences between sound-evoked responses to self-initiated sounds and sounds that are played back passively were analyzed separately for the voluntary and the involuntary condition (see below). Consequently, the effects on auditory responses due to the TMS in the involuntary condition are controlled for.

In order to quantify attenuation of brain responses to sounds elicited by button presses relative to passive exposure to the same sounds, we added an “auditory-only” control to both the voluntary and the involuntary conditions, in which we measured EEG responses to the sounds alone, without preceding finger movements. This was achieved by playing back the auditory stimuli of the active conditions to the passively listening participants. In the involuntary auditory-only condition, the exact sequence of TMS pulses and sounds was replayed, but we tilted the TMS coil by 90°, which does not result in motor cortex stimulation.

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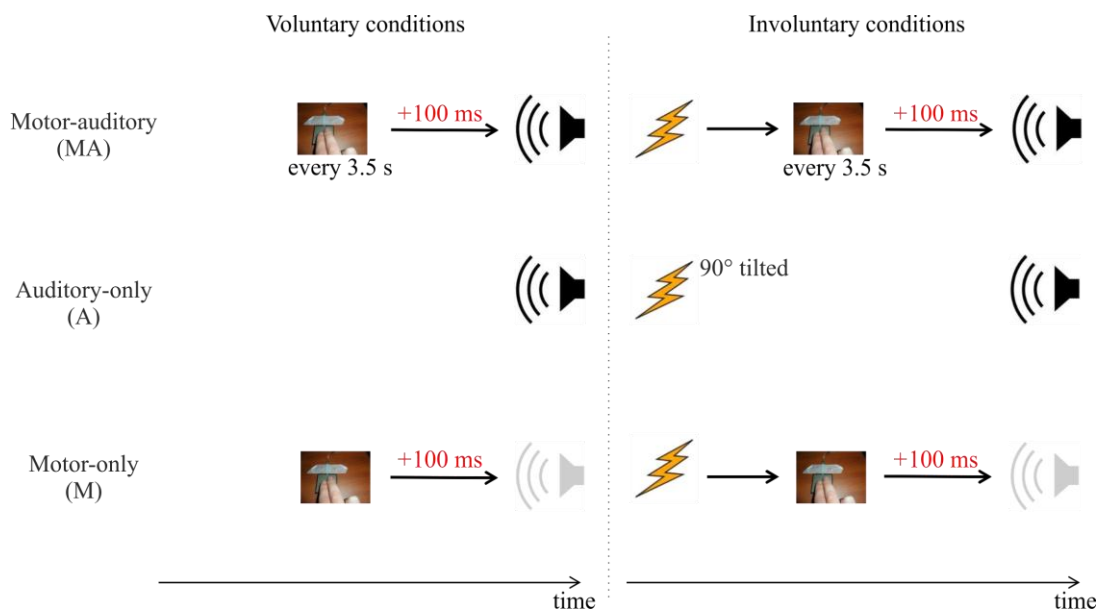
To account for motor activity in the EEG recordings, we added a further “motor-only” control to both the voluntary and the involuntary conditions. In the motor-only voluntary condition, participants pressed the button in the same self-paced interval as in the voluntary condition, but no sounds were played. In the motor-only involuntary condition, TMS pulses were applied to elicit button presses every 2.5-4.5 s (mean 3.5 s), but again, no sounds were played (see Figure 10). Each of the six conditions was presented in four blocks of 45 trials (180 trials per condition). With 1080 trials (6 conditions  $\times$  180 trials) at an average duration of 3.5 s, the experiment took approximately 1 hour, excluding subject preparation and breaks. Blocks for voluntary and involuntary conditions were always followed by the respective auditory-only and motor-only blocks. Apart from that constraint; the order of the voluntary and involuntary conditions was counterbalanced across participants. Before the main experiment, participants performed a short training session of the voluntary condition and the motor-only voluntary condition to get accustomed to the procedures and to improve their ability to produce button presses within intervals of 2.5 to 4.5 s. After each press during training, participants were shown the time elapsed since the previous button press. At the end of each training block (20 trials) participants were shown the number of produced intervals that were above and below the required range. Furthermore, participants were accustomed to the involuntary condition to get familiar with the TMS procedure. While applying a single TMS pulse to the left primary motor cortex to elicit an involuntary finger movement, participants were instructed to relax their right hand and to fixate the cross on the screen.

### 3.2.2.3 TMS stimulation

TMS was applied with a Rapid<sup>2</sup> system with a hand-held 70-mm figure-eight coil (Magstim, [www.magstim.com](http://www.magstim.com)). ABrainsight 2 neuro-navigation system (Rogue Research, [www.rogue-research.com](http://www.rogue-research.com)) was used to aid localizing and verifying the TMS target position. We registered a magnetic resonance image of a template head to the head of each participant. The neuro-navigation system tracked the relative positions of the TMS coil and the participant’s head during the experiment and displayed anatomical locations on the template brain corresponding to the current coil position. The approximate location of the left primary motor cortex was identified on the template brain. The position of the coil was then adjusted so that a TMS pulse produced a motor potential in the right first dorsal interosseus muscle. This muscle flexes the index finger and is involved in the voluntary finger movement that participants executed when pressing the button. Muscle activity was measured with an

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electromyography (EMG) system integrated with the TMS apparatus. The intensity of the TMS stimulation during the experiment was set to 110 % of the smallest intensity that produced a motor potential and a visible finger movement. A trigger was generated whenever the force measured by the pad deviated by a set amount from the reference value, which was defined as the weight of the relaxed finger on the pad and was constant across conditions. Significant movements that led to button presses were elicited in 81 % (standard deviation: 14.27 %) of involuntary trials. The 19 % of failed trials can be explained by two reasons: the experimenter either missed the spot in primary motor cortex so that no finger movement was elicited or the movement that was generated was not large enough. Participants were instructed to hold their hand relaxed while TMS stimulation to avoid possible corrections of button presses, which were too soft.



**Figure 10: Schematic illustration of the experimental design**

Two main conditions were applied. In the voluntary condition participants pressed a force sensor voluntarily approximately every 3.5 s. (range 2.5 - 4.5 s). A short sound followed each button press after 100 ms (Motor-auditory, MA). Afterwards, participants listened passively to the same sequence of sounds (Auditory-only, A). Additionally, to control for motor activity participants pressed the button and no sound occurred (Motor-only, M). In the involuntary condition the button was pressed involuntarily (Motor-auditory, MA). Single pulse TMS over primary motor cortex elicited short finger movements every 3.5 s (range 2.5 - 4.5 s). During the passive replay of the sound sequence the TMS-coil was tilted 90° (Auditory-only, A). To control for motor-activity involuntary button presses elicited no sounds (Motor-only, M).

### 3.2.2.4 EEG recording

EEG activity was recorded continuously throughout the experiment with a SynAmps2 amplifier (Neuroscan, [www.neuroscan.com](http://www.neuroscan.com)) and TMS-compatible sintered Ag/AgCl electrodes from 64 positions on the scalp, including the left and right mastoid (M1, M2). In addition, a ground electrode was placed on the head, and a reference electrode was placed on the tip of the nose. Eye movements were monitored with bipolar recordings from electrodes placed above and below the left eye (vertical electro-oculogram, VEOG) and lateral to the outer canthi of both eyes (horizontal electro-oculogram, HEOG). EEG and EOG signals were sampled at 2000 Hz.

### 3.2.2.5 Data analysis

Epochs of 3 s duration, starting 1.5 s before the onset of the sound stimuli, were extracted from the raw EEG data. A linear trend was removed from each epoch and power line noise was removed by rejecting the 60 Hz bin from the epoch's spectrum using a discrete Fourier transform. Electrical artefacts caused by the TMS pulses were removed from the EEG data using spline interpolation as described by (Thut et al., 2011). Epochs were resampled at 512 Hz. We applied a 2nd-order two-way 1 Hz Butterworth high-pass filter and a 16th-order two-way 25 Hz Butterworth low-pass filter to the epochs. The data were visually inspected and epochs with excessive EOG, movement, or other artefacts were removed. Epochs containing button presses outside the required interval range (see above) were also removed. Epochs were then shortened to 600 ms duration, starting 300 ms before the onset of the sound stimulus. Epochs were averaged separately for each experimental condition and participant.

To isolate sound-evoked brain activity from motoric activity associated with the finger movements, we subtracted the respective motor-only conditions from the voluntary and involuntary conditions. The resulting responses were then compared with responses in the respective auditory-only conditions. In this comparison, we focused on the amplitudes of the N1 and P2 components of the evoked response. We defined the amplitude of the N1 component as the minimum of the response waveform in a latency window of 70 to 140 ms after sound onset, and the amplitude of the P2 component as the maximum of the response waveform in a latency window of 135 to 265 ms after sound onset. We subtracted N1 and P2 amplitudes (“peak-to-peak amplitude”) and performed a repeated measurement analysis of



variance (ANOVA) with the factors *Agency* (voluntary vs. involuntary) and *Task* (active vs. passive) on the mean peak-to-peak amplitude of the fronto-central electrodes F3, Fz, F4, FCz, FC3, FC4, Cz, C3, and C4. Post-hoc tests were conducted to clarify the origin of significant interactions. Greenhouse-Geisser correction was applied when appropriate. We used peak-to-peak analysis to minimize potential influences of the TMS artifact and to increase signal-to-noise ratio compared to a single component analysis. The downside of this procedure is that it is not possible to dissociate attenuation effects on the N1 and P2 components. Although some studies have found differentiated attenuation effects on these two components (Knolle, Schröger, & Kotz, 2012; Sowman, Kuusik, & Johnson, 2012), effects on the N1 and P2 in common attenuation paradigms mostly go along with each other (Horváth et al., 2012; Schafer & Marcus, 1973).

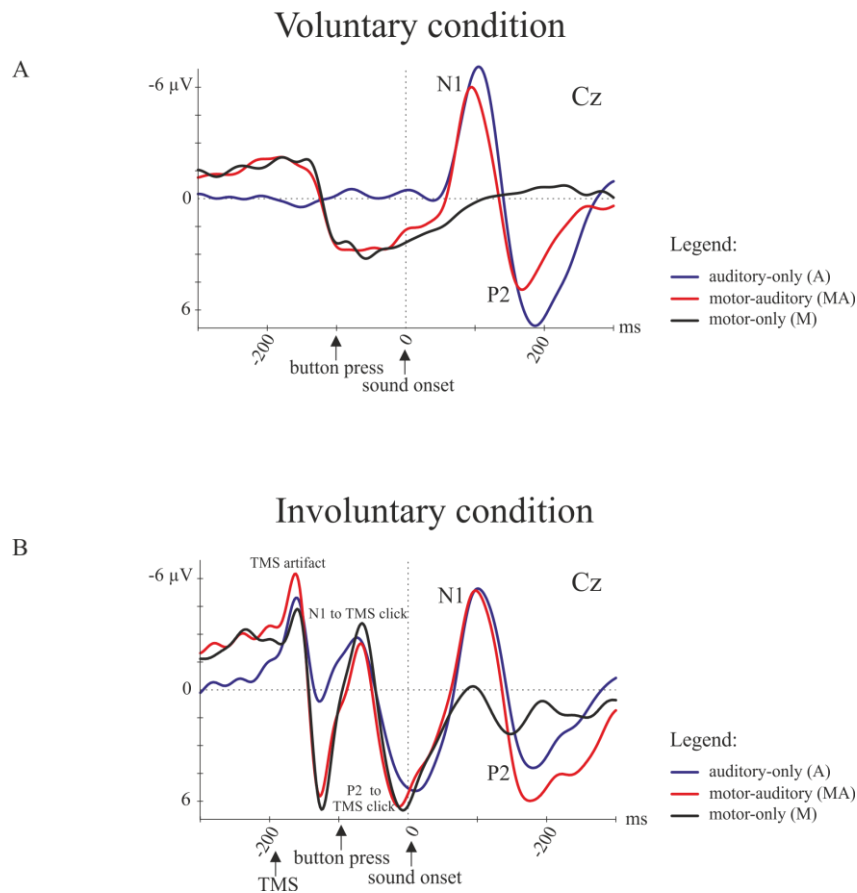
### 3.2.3 Results

In Figure 11 original grand-average ERP waveforms at electrode Cz elicited by passive sound exposure (auditory-only) and self-initiated sounds (motor-auditory) as well as motor activity (motor-only) are shown, separately for the voluntary (Figure 11A) and involuntary condition (Figure 11B). The ERP waveform in response to the self-initiated sounds shows a negative deflection in the typical N1 latency range and a positive deflection in the typical P2 latency range.

For further analysis evoked responses to passive sound exposure will be compared to evoked responses to motor-corrected self-initiated sounds within each condition (see Figure 12A and B). The analysis revealed a significant difference between the sound-evoked responses in the voluntary condition (in which participants initiate a finger movement to press a button) and the involuntary condition (in which the movement is initiated by TMS; significant main effect of *Agency* on peak-to-peak amplitude of the N1-P2 complex,  $F_{1,16} = 21.90$ ,  $p < .001$ ). Furthermore, no differences between the sound-evoked responses were observed in the active condition (in which the sound was initiated by the participants button press) and the passive condition (in which sounds were played back passively; no significant main effect of *Task* on peak-to-peak amplitude of the N1-P2 complex,  $F_{1,16} = 0.52$ , ns). However, a significant interaction of *Agency* and *Task* was found ( $F_{1,16} = 7.53$ ;  $p = .014$ ). Post-hoc tests revealed stronger response attenuation, i.e. smaller peak-to-peak amplitudes for self-initiated sounds than passive sound exposure, in the voluntary condition (see Figure 12A, upper panel) than in

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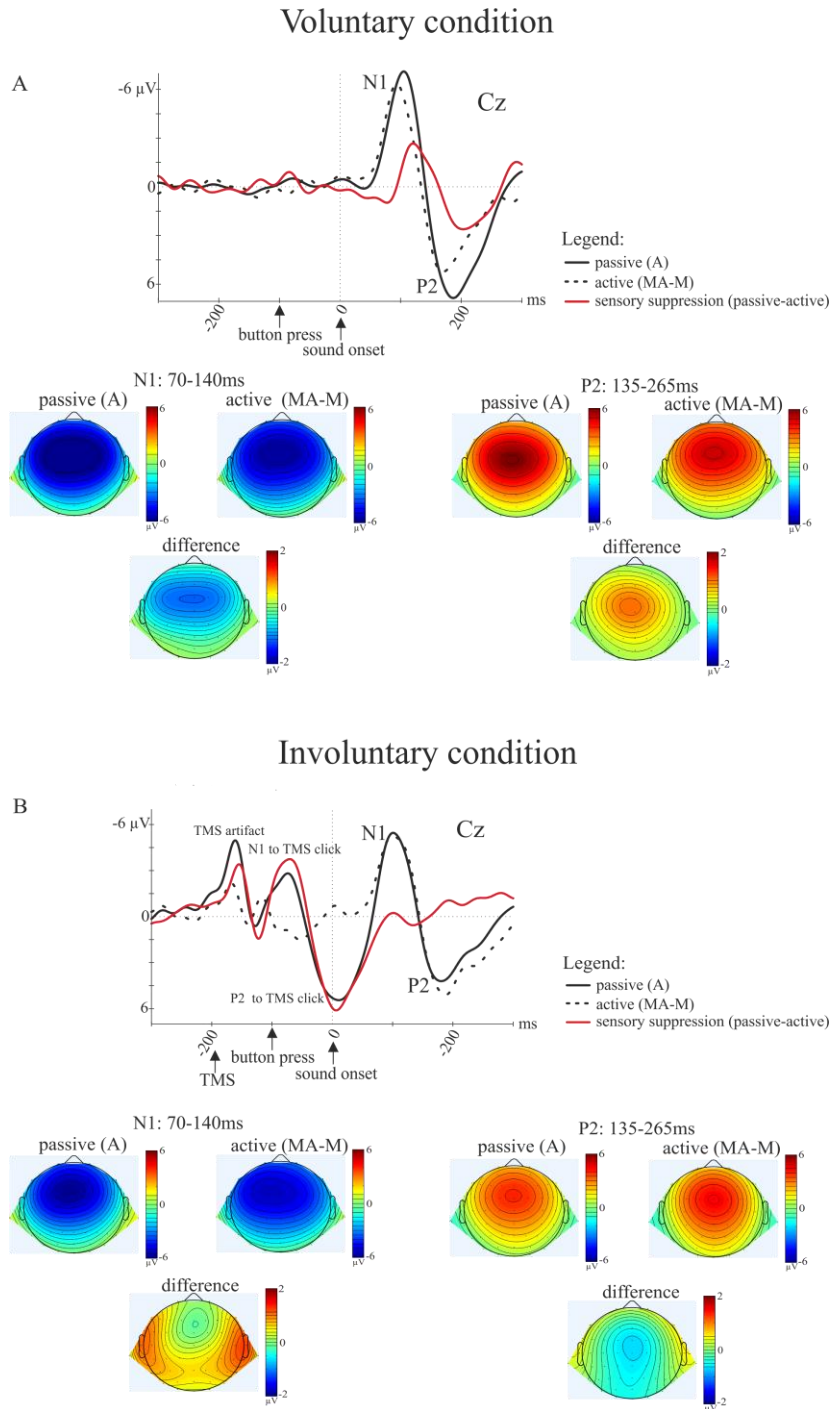
the involuntary condition (see Figure 12B, upper panel,  $t(16) = 2.28$ ;  $p = .037$ ). This is also apparent in the topographical scalp distributions of the separate N1- and P2 components of each condition (see Figure 12A and 12B, lower panel). For passive sound exposure in both the voluntary and the involuntary condition the N1 component shows a typical negative-going fronto-central scalp distribution and the P2 component shows a typical positive-going, somewhat more central distribution. However, in the voluntary condition a clear modulation of the N1- and P2 components is observable for self-initiated sounds. This self-initiation effect is reflected in the difference wave (passive-minus-active, see Figure 12A, lower panel). In contrast, in the involuntary condition the N1- and P2 components do not show a modulation for self-initiated sounds. The absence of the self-initiation effect in the involuntary condition is also supported by the difference wave (see Figure 12B, lower panel).



**Figure 11: Illustration of the original grand-average ERPs at Cz**

Grand-average ERPs at Cz elicited by passive sound exposure (blue line), self-initiated sounds (red line) and motor activity (black line) are depicted for the voluntary condition (A) and the involuntary condition (B).

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**Figure 12: Illustration of the self-initiation effects at Cz**

Grand-average ERPs at Cz elicited by passive sound exposure (black solid line), motor-corrected self-initiated sounds (black dotted line) and the corresponding difference wave (passive minus self-initiated, red line) as well as the topographical distribution to passive sound exposure, to self-initiation of sounds and the difference wave during the latency ranges of the separate N1- (70 - 140 ms) and P2 (135 - 265 ms) components are depicted for the voluntary condition (A) and the involuntary condition (B).

### 3.2.4 Discussion

The present study aimed to determine whether attenuation of brain responses to self-initiated sounds can be explained by brain activity involved in movement planning rather than movement execution. We recorded ERPs in response to a sound initiated by a button press. Sounds were initiated either by voluntary finger movements made by the participants, or by similar, but involuntary, movements induced by stimulating primary motor cortex with TMS. We hypothesized that CD signals involved in the processing of self-initiated sounds are sent during movement planning, rather than movement execution. Thus, an attenuation of the sound-evoked N1-P2 complex was expected only for voluntary movements, but not for involuntary movements, because no CD signals should be available to the predictive forward model during involuntary movements.

As expected, our results revealed an attenuated auditory N1-P2 complex to self-initiated sounds following voluntary finger movements. This finding strengthens previous electrophysiological research investigating self-initiation effects in the auditory modality (Aliu et al., 2009; Baess et al., 2011; Bässl et al., 2008; Knolle, Schröger, & Kotz, 2012; Martikainen et al., 2005; Schafer & Marcus, 1973). Furthermore, our results are in line with behavioral findings showing sensory attenuation to self-initiated sounds (Desantis, Weiss, et al., 2012; Sato, 2008, 2009; Weiss et al., 2011a, 2011b). Our main experimental manipulation showed that if the finger movement that initiated the sound was caused by motor cortex stimulation, no attenuation of the N1-P2 complex to self-initiated sounds was detectable. That is, the auditory self-initiation effect was abolished when the movement was not planned by the participants. These results demonstrate that the intention to move determines sensory attenuation of self-initiated sounds, and that activity in primary motor cortex is insufficient to drive the attenuation. Thus, we provide direct evidence that the CD circuits that are engaged in the processing of self-initiated sounds originate upstream from primary motor cortex where the motor command is executed. Our results are in agreement with previous studies in the somatosensory modality (Christensen et al., 2007; Haggard & Whitford, 2004; Voss et al., 2007) that found no sensory attenuation for involuntary body movements, irrespective of whether movements were artificially induced via peripheral (muscle) or central (single pulse TMS to motor cortex) stimulation. Moreover, it has been shown that self-generation effects such as sensory attenuation are disrupted when repetitive TMS is applied over areas prior to motor cortex (Haggard & Magno, 1999; Haggard & Whitford, 2004; Moore et al., 2010).

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Conversely, there is some evidence that motor planning (Voss et al., 2006) and anticipated movement (Voss et al., 2008), without actual movement execution, may lead to sensory attenuation effects. Our findings show that the same mechanism seems to hold in the auditory modality and thus support the notion of an universal predictive mechanism for sensory processing of voluntary movements that operates prior to the activation of the primary motor cortex (Crapse & Sommer, 2008a; Wolpert et al., 1995). However, because TMS-induced movements were not fully identical to voluntary movements in the present study it cannot be ruled out entirely that the observed effects might be affected by differences between TMS-induced movements and voluntary movements.

There exists converging evidence that the experience of conscious motor intention and the associated sense of agency mainly arises from motor preparation in premotor and parietal cortex (Haggard, 2005). This hypothesis is supported by findings showing that cortical electrical stimulation of parietal brain regions can generate feelings of intending to move and even the conviction of having executed the movement (Desmurget et al., 2009). In line with this, (Desmurget & Sirigu, 2009) proposed a parietal-premotor network for movement intention suggesting that CD signals are emitted through forward modeling within the parietal cortex, and that these signals are the basis of motor awareness. In agreement with this proposal our findings provide evidence for a direct relationship between the N1-P2 attenuation effect for self-initiated sounds and the sense of agency. We reported an attenuated N1-P2 complex only for intended movements that is, when participants experienced agency. Thus, the N1-P2 attenuation effect seems to reflect a sense of self in action which allows us to recognize whether an external event was linked to our own movement or not. Our results support previous studies interpreting a lack of N1-P2 attenuation as an indicator of agency disruptions (Gentsch & Schütz-Bosbach, 2011; Kühn et al., 2011).

Importantly, our results contradict previous non-predictive accounts of attenuation of self-generated sensory events (Horváth et al., 2012; Horváth, 2013a, 2013b; Synofzik et al., 2008; Tsakiris & Haggard, 2005). Those models propose that at least a part of the sensory attenuation effect may be the basis for the initial formation of contingent associations between motor and sensory events. Thus, sensory attenuation effects would be rather unspecific: any sound in the temporal vicinity of the motor act would receive attenuated processing, not indicating a specific motor-sensory prediction. Motor-sensory prediction would only be formed in a later step, once contingency can be extrapolated from repeated pairing. For

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example, Horváth and colleagues (2012) previously suggested that sensory attenuation for self-initiated sounds reflects coincidence detection between button press and sound. However, the present data argue against this hypothesis. That is, although button press and sound were coincident in both voluntary and involuntary movements, no attenuation of the N1-P2 complex for self-initiated sounds was observed for involuntary motor acts. It has been suggested that attenuation effects may be due to attentional differences between active and passive conditions. In particular, performing an action may briefly draw attention away from auditory processing, which results in attenuated auditory responses for sounds close to a button press (Horváth et al., 2012; Makeig et al., 1996). According to this notion, one may speculate that the TMS click in the involuntary condition could draw participants' attention to the subsequent auditory stimulus, which could reduce the attenuation effect. However, in the present study we identified sensory attenuation effects only within conditions, i.e. conditions in which the TMS was either present (corrected motor-auditory involuntary vs. auditory-only involuntary) or not (corrected motor-auditory voluntary vs. auditory-only voluntary) were compared in the analysis. Thus, possible attention effects of the preceding TMS clicks on forthcoming processing are the same in the active and the passive TMS condition. Therefore, attentional effects caused by the TMS stimulation should be canceled out in the calculation of the attenuation effects. Consequently, the observed effects exclusively depend on whether the sound was self-initiated or not. However, it is possible that the voluntary and involuntary conditions are different in attention. As mentioned above, the difference in the attenuation effect depends on whether the movement is voluntary or involuntary, that is whether participants experience agency or not. It is possible that differences in agency result in attentional differences. That is, it cannot be ruled out that the planning of the action draws attention away from the sounds, but the involuntary execution of the movement does not.

In sum, our findings demonstrate that the origin of the sensory attenuation of brain responses to self-initiated sounds is prior to motor cortex activation. The intention to move and the corresponding feeling of agency rather than the mere movement execution seem to play an essential role for the attenuation of the auditory N1-P2 complex. The present result is in favor of a predictive internal forward-model account.

### 3.3 Sensation of agency and perception of temporal order<sup>6</sup>

#### Abstract

After adaptation to a fixed temporal delay between actions and their sensory consequences, stimuli delivered during the delay are perceived to occur prior to actions. Temporal judgments are also influenced by the sensation of agency (experience of causing our own actions and their sensory consequences). Sensory consequences of voluntary actions are perceived to occur earlier in time than those of involuntary actions. However, it is unclear whether temporal order illusions influence the sensation of agency. Thus, we tested how the illusory reversal of motor actions and sound events affect the sensation of agency. We observed an absence of the sensation of agency in the auditory modality in a condition in which sounds were falsely perceived as preceding motor acts relative to the perceived temporal order in the control condition. This finding suggests a strong association between the sensation of agency and the temporal order perception of actions and their consequences.

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<sup>6</sup> This study is based on the article: Timm, J., Schönwiesner, M., SanMiguel, I., & Schröger, E. (under revision II). Sensation of agency and perception of temporal order.

### 3.3.1 Introduction

Precise temporal judgments of actions and their corresponding sensory consequences are an important component of human time perception. Several studies showed that temporal order judgments are constructions of the brain, which are easily manipulated in the laboratory (Eagleman, 2008; Haggard, Clark, et al., 2002; Haggard & Clark, 2003; Haggard, 1999; Tsakiris & Haggard, 2003). Particularly, it has been shown that when a fixed temporal delay is consistently introduced between a motor act and its sensory consequences, participants' perception adapts to this delay. If, subsequently, the delay between the action and its effect is shortened, participants may perceive that the sensory consequence preceded the motor act (i.e., they perceive an illusion of reversed temporal order between actions and sensory consequences). This illusion was first described for visual stimuli generated via button presses (Stetson et al., 2006). Specifically, participants were asked to press a button, which was followed by a flash. A fixed temporal delay between button presses and flashes was introduced. After participants had adapted to this delay, they perceived unexpected flashes presented at shorter delays as occurring before the button press. The illusion has subsequently been replicated in the tactile and the auditory modality (Heron et al., 2009; Sugano et al., 2010) and with more complex stimuli (Keetels & Vroomen, 2012; Yamamoto & Kawabata, 2011). The illusion has been explained as a recalibration of motor-sensory timing, resulting from the participants' prior expectation that there should be little or no delay between actions and their sensory consequences (Stetson et al., 2006). Recalibrating the temporal interpretation of motor acts and sensory consequences may also be crucial to the perception of causality, because causality requires a judgment of whether the motor act precedes or follows the sensory input. It has been proposed that this can only be achieved by a multisensory integration mechanism that calibrates the relative timing of sensory events from different modalities, so that 'before' and 'after' can be accurately determined (Eagleman, 2008). The illusion has been replicated in different sensory modalities, which suggests that the recalibration mechanism is supramodal (Heron et al., 2009).

There is some evidence that voluntary action is required for the perceptual recalibration of motor-sensory timing to take place. Specifically, Stetson and colleagues (2006) found that illusory reversals occurred only when participants moved their finger actively, but not when the button was moved with a motor to tap the finger of the participants. The finding that voluntary movements strongly influence the temporal order perception of actions and sensory



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effects is also reflected in the intentional binding phenomenon, where participants perceive a sensory event earlier in time when it is the consequence of a voluntary action than when it is not (Engbert et al., 2008; Haggard, Clark, et al., 2002; Haggard & Clark, 2003; Moore & Haggard, 2008; Moore & Obhi, 2012; Tsakiris & Haggard, 2003; Voss et al., 2010). Voluntary movements involve a strong sensation of agency, that is, an experience of causing an action and its sensory consequences (Haggard, 2005). It has been suggested that the sensation of agency is strongly related to the concept of causality (Hume, 1888, 1900; Wegner, 2003, 2004). Those models assume that causation is inferred from the temporal relation between cause and sensory effect. That is, causality can only be established when an action precedes its sensory consequences. The sensation of agency, in turn, reflects the experience of being a causal agent (Wegner, 2004). Thus, temporal order judgments should be directly linked to sensation-of-agency judgments. This assumption is supported by previous findings showing that temporal order judgments are influenced by the belief of causing an effect (Desantis et al., 2011; Haering & Kiesel, 2012). Desantis and colleagues (2011) revealed a stronger intentional binding effect, which is an implicit measure of the sensation of agency, when participants believed that they triggered a sound, compared to when they believed that another person triggered the sound. This coupling between temporal order judgments and sensation of agency seems intuitive: if we perceive an effect occurring simultaneously with or shortly after an action, then we have likely caused it. Conversely, if we are certain we caused an effect, then it could not have happened before the action. Nevertheless, the relationship between temporal order judgments and sensation-of-agency judgments is not that trivial. People are in general readily able to experience perceptions that are rationally contradictory, indicated in the large variety of perceptual illusions (Eagleman, 2008). Furthermore, motor-to-sensory links can be highly automatic, especially in the auditory modality. Thus, motor acts could affect sensory processing independently of the subject's sensation of agency over the stimuli. For example, self-initiated sounds elicit attenuated auditory brain responses compared to externally initiated sounds, an effect commonly related to the subject being the agent of the stimuli (Aliu et al., 2009; Baess et al., 2011; Bässl et al., 2008; Ford et al., 2007; Horváth et al., 2012; Knolle, Schröger, Baess, et al., 2012; Knolle, Schröger, & Kotz, 2012; Martikainen et al., 2005; McCarthy & Donchin, 1976; SanMiguel et al., 2013; Schafer & Marcus, 1973; Timm, SanMiguel, Saupe, & Schröger, 2013). However, several studies have shown that a contingent relationship between the motor act and the sound is not necessary for this effect to occur, as sensory processing of sounds seems to be also attenuated when the sound is merely coincidentally concurrent with the

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motor act (Horváth et al., 2012; Makeig et al., 1996). Given these examples, it is conceivable that sensation-of-agency judgments may be independent from temporal order perceptual illusions, particularly in the auditory modality. We tested whether subjective temporal order judgments are directly related to the sensation of agency, using the experimental design of Stetson and colleagues (2006). We asked participants to report their sensation of agency over the production of a sound in conditions in which they either perceived an illusory reversal of the temporal order of events or not. Assuming a direct relationship, we hypothesized that in conditions, in which the recalibration of the timing between actions and sensory consequences causes an illusory perception of temporal order (i.e. the stimulus is perceived as occurring before the motor action), it should also cause a lack of a sensation of agency, that is, participants should not have the feeling that their action caused the sensory event.

We also addressed three additional unresolved issues in this study. The first relates to the counterintuitive finding that, under normal circumstances, participants perceive motor actions and sensory consequences as simultaneous when the sensory event precedes the motor action by up to 100 ms (McCloskey, Colebatch, Potter, & Burke, 1983). Several studies investigating perceptual effects of voluntary movements have reported this finding without directly discussing it (Haggard, Clark, et al., 2002; Haggard & Clark, 2003; Haggard, 1999; Tsakiris & Haggard, 2003). Stetson and colleagues (2006) circumvented this issue in their experiment by first training participants so that their perception of the relative timing between actions and effects closely matched the real timing. It is unclear how this training might have influenced the illusion results. Thus, we further tested whether the visual temporal order illusion reported by Stetson and colleagues (2006) can be replicated with untrained participants, first in the visual, and subsequently in the auditory modality. Previous studies have shown that temporal recalibration can also take place when the motor acts result in auditory instead of visual stimuli (Heron et al., 2009; Sugano et al., 2010; Yamamoto & Kawabata, 2011), hence we expected to observe the illusion in the auditory modality as well. However, as temporal resolution (Recanzone, 2003, 2009; Wada, Kitagawa, & Noguchi, 2003) and duration discrimination (Grondin, 1993) are much better in the auditory than in the visual system, it is possible that the auditory system is less prone to temporal order illusions. Moreover, to the best of our knowledge, replications of the original illusion effect described by Stetson and colleagues (2006) in other sensory modalities have never presented the participants with real temporal order reversals. This is particularly relevant with untrained participants, given that the point of subjective simultaneity (PSS) seems to lie in the negative

latency range (stimulus comes before motor act) under these circumstances. Thus, we aimed to establish the real PSS, and corroborate that it can be recalibrated by adapting to a constant motor-sensory delay, leading to the temporal order reversal illusion when shorter delays are presented in both the visual and the auditory modality.

Taken together, three experiments were conducted. In the first experiment we replicated the visual temporal order illusion reported by Stetson and colleagues (2006) with untrained participants and extended it in a second experiment to the auditory modality. In a third experiment we finally tested the relationship between subjective temporal order judgments and the sensation of agency.

### 3.3.2 Materials and Methods

#### 3.3.2.1 General experimental procedure

Participants were seated facing a computer screen, showing a uniformly black background, at a distance of about 100 cm and held a gamepad. They were asked to press a button on the gamepad as fast as possible whenever a red cross (cue) appeared on the screen with their dominant hand. A specific stimulus (see Experiment I, II and III for detailed information) was presented for 50 ms at a point in time after the cue and either before or after the button press. Sensory stimulation was run via MATLAB using the Cogent2000 toolbox ([http://www.vislab.ucl.ac.uk/cogent\\_2000.php](http://www.vislab.ucl.ac.uk/cogent_2000.php)). Stimuli were presented in two conditions: a real-time condition and a delay-time condition. In 60 % of the trials of both conditions, the stimulus appeared at a fixed time point with regard to the button press. In the real-time condition the stimulus appeared immediately after the button press with a negligible delay (1-2 ms). In the delay-time condition the stimulus appeared 100 ms after the button press. In the remaining 40 % of the trials the stimulus appeared at an unexpected time within a window of 140 ms before to 140 ms after the button press. The sampling of these delays followed a normal distribution with a mean of 60 ms after the button press and a standard deviation of 80 ms. In the trials in which the stimulus was intended to appear before a participant's button press, the time of presentation was estimated from a running average of the participant's reaction time in the previous five trials. Since this estimation was not precise, the resulting distributions were not exact (see the histograms in Figure 13B for the actual final distribution of trials). For the first five trials the running average was calculated from five pre-trials,

which were presented with the temporal delay of the respective condition (real-time, delay-time). The pre-trials were not taken into account for the later analysis (Figure 13 as an example for Experiment I). After each trial participants reported either the perceived temporal order of button press and stimulus (see Experiment I and II for detailed information) or the perception of agency (see Experiment III for detailed information). Each experiment consisted of six experimental blocks, three for each of the two conditions. In each block 118 trials were presented, resulting in 354 trials per condition. The condition order was counterbalanced across participants such that either the real-time condition or the delay-time condition was presented first. Participants performed a two minute dummy block before the main experiment to get acquainted with the task procedures however they were given no feedback as to the accuracy of their temporal order reports.

### 3.3.2.2 Data analysis

#### 3.3.2.2.1 Psychometric functions

From the temporal order (Experiment I and II) and sensation-of-agency (Experiment III) reports of each participant a psychometric function was computed for both conditions (real-time, delay-time). To this end, time ranges of 20 ms within the time window of -200 ms to +140 ms with regard to the button press were defined. Although the intended time-window around the button press within which stimuli could be presented ranged from -140 ms to +140 ms, a broader time window was taken into account for the analysis. This is due to variations between the intended and actual time of delivery of the stimuli preceding the buttons press, as in these cases delivery times had to be calculated on the basis of an inaccurate estimation of the reaction time in each particular trial. For each time range the proportions of ‘before’ and ‘after’ (Experiment I and II) or ‘agency’ and ‘no agency’ (Experiment III) reports were calculated. Afterwards, a psychometric function was fitted to the behavioral data, separately for each participant and condition, by the least squares optimization method. A logistic function was used as follows:

$$y = 1./(1+e^{-1*(x-PSS)/SL})$$

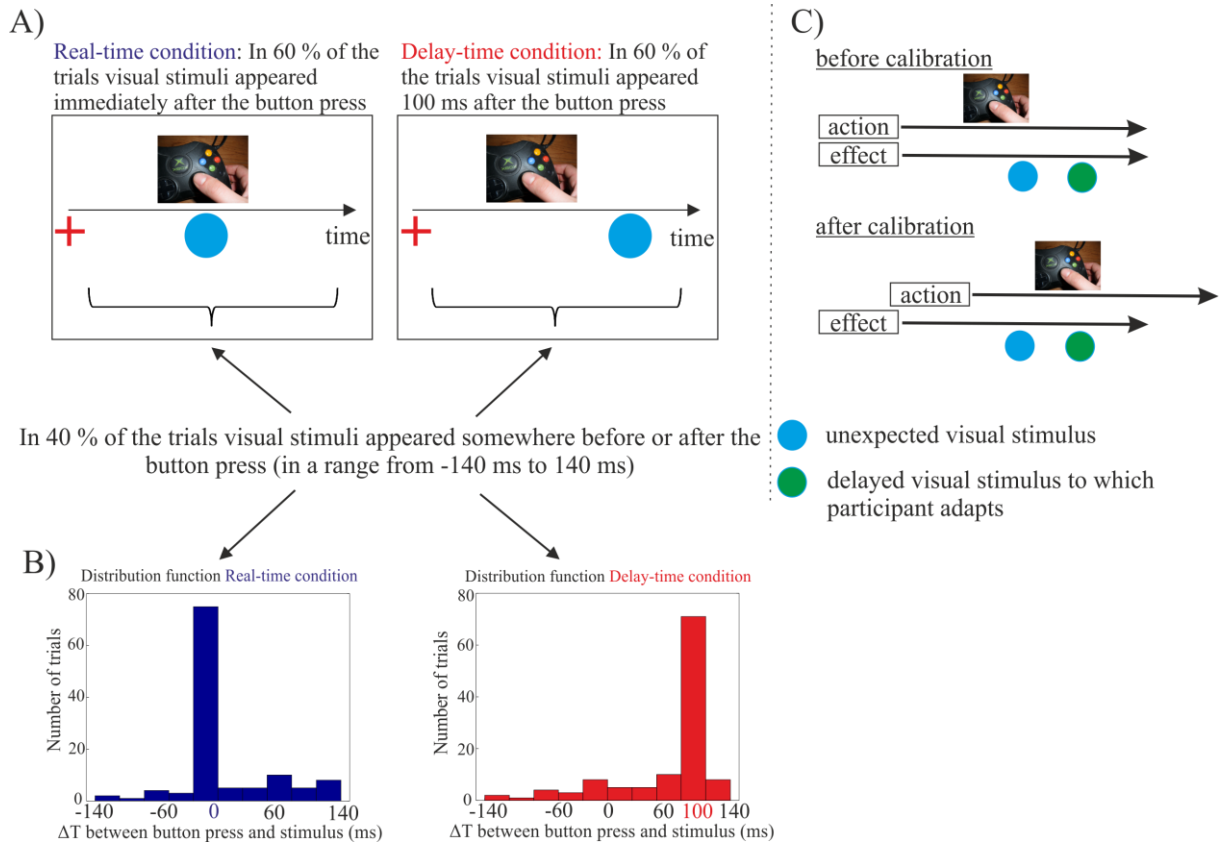
where x is the real asynchrony between button press and stimulus, y is the modeled proportion of perceiving the stimulus after the button press, PSS is the point of subjective simultaneity of

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button press and stimulus (50 % point of the psychometric function), and SL is the slope (steepness, indicating the judgment precision) of the psychometric function. The slope was calculated as a separate parameter. The slope of the curves reflects the precision of the temporal order (Experiment I and II) and sensation-of-agency judgments (Experiment III). In an iterative procedure, PSS and SL were independently varied in a stepwise manner to find the parameter combination that yields the best approximation to the experimentally observed proportions (of perceiving the stimulus after the button press) for the given participant and condition. The step size was 0.1 for both parameters. The parameter values explored ranged from -400 to +160 ms for PSS and from 0.1 to 100 for SL. Model fit was assessed by the sum of squared deviations between the proportions of perceiving the stimulus after the button press that were observed in the experiment and those that were predicted by the logistic function. From the parameter combination that yielded the best fit, the SL and PSS values were used as estimates for the slope and the point of subjective simultaneity for the given participant and condition in all subsequent analyses. For the figures the average of the experimental data of all participants was calculated. Out of this average the parameter values were fitted in the same iterative procedure explained above.

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**Figure 13: Basic experimental design and the recalibration mechanism**

A) Basic experimental design: Participants were cued to press a button. A visual stimulus appeared on the screen after the cue and somewhere before or after the button press. Two conditions were applied – the real-time condition and the delay-time condition. In 60 % of the trials the visual stimulus appeared at a fixed time point with regard to the button press (real-time condition = immediately after the button press, delay-time condition = 100 ms after the button press). In the remaining 40 % of the trials the visual stimulus occurred either before or after the button press (ranging from -140 ms to +140 ms). After each trial participants reported if they perceived the visual stimulus before or after the button press.

B) The histograms show the distribution of the number of trials sampled for each delay in the real-time condition and the delay-time condition.

C) Recalibration mechanism: Due to delayed sensory feedback in the delay-time condition participants calibrate temporal order judgments to reduce the delay between the action and its sensory consequences. After recalibration, the delayed sensory feedback is perceived as occurring closer in time to the button press. This causes an unexpected stimulus appearing sooner but actually still after the button press to be perceived as occurring before the button press.

### 3.3.2.2.2 Statistical analysis

For each Experiment (I to III) the reaction times for the decision were compared between conditions to test whether the reaction to the specific stimuli differed significantly between the real-time and the delay-time condition. To test for statistical differences between conditions with regard to the PSS an analysis of variance with the within-subject factor *condition* (real-time, delay-time) and the between-subject factor *condition order* (real-time condition presented first, delay-time condition presented first) was conducted for all experiments (Experiment I to III). This analysis tests whether the experimental manipulation effectively induced a shift in the perception of action-effect timing across conditions. However, as noted, under normal conditions the perceived timing of actions and effects does not accurately reflect the actual timing of actions and events (see Introduction). Therefore, the amount of discrepancy between the real and perceived action-effect timing was also quantified and compared across conditions. Particularly, the proportion of trials in which the stimulus occurred together with, or slightly after the button press (0 - 25 ms after button press) but participants reported ‘before’ (Experiment I and II) or ‘no agency’ (Experiment III) was calculated in both conditions (real-time and delay-time). To test potential differences in the slope values of the curves in the real-time and delay-time condition an analysis with the factor *slope* with the two levels real-time condition and delay-time condition was computed. Furthermore, to investigate differences in the magnitude of the temporal order illusion and the judgment precision across sensory modalities an analysis including the within subject factor *condition* and the between-subject factor *modality* (visual, auditory) was calculated for the PSS and the slope of the curves for Experiment I and Experiment II. To test for differences in the psychometric functions between temporal order judgments and sensation-of-agency judgments in Experiment II and Experiment III two analyses with the between-subject factor *judgment* (temporal order, agency) and the factors *condition* and *slope* were conducted, respectively. Post-hoc tests were computed when appropriate to clarify the origin of significant effects. Greenhouse-Geisser correction was applied where appropriate. The sample size and the proportions of participants’ gender differed between experiments.

### 3.3.3 Experiments and results

#### 3.3.3.1 Experiment I

The purpose of Experiment I was to replicate the temporal order illusion of actions and their sensory consequences in the visual modality (Stetson et al., 2006).

##### 3.3.3.1.1 Methods

###### 3.3.3.1.1.1 Participants

Eight healthy female volunteers (2 left-handed) participated in the experiment. The mean age of the participants was 25.3 years (range: 21 to 30 years). In this and all following experiments participants reported normal or corrected-to-normal vision. None were taking any medication affecting the central nervous system. All participants gave informed consent prior to the measurements and received either course credit or payment for their participation.

###### 3.3.3.1.1.2 Experimental procedure

Visual stimuli were presented for 50 ms on the middle of the screen (ViewSonic Graphics Series G90fB, 100 Hz refresh, Truecolor 32 bit, 1024x768). Visual stimuli were blue circles (4 cm diameter, RGB values: 0 0 255), which were presented on a black background (RGB values: 0 0 0). After each trial, participants reported whether they had perceived the visual stimulus occurring before or after the button press.

###### 3.3.3.1.2 Results

The analysis of the reaction times for the decision revealed no significant differences between the real-time condition (mean: 254 ms) and the delay-time condition (mean: 271 ms;  $t(7) = -1.34$ ;  $p = .222$ ), indicating comparable reaction times across conditions. In the real-time condition, visual stimuli and button presses were perceived as simultaneous when visual stimuli preceded button presses by 48.5 ms on average across participants (PSS = -48.5 ms). In the delay-time condition this time was reduced to 10.2 ms, and the entire psychometric function for the perception of temporal order of button press and visual stimulus was shifted

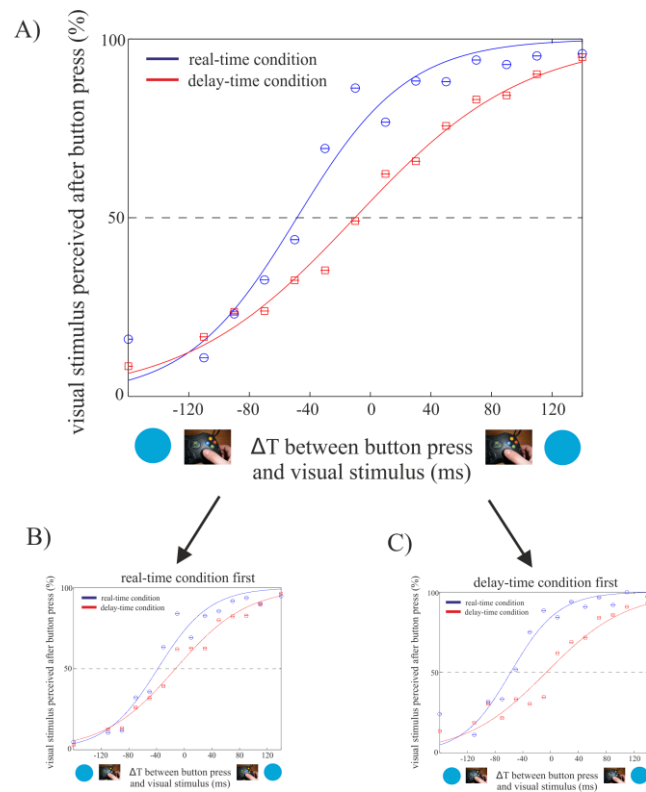


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towards positive values with respect to the real-time condition (mean shift = 38.3 ms, standard deviation = 50.8 ms, Figure 14A). The analysis showed that this shift was significant (main effect of *condition*,  $F_{1,6} = 19.16$ ;  $p = .005$ ,  $\eta^2 = 0.76$ ). Thus, a visual stimulus occurring just after the perceived time of simultaneity between button press and visual stimulus in the real-time condition was perceived as occurring before the button press in the delay-time condition, i.e. the perceived temporal order of actions and their sensory consequences was reversed in the delay-time condition with regard to the temporal order perceived in the real-time condition. There was a significant interaction of *condition* and *condition order* ( $F_{1,6} = 6.07$ ;  $p = .049$ ,  $\eta^2 = 0.50$ ; Figure 14B and C), indicating a stronger illusion when the delay-time condition blocks were presented before the real-time condition blocks. That is, the PSS difference was larger when the delay-time condition was administered first. However, post-hoc comparisons did not reveal any significant differences between condition orders in the delay-time- and the real-time condition. There was no change in the precision of the temporal order judgments across conditions, as indicated by similar slopes of the psychometric functions in both conditions ( $F_{1,6} = 0.02$ ; *n.s.*). Finally, the probability of an illusion with respect to the real temporal order of events was higher in the delay-time condition (36.92 %) compared to the real-time condition (11.67 %,  $F_{1,7} = 9.95$ ;  $p = .016$ ,  $\eta^2 = 0.58$ ).

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**Figure 14: Illustration of the temporal order illusion in the visual modality**

A) Mean data of all participants, showing the psychometric functions of the real-time condition (blue curve) and the delay-time condition (red curve). The dashed line indicates the point of subjective simultaneity (PSS) of each condition at which participants reported “visual stimulus after button press” with a 50 % probability. B) and C) Illustration of the condition order effect. The horizontal dashes in the circles and the squares indicate the error bars.

### 3.3.3.2 Experiment II

The purpose of Experiment II was to verify that the temporal order illusion described above exists for sounds as sensory consequence of the button press.

#### 3.3.3.2.1 Methods

##### 3.3.3.2.1.1 Participants

Sixteen healthy volunteers (7 male, 1 left-handed) participated in the experiment. Mean age of the participants was 22.6 years (range: 18 to 27 years).

### 3.3.3.2.1.2 Experimental procedure

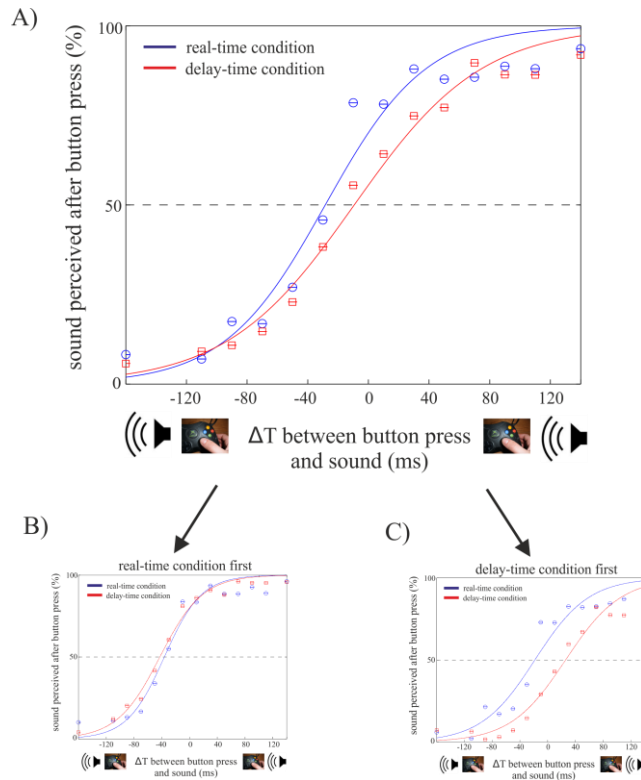
The experimental procedure was identical to the one used in Experiment I, with the exception that the visual stimuli were replaced by auditory stimuli. We presented 1000 Hz sine tones of 50 ms duration (including 10-ms rise and fall times) through circumaural headphones. Under the headphones, participants wore soft foam earplugs to attenuate other sounds, in particular sounds made by pressing the button. The intensity of the stimuli was adjusted to a comfortable loudness by the participant. After each trial, participants reported whether they had perceived the sound occurring before or after the button press.

### 3.3.3.2.2 Results

The comparison of the reaction times for the decision did not show any significant differences between conditions ( $t(15) = 0.29$ ;  $p = \text{ns.}$ ), indicated by comparable reaction times for the real-time (mean: 327 ms) and delay-time condition (mean: 322 ms). We found a similar, but smaller, shift between psychometric functions in the real-time and delay-time conditions for sound stimuli compared to visual stimuli (PSS shift = 19.1 ms, standard deviation = 30.8 ms, Figure 15A). The shift between real-time and delay-time conditions is significant (main effect of *condition*,  $F_{1,14} = 17.94$ ;  $p < .001$ ,  $\eta^2 = 0.56$ ) and indicates an illusory reversal of the perceived temporal order of button presses and sounds in the delay-time condition with regard to the temporal order perceived in the real-time condition. The difference in the magnitude of the illusion across sensory modalities is significant (interaction of factors *condition* and *modality*,  $F_{1,22} = 4.42$ ;  $p = .047$ ,  $\eta^2 = 0.17$ ), indicating a considerably stronger temporal order illusion for the visual modality. The difference is due to the real-time condition, in which sounds and button presses were perceived as simultaneous when sounds preceded button presses by 28.4 ms, as compared to 48.5 ms when visual stimuli were used. In the delay-time condition this time was reduced to 9.3 ms, which is comparable to the 10.2 ms measured with visual stimuli. No significant difference in judgment precision across sensory modalities was observed (no interaction of factors *slope* and *modality*,  $F_{1,22} = 0.28$ ;  $p = .869$ ). As in the previous experiment, the temporal order illusion was stronger when the blocks of the delay-time condition were presented before those of the real-time condition (interaction of *condition* and *condition order*,  $F_{1,14} = 11.55$ ;  $p = .004$ ,  $\eta^2 = 0.45$ ; Figure 15B and C). This condition order effect was driven by differences in the delay-time condition between condition orders: when the delay-time condition was presented first, the curve is shifted to more positive values

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(real-time:  $t(14) = -1.19$ ;  $p = .282$ ; delay-time:  $t(14) = -3.02$ ;  $p = .009$ ). As in Experiment I, no differences in the precision of judgments were found between conditions ( $F_{1,14} = 2.24$ ;  $p = .157$ ). As for Experiment I the probability of an illusion with respect to the real temporal order of events was higher in the delay-time condition (34.39 %) compared to the real-time condition (20.43 %,  $F_{1,15} = 8.68$ ;  $p = .010$ ,  $\eta^2 = 0.37$ ).



**Figure 15: Illustration of the temporal order illusion in the auditory modality**

A) Mean data of all participants, showing the psychometric functions of the real-time condition (blue curve) and the delay-time condition (red curve). The dashed line indicates the point of subjective simultaneity (PSS) of each condition at which participants reported “sound after button press” with a 50 % probability. B) and C) Illustration of the condition order effect. The horizontal dashes in the circles and the squares indicate the error bars.

### 3.3.3.3 Experiment III

The purpose of Experiment III was to investigate whether the illusory reversal of perceived temporal order of button presses and sounds affects the sensation of agency that a participant experiences over the generation of the sound.

### 3.3.3.3.1 Methods

#### 3.3.3.3.1.1 Participants

Seventeen healthy volunteers (4 male, 1 left-handed) participated in the experiment. Mean age of the participants was 21.3 years (range: 18 to 32 years).

#### 3.3.3.3.1.2 Experimental procedure

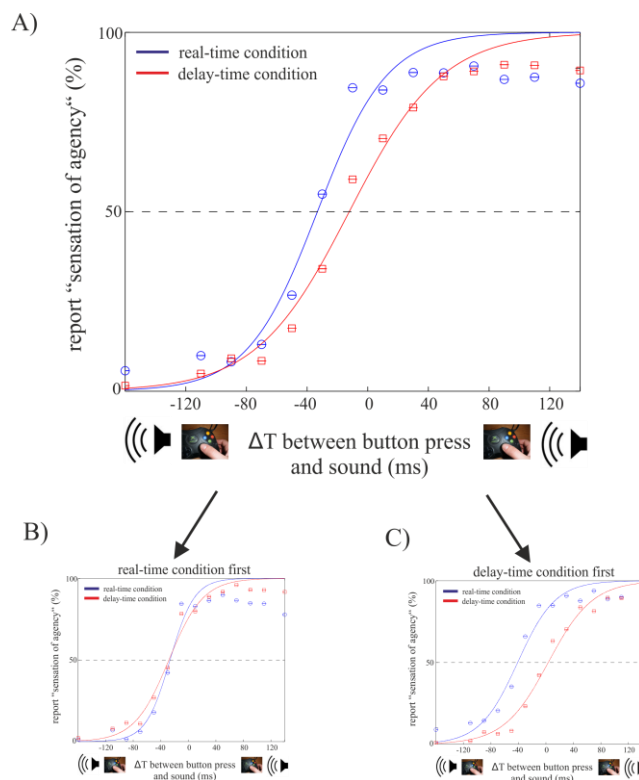
The experimental procedure was identical to the one used in Experiment II, with the exception that the task to judge temporal order was replaced by a task to judge sensation of agency. Participants were asked to report if they had the impression of having generated the sound with their voluntary button press or not (“Did you generate the sound with your button press?”). We expected that in trials in which the sound was perceived as preceding the button press the sensation of agency (‘causing’ the sound by the volitional action of pressing the button) would be reduced or abolished. This expectation was based on the assumption that temporal order perception and sensation of agency rely on a perceived causal relationship between actions and sensory consequences (Cai, Stetson, & Eagleman, 2012).

#### 3.3.3.3.2 Results

As in the previous experiments the reaction times for the decision were comparable for the real-time (mean: 290 ms) and the delay-time condition (mean: 300 ms;  $t(16) = -1.45$ ;  $p = .166$ ). The psychometric functions for sensation-of-agency judgments are virtually indistinguishable from those measured for temporal order judgments (no significant interaction of *condition* and *judgment*,  $F_{1,31} = 0.09$ ; *n.s.*, no significant interaction of *slope* and *judgment*,  $F_{1,31} = 0.91$ ;  $p = .346$ ), including the shift between real-time and delay-time conditions (21.0 ms, standard deviation = 31.3 ms, Figure 16A). In the real-time condition, agency was perceived when sounds preceded button presses by 33.2 ms. This time was significantly reduced to 12.2 ms in the delay-time condition (main effect of *condition*,  $F_{1,15} = 16.98$ ;  $p = .001$ ,  $\eta^2 = 0.53$ ). Comparison of these results with the point of perceived simultaneity measured in the previous experiment shows that participants have a reduced sensation of agency for sounds presented earlier than the perceived time of simultaneity. This means that in otherwise identical trials, participants perceived no agency over the sounds in

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the delay-time condition, whereas they perceived agency in the real-time condition. As in the previous experiments, the illusion was stronger when the delay-time condition blocks were presented before the real-time condition blocks (interaction of *condition* and *condition order*,  $F_{1,15} = 23.47$ ;  $p < .001$ ,  $\eta^2 = 0.61$ ; Figure 16B and C). As in experiment II, the comparison of the curves of the real-time condition and the delay-time condition of both condition orders revealed a significant difference between the delay-time conditions: when the delay-time condition was presented first, the psychometric curve was shifted to more positive values, thus increasing the difference with the real-time condition for this condition order (real-time:  $t(15) = 0.71$ ;  $p = .487$ ; delay-time:  $t(15) = -2.31$ ;  $p = .035$ ). Moreover, the judgments were of similar accuracy in both conditions ( $F_{1,15} = 0.12$ ; *n.s.*). Comparable to both previous experiments, the probability of an illusion with respect to the real temporal order of events was higher in the delay-time condition (29.64 %) compared to the real-time condition (12.82 %,  $F_{1,16} = 7.48$ ;  $p = .015$ ,  $\eta^2 = 0.32$ ).



**Figure 16: Illustration of the sensation-of-agency illusion in the auditory modality**

A) Mean data of all participants, showing the psychometric functions of the real-time condition (blue curve) and the delay-time condition (red curve). The dashed line indicates the point of subjective simultaneity (PSS) of each condition at which participants reported “agency” with a 50 % probability.

B) and C) Illustration of the condition order effect. The horizontal dashes in the circles and the squares indicate the error bars.

### 3.3.4 Discussion

The present study aimed to discover the relationship between the sensation of agency and the perception of temporal order of motor and sensory events in the auditory modality. We used an illusion of temporal order perception to decouple the perceived from the real temporal order of events. This illusion, first introduced by Stetson and colleagues (2006) using visual stimuli, allowed us to create a situation in which participants pressed a button to play a sound, but perceived a reversed temporal order of button press and sound. In this situation, participants also experienced an illusory lack of agency over the production of the sound. We measured virtually identical psychometric functions for the dependence of sensation-of-agency judgments and temporal order judgments on stimulus timing, which suggests that a common mechanism underlies both types of sensations.

#### 3.3.4.1 Temporal order illusion in vision and audition

We first replicated the reported temporal order illusion for actions and visual stimuli (Stetson et al., 2006), which confirms the stability of the illusion effect in vision. We extended the experiment to include auditory stimuli. That is, we demonstrated an illusory perception of actions and sensory consequences in the auditory modality as well. However, compared to the study of Stetson and colleagues (2006), we did not train participants to eliminate the normal offset in the perceived simultaneity. Thus, it seems that the temporal order illusion represents a robust effect which occurs irrespective of the actual order of events. In addition to a shift in perceived timing in the (non-adapted) control conditions, we also obtained an illusion with respect to the order of physical events in a considerable number of trials in both modalities. Our findings confirm previous results obtained with different paradigms (Heron et al., 2009; Sugano et al., 2010; Yamamoto & Kawabata, 2011). However, unlike the study of Stetson and colleagues (2006), these later studies used paradigms in which sensory stimuli never preceded the motor action. That is, the participants were never presented with actual order reversals. This may have facilitated the occurrence of illusory order reversals, because there was no reference exemplar of an actual order reversal. Our results show that the temporal order illusion in the auditory modality occurs even when such reference exemplars are presented. Our data revealed a significantly stronger illusion in the visual (PSS shift = 38.3 ms) compared to the auditory modality (PSS shift = 19.1 ms). This difference may be

due to the auditory system's superior temporal precision and thus greater ability to provide veridical timing information compared to the visual system (Shams, Ma, & Beierholm, 2005).

### 3.3.4.2 Sensation of agency

We found an illusion in the perception of agency that was tightly coupled to the perception of temporal order. After adaptation to a fixed temporal delay between actions and sensory consequences, participants ceased to perceive agency for the production of sounds, for which they perceived agency in the control condition. In fact, the psychometric functions for sensation of agency and temporal order perception were virtually identical. This finding strengthens the assumption that both temporal order judgments in audition and the sensation of agency are computed from the same underlying neural mechanism. This assumption is not that trivial as it has been pointed out that temporal order judgments are prone to a large variety of perceptual illusions (Eagleman, 2008) and that other effects on the sensory processing of sounds seem to be merely dependent on the presence of a concurrent motor act, irrespective of any contingent relationship between motor act and sensory effect, which would hypothetically be the basis for extrapolating causation (Horváth et al., 2012; Makeig et al., 1996). However, the fact that sensation-of-agency judgments were found to be directly affected by temporal order illusions supports the notion of shared neural processes. It could be that the sensation of agency is simply directly constrained by temporal order judgments, because participants may refrain from reporting that they caused an effect that preceded their own actions. However, several experiments show that it is relatively easy to generate a sensation of agency for events that could not physically have been caused by the participants as long as the timing is appropriate (Sato & Yasuda, 2005; Wegner et al., 2003, 2004; Wegner & Wheatley, 1999; Wohlschläger, Engbert, et al., 2003). We explicitly avoided a situation in which participants would have to make temporal order judgments and sensation of agency judgments at the same time, in order to decrease the possibility that participants make only one judgment and use it to answer both questions. Previous results suggested that the belief of causing an effect influences temporal order judgments (Desantis et al., 2011; Haering & Kiesel, 2012). Here, we show that the reverse is also true: illusory reversals of the temporal order of actions and sensory effects abolish the sensation of agency. These findings suggest a shared mechanism for both types of perceptions. If that is the case, then neural models of context-dependent temporal order judgments (Cai et al., 2012) might apply to sensation-of-agency judgments as well. This model postulates a neural code for the temporal disparity



between the motor act (computed from an efference copy) and the sensory signal. In particular, Cai and colleagues (2012) propose a two stage process which determines the behavioral output. On a low-level stage different temporal delays between motor acts and sensory events are encoded by delayed-tuned neurons. The output of this physiological stage is fed to a higher-level processing stage that pools evidence for “motor act precedes sensory signal” decisions and for “sensory signal precedes motor act” decisions. In fact, they propose that this may form the basis of causality judgments. The present results are fully compatible with this account and its extension to agency judgments.

### **3.3.4.3 Sensory events that precede motor actions are perceived as simultaneous with them**

We encountered another illusion according to which sensory events that shortly preceded motor actions are perceived as simultaneous with them in the real-time conditions (cf. the point of subjective simultaneity in the real-time condition). This effect has been reported earlier (McCloskey et al., 1983), and has been discussed as indicating that voluntary actions not only attract sensory stimuli that follow, but also those that precede the motor actions (Haggard, Clark, et al., 2002). In general, there seems to be a tendency to link sensory events that occur in the process of motor preparation to the actual motor action (Deecke, Scheid, & Kornhuber, 1969; Eagleman, 2008; Hazeman, Audin, & Lille, 1975; Libet et al., 1983). Moreover, several studies have shown that participants estimate the starting time of a finger movement consistently around 50-80 ms too early (Haggard & Eimer, 1999; Libet et al., 1983; Sirigu et al., 2004). This postdiction of actions may indicate that the feeling of starting a movement is not coupled to the start of the movement itself, but to its preparation. Thus, it appears plausible that in order for a sensory event to be perceived as simultaneous with a movement, it should be simultaneous with these preparatory processes. Our finding that, in the real-time condition, sensory events had to precede motor acts by up to 48.5 ms to be perceived as simultaneous with the motor acts is consistent with this hypothesis. Moreover, the fact that this illusion was also present for sensation of agency judgments again indicates a shared mechanism for both types of perceptions.

### 3.3.4.4 Effect of condition order

We observed a significant effect of condition order: the illusion effect obtained in all three experiments was strongest when participants performed the delay-time condition before the real-time condition. To our knowledge such an asymmetry has not been reported before and may challenge previously suggested mechanisms of the illusion effect (Cai et al., 2012; Heron et al., 2009; Stetson et al., 2006). The condition order effect is an incidental finding that will need further investigation. However, we speculate that when participants are exposed to the real-time condition first, the natural performance is reinforced and they find it difficult to adapt to the temporal delay in the subsequent delay-time condition. It is also conceivable that the order effect originates from hysteresis in the long-term adaptation of populations of neurons representing temporal differences between motor acts and sensory effects. We suggest future studies take note of this condition order effect to optimize the design of experiments on temporal order illusions.

In summary, we report evidence for an illusory temporal order perception of a motor act and a sound and for a strong association between the sensation of agency and the illusory perception of the temporal order of actions and effects. These findings provide further evidence that motor intentions partly determine human time perception, which in turn influences the sensation of agency. The observed effect of condition order may offer new insights into the underlying mechanisms of the illusion effect and will help to optimize future illusion experiments.

### **3.4 Agency judgments are independent of sensory attenuation of brain responses to self-initiated sounds<sup>7</sup>**

#### Abstract

Stimuli caused by our own movements are treated specially in the brain. In auditory processing, self-initiated sounds evoke a smaller brain response than externally-generated ones. Previous work suggests that this response attenuation reflects a predictive mechanism to differentiate the sensory consequences of one's own actions from other sensory input, which is directly associated with a feeling of being the agent of the movement. However, little is known about how sensory attenuation of brain responses to self-initiated sounds is related to judgments of agency. Thus, the present study addresses the question whether agency judgements are affected by attenuation of brain responses to self-initiated sounds. We recorded event-related potentials in response to sounds initiated by button presses. In one condition, participants perceived agency over the production of the sounds, whereas, in another condition, participants experience an illusory lack of agency. Importantly, the button press-sound sequence was physically identical, only participants' agency judgment differed across conditions. Results show sensory attenuation irrespective of agency experience, indicated by reduced amplitudes of the auditory N1 component in response to self-initiated sounds. Our findings demonstrate that sensory attenuation of brain responses to self-initiated sounds and agency judgments are independent. The results are discussed in the framework of a predictive modeling account in audition.

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<sup>7</sup> This study is based on the article: Timm, J., SanMiguel, I., Schönwiesner, M., & Schröger, E. (in prep). Agency judgments are independent of sensory attenuation of brain responses to self-initiated sounds.

### 3.4.1 Introduction

Sensory input caused by our own voluntary movements is processed differently than sensory input caused by external sources. Specifically, self-generated stimuli are attenuated in comparison to externally-generated ones (Blakemore, Wolpert, et al., 1998). Sensory attenuation has been suggested to indicate the successful prediction of the sensory consequences of our motor actions via forward modeling (Wolpert et al., 1995). In this scenario, a forward model would receive a copy of the current motor command (corollary discharge, Sperry, 1950) and predicts a representation of the expected sensory consequences. Actual sensory consequences that match the prediction are attenuated (Tsakiris & Haggard, 2005). The prediction also enables differentiating the sensory consequences of one's own actions from other sensory input and may thus contribute to the experience of agency (Blakemore et al., 2002; Frith et al., 2000).

Sensory attenuation for self-generated stimuli was used as an index of internal predictive processing in several studies across different sensory modalities (Blakemore, Wolpert, et al., 2000; Gentsch & Schütz-Bosbach, 2011; Voss et al., 2006; Weiskrantz et al., 1971). In auditory processing, self-initiated sounds elicit an attenuated N1 and/or P2 component in the auditory event-related potential (ERP) compared to passive sound exposure (Aliu et al., 2009; Baess et al., 2011; Bäсс et al., 2008; Ford et al., 2007; Horváth et al., 2012; Knolle, Schröger, Baess, et al., 2012; Knolle, Schröger, & Kotz, 2012; Martikainen et al., 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973; Timm et al., 2013). The attenuation of the N1 and/or P2 component is thought to reflect a match between predictions of the internal forward model and actual sensory feedback. We have recently provided direct proof for this assumption by demonstrating that sensory attenuation of the N1 and P2 component to self-initiated sounds depends on brain activity involved in movement planning rather than movement execution (Timm, SanMiguel, Keil, Schröger, & Schönwiesner, under revision). Furthermore, we have found evidence for a direct relationship between the N1 and P2 attenuation effect for self-initiated sounds and the feeling of agency (Timm, SanMiguel, et al., under revision): attenuation of the N1 and P2 component was only observed for intended movements but not for movements initiated by stimulating primary motor cortex with transcranial magnetic stimulation (TMS), that is, only when predictive sensorimotor signals were available. Thus, the N1 and P2 attenuation may indicate a sense of self in action, which allows us to recognize whether an external event is linked to our own movement or not.

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However, recent conceptual refinements on the sense of agency distinguish two different levels of agency representations – the feeling of agency and judgments of agency (Gallagher, 2006; Synofzik et al., 2008). On a first perceptual level the feeling of agency represents a non-conceptual feeling of being the agent of an action. The authors argue that the feeling of agency is affected by the match between predictions made by the forward model and actual sensory feedback based on automatic processing of sensorimotor signals generated by the acting self. On a second perceptual level feeling of agency is further processed and judgments of agency are formed, reflecting the belief of being the agent of an action. This belief formation represents an interpretative and inferential process looking for the best explanation of the cause of the action. Thus, according to the authors the sense of agency represents a combination of predictive and inferential mechanisms. Recent findings on intentional binding, i.e. the finding that sensory consequences are perceived closer in time to a voluntary movement (Desantis et al., 2011; Haering & Kiesel, 2012; Moore & Haggard, 2008; Moore et al., 2009), are consistent with these assumptions. These studies showed that the intentional binding effect, as an implicit measure of agency, depends on both predictive and interpretative mechanisms.

Research on action-driven predictions proposes that predictive sensorimotor signals contribute to both sensory attenuation in response to self-initiated sounds and the emergence of agency judgments (Blakemore et al., 2002; Sato, 2009; Weiss et al., 2011a). The assumption that sensory attenuation and agency judgments are directly related is supported by recent behavioral evidence in the auditory domain. Desantis and colleagues (2012) showed that the perceived loudness of sounds is attenuated when participants believed that the sounds are self-initiated compared to when they believe that sounds were generated by another person. However, up to now only a few studies investigated the relation between sensory attenuation of cortical brain responses and judgments of agency, showing ambiguous results across different sensory modalities (Gentsch et al., 2012; Gentsch & Schütz-Bosbach, 2011; Kühn et al., 2011). Thus, the present study addresses the question in which way sensory attenuation of brain responses to self-initiated sounds can be associated with judgments of agency. To this aim, we used electroencephalography (EEG) to record ERPs from the human scalp in response to a sound initiated by a button press. Although sounds were always initiated by the participants' button presses, critically, in different conditions, participants perceived themselves as the agent of the sounds or not. In this way, we could compare sensory attenuation effects to self-initiated sounds when participants believed they themselves

had generated the sound with their button press and when they did not believe that they had been the agent of the sound. We manipulated the participants' sensation of agency for the sounds, using a well-established perceptual illusion (Heron et al., 2009; Keetels & Vroomen, 2012; Stetson et al., 2006; Sugano et al., 2010; Timm, Schönwiesner, SanMiguel, & Schröger, under revision). In particular, Timm and colleagues (under revision) showed that after adaptation to a fixed temporal delay between actions and sensory consequences, participants ceased to perceive agency for sounds presented with shorter delays. Based on the hypothesis that predictive sensorimotor signals contribute to both sensory attenuation and agency judgments, we expect to find attenuated auditory N1 or P2 components only when participants perceived agency but not when participants experienced an illusory lack of agency over the production of the sound. Contrary, if agency judgments depend more on inferential than on predictive processes, attenuated auditory N1 or P2 components could be also expected when participants experience an illusory lack of agency because actually participants always self-initiate the sound, that is, predictive signals should be always available to the internal forward model.

The study comprised first a behavioral experiment, followed by the EEG experiment. In the behavioral experiment, participants rated their sensation of agency on every trial under the different conditions. Based on these ratings, we selected participants in which a consistent illusion could be induced for the EEG experiment. The same conditions tested in the behavioral experiment were used in the EEG experiment, where subjective ratings of the sensation of agency were not anymore performed. We compared auditory ERPs between conditions for which participants had given opposing sensation of agency ratings, while the temporal delay between the button press and the sound was identical.

### **3.4.2 Behavioral experiment**

#### **3.4.2.1 Materials and Methods**

##### **3.4.2.1.1 Participants**

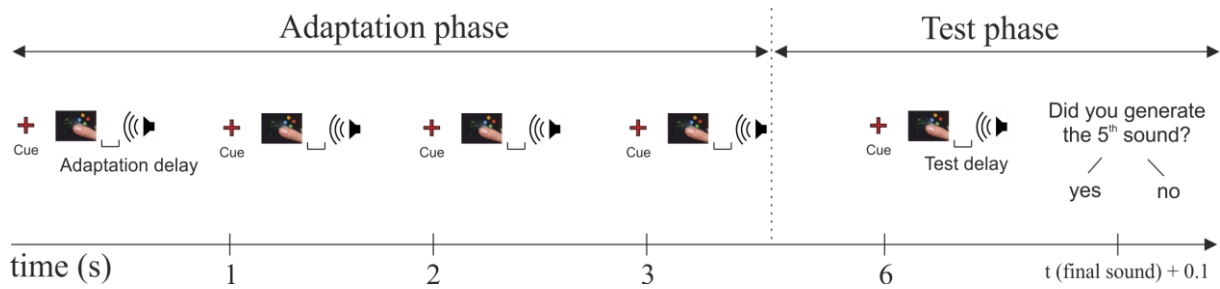
Fifty healthy volunteers (8 male, 6 left-handed) participated in the experiment. Mean age of the participants was 23.82 years (range: 18 to 30 years). All participants reported normal hearing and normal or corrected-to-normal vision. None were taking any medication affecting

the central nervous system. All participants gave informed consent prior to the measurements and received either course credit or payment for their participation.

### 3.4.2.1.2 Procedure

Participants were asked to press a button every time a visual cue was presented. Each button press triggered a short sound. Trials were divided into an adaptation phase, comprising four button presses, and a test phase, comprising one last button press. In the adaptation phase the temporal delay between button press and sound was fixed at a certain value (see below for each condition). In the test phase this temporal delay was either the same or shorter than in the adaptation phase. At the end of each trial, participants were required to judge whether the sound presented in the test phase was generated by their own button press or not. Based on previous studies (Heron et al., 2009; Keetels & Vroomen, 2012; Stetson et al., 2006; Sugano et al., 2010; Timm, Schönwiesner, et al., under revision; Yamamoto & Kawabata, 2011), we expected to induce an illusory lack of the sensation of agency for the final sound when participants adapted to a delay between press and sound during the first four button presses, and this delay was eliminated in the final test button press. Stimulus generation and acquisition of behavioural responses were controlled by a computer using MATLAB (The MathWorks, [www.mathworks.com](http://www.mathworks.com)) and the Psychtoolbox (Brainard, 1997; Pelli, 1997). Participants seated in a sound-attenuated chamber, fixating on a grey cross displayed at the center of a black screen at a distance of about 1 m. They held a gamepad with their dominant hand and were instructed to press one of the buttons as fast as possible with their thumb whenever the grey cross changed its color to red (visual cue). Each button press triggered a short sound. The sounds were 1000-Hz sine tones of 50 ms duration (including 10-ms rise and fall times), presented through circumaural headphones (Sennheiser HD 25-1). In addition to the headphones, participants wore soft foam earplugs to attenuate other sounds, in particular sounds made by pressing the button. Participants adjusted the intensity of the sounds to a comfortable loudness prior to the experiment. In the adaptation phase four visual cues were presented with a stimulus-onset asynchrony (SOA) of 1 s. The test phase consisted of a fifth visual cue, presented 3 s after the onset of the last cue of the adaptation phase (see Figure 17). 100 ms after the final sound, the question: “Did you generate the 5<sup>th</sup> sound?” was presented on the screen. Participants were required to provide a yes/no response on every trial via two additional buttons on the gamepad. Successive trials were separated by a 1 s inter-trial-interval.

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**Figure 17: Schematic illustration of one experimental trial**

Participants were asked to press a button every time a visual cue was presented. Each button press triggered a short sound. Trials were divided into an adaptation phase, comprising four button presses, and a test phase, comprising one last button press. In the adaptation phase four visual cues were presented with a SOA of 1 s and the temporal delay between button press and sound was fixed at a certain value (see Table 3). The test phase consisted of a fifth visual cue, presented 3 s after the onset of the last cue of the adaptation phase. In the test phase the temporal delay was either the same or shorter than in the adaptation phase. At the end of each trial (100 ms after the final sound), participants were required to judge whether the sound presented in the test phase was generated by their own button press or not.

The experiment included the *illusion condition* and several control conditions (see Table 3). For each condition, a different adaptation button press – sound delay and test button press – sound delay combination was used. Following previous studies, in the *illusion condition* participants adapted to a constant 200 ms delay between button press and sound during the adaptation phase, and this delay was then shortened (in this case eliminated) to 0 ms in the test phase. In this condition, we expected a lack of agency, because participants adapt to the delay in the adaptation phase and tend to perceive sounds presented with a shorter delay as preceding the button press (Heron et al., 2009; Keetels & Vroomen, 2012; Stetson et al., 2006; Sugano et al., 2010; Timm, Schönwiesner, et al., under revision; Yamamoto & Kawabata, 2011). For comparison, the *real-time condition* was introduced. In the *real-time condition*, sounds appeared immediately after the button press with a negligible delay (1-2 ms) in both the adaptation and test phases. Here we expected participants to report that they were the agent of the fifth sound. Hence, the same delay (0 ms) was presented in the test phase of the *real-time-* and *illusion condition*, but opposing agency reports were expected. Two more conditions were introduced to control for possible confounding effects in the later ERP experiment (see below): the *delayed-time control condition* and the *deviant-control condition*. In the *delayed-time control condition* sounds were presented 200 ms after the



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button press in both the adaptation and test phases. No illusory perception of agency was expected in the test phase of this condition. In the *deviant-control condition* sounds were presented 400 ms after the button press in the adaptation phase and 200 ms after the button press in the test phase. For this last condition, although the delay was shortened during the test phase, we expected no illusory lack of agency. This hypothesis was based on the results of earlier pilot studies, in which we observed that even when participants adapt to a considerable delay between button press and sound, the subsequent test delay has to be shorter than 50 ms for an illusion of lack of agency to occur.

The conditions were presented in blocks, which included trials from two different conditions, presented randomly with 50 % probability for each condition. Because previous results demonstrated that the condition order influences the agency illusion (Timm, Schönwiesner, et al., under revision), the *illusion condition* and *deviant-control condition* were presented first in four blocks of 18 trials each. This was followed by another four blocks of 18 trials each, in which the *real-time condition* and the *delayed-time control condition* trials were mixed. Participants performed a two-minute dummy block before the main experiment to get acquainted with the task procedures, but were given no feedback as to the accuracy of their agency reports. The total duration of the behavioral experiment was 90 minutes, including pauses.

**Table 3: Experimental conditions with respective button press – sound delays in adaptation and test phase as well as expected agency judgment**

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	Adaptation delay (ms)	Test delay (ms)	Expected agency judgment
<i>Illusion condition</i>	200	0	no
<i>Real-time condition</i>	0	0	yes
<i>Delayed-time control condition</i>	200	200	yes
<i>Deviant-control condition</i>	400	200	yes

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### 3.4.2.1.3 Data analysis

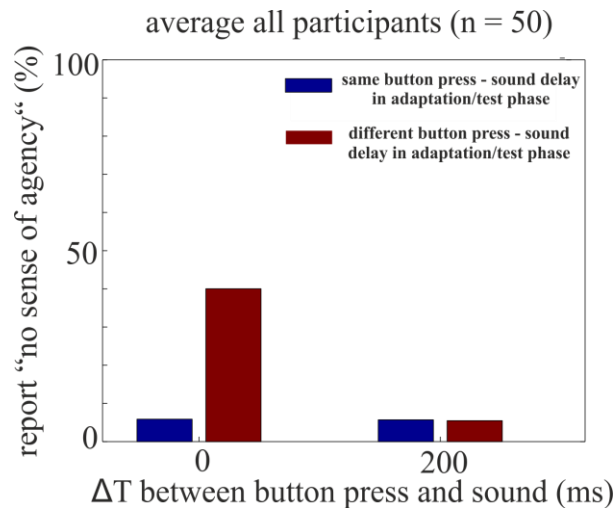
We calculated the proportion of ‘agency’ and ‘no agency’ responses in each condition. On average, participants reported a lack of agency more often in the *illusion condition* than in the other conditions. We quantified the magnitude of the illusion as the difference of the proportions of ‘no agency’ responses between the *illusion condition* and the other conditions (*real-time*, *delayed-time control* and *deviant-control condition*). We discovered that not all participants experienced the illusion to the same degree. We therefore divided the participants in three post-hoc groups according to the magnitude of the illusion: a “high illusion” group (n = 19), in which the magnitude of the illusion was higher than 40 % (average magnitude = 70.9 %), a “moderate illusion” group (n = 15), in which the magnitude of the illusion was between 20 and 40 % (average magnitude = 34.7 %), and a “low illusion” group (n = 16), in which the magnitude of the illusion was less than 20 % (average magnitude = 8.3 %). To test for statistical differences in the agency reports between conditions we conducted an analysis of variance (ANOVA) with the within-subject factors *condition* (agency, agency-illusion) and *delay* (no delay, 200 ms delay) in each group. Post-hoc tests with Bonferroni correction were computed when appropriate to clarify the origin of significant effects. Greenhouse-Geisser correction was applied where appropriate.

### 3.4.2.2 Results

We observed the expected illusory lack of agency in the *illusion condition* on the average across the participants. After adaptation to an artificially induced delay in the adaptation phase, participants reported no experience of agency for sounds presented with shorter delays in the test phase (Figure 18). We obtained individual differences in the magnitude of the illusion effect, thus we divided participants into high, medium, and low groups for further analysis. In all three groups (high, moderate, low) the illusion effect could be induced. That is, the analysis revealed a significant difference between conditions with same button press - sound delays of the adaptation and test phase (*real-time*, *delayed-time control*) and conditions with different button press - sound delays of the adaptation and test phase (*illusion*, *deviant-control*; significant main effect of *condition*, *high*:  $F_{1,18} = 471.60$ ,  $p < .001$ ; *moderate*:  $F_{1,14} = 454.19$ ,  $p < .001$ ; *low*:  $F_{1,15} = 16.96$ ,  $p = .001$ ). Furthermore, significant differences were found for the different temporal delays of button press and sound (no delay vs. 200 ms delay) in the “high illusion” group (significant main effect of *delay*,  $F_{1,18} = 320.13$ ,  $p < .001$ ) and

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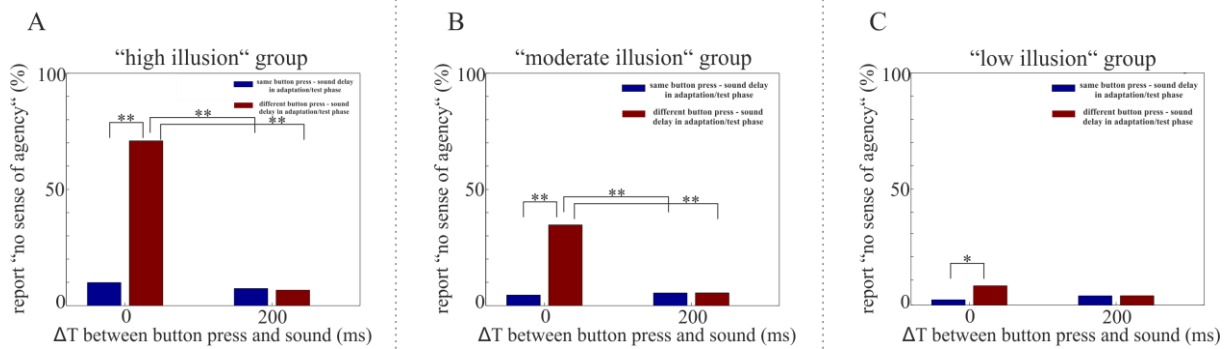
“moderate illusion” group (significant main effect of *delay*,  $F_{1,14} = 101.28$ ,  $p < .001$ ), indicating a stronger illusion effect for sounds presented immediately after the button press. In contrast, the analysis of the “low illusion” group revealed no main effect of the factor *delay* ( $F_{1,15} = 1.34$ ,  $p = .264$ ). However, a significant interaction of *condition* and *delay* was found in all illusion groups (*high*:  $F_{1,18} = 439.50$ ,  $p < .001$ ; *moderate*:  $F_{1,14} = 309.23$ ,  $p < .001$ ; *low*:  $F_{1,15} = 14.05$ ,  $p = .002$ ). Post-hoc tests revealed higher proportions of “no agency” reports in conditions with different button press – sound delays in the adaptation and test phase (*illusion*, *deviant-control*) compared to conditions with same button press – sound delays in the adaptation and test phase (*real-time*, *delayed-time control*) when the sound was presented immediately after the button press (*high*:  $t(18) = 21.79$ ;  $p < .001$ ; *moderate*:  $t(14) = 20.14$ ;  $p < .001$ ; *low*:  $t(15) = 4.19$ ;  $p = .006$ ). Thus, these effects indicate an illusory perception of agency in the *illusion condition* compared to the *real-time condition*. Such a perceptual agency illusion for the *illusion condition* was also observed in relation to both 200 ms delay conditions (*delayed-time control*, *deviant-control*) for the “high illusion” group (*delayed-time control*:  $t(18) = 20.48$ ;  $p < .001$ , *deviant-control*:  $t(18) = 20.32$ ;  $p < .001$ ) and the “moderate illusion” group (*delayed-time control*:  $t(14) = 15.46$ ;  $p < .001$ ; *deviant-control*:  $t(14) = 14.43$ ;  $p < .001$ , see Figure 19A-C).



**Figure 18: Illustration of the averaged illusion effect**

Proportions of “agency” and “no agency” reports for the average of all participants ( $n = 50$ ) for conditions with same button press – sound delays in the adaptation and test phase (*real-time*, *delayed-time control*, blue bars) and conditions with different button press – sound delays in the adaptation and test phase (*illusion*, *deviant-control*, red bars) for both temporal delays (no delay, 200 ms delay), respectively.

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**Figure 19: Illustration of the illusion effect in different illusion groups**

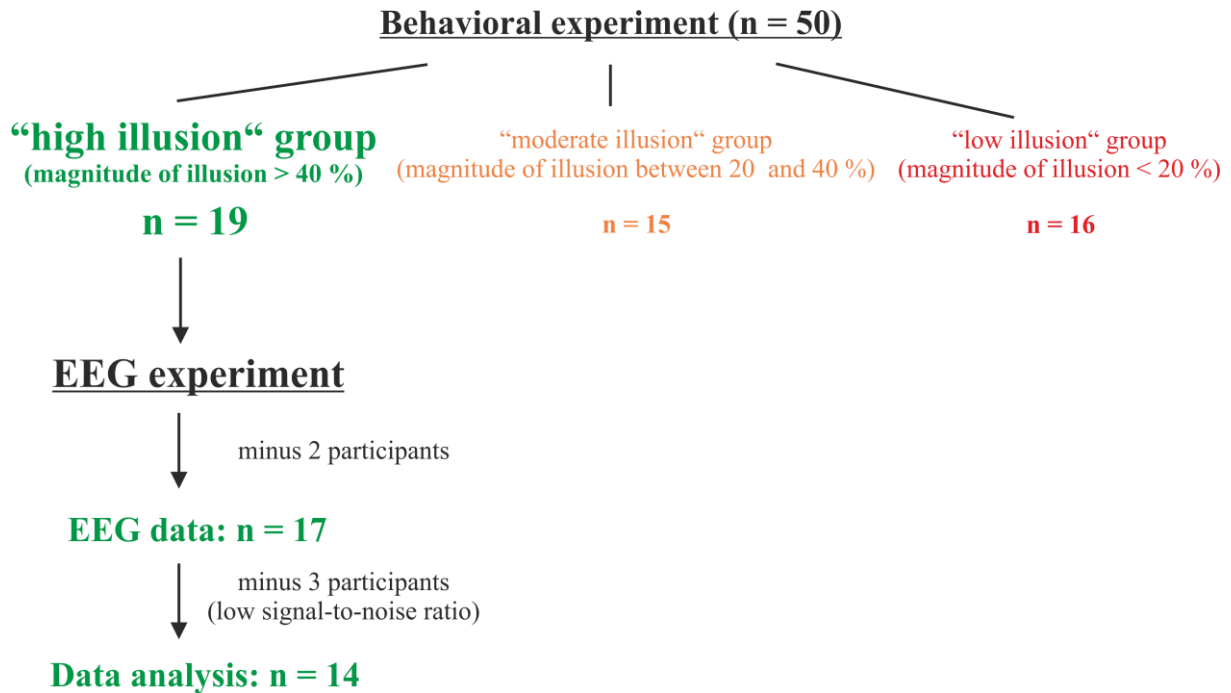
Proportions of “agency” and “no agency” reports for conditions with same button press – sound delays in the adaptation and test phase (*real-time, delayed-time control*, blue bars) and conditions with different button press – sound delays in the adaptation and test phase (*illusion, deviant-control*, red bars) for both temporal delays (no delay, 200 ms delay), respectively. A: Illusion effect in the “high illusion” group, B: Illusion effect in the “moderate illusion” group, C: Illusion effect in the “low illusion” group. Significant differences are indicated (\*\*  $p < .001$ ; \*  $p < .01$ ).

### 3.4.3 EEG experiment

#### 3.4.3.1 Materials and Methods

##### 3.4.3.1.1 Participants

We conducted an EEG experiment to investigate effects of the illusionary perception of agency on sensory attenuation of auditory brain responses to self-initiated sounds. Thus, the EEG experiment was conducted only with participants who reliably experienced the illusion (“high illusion” group of the behavioral experiment). Seventeen of the participants in that group (2 male, 4 left-handed) agreed to take part in the EEG experiment. Of these, three female participants had to be excluded from the analysis due to low signal-to-noise ratio in the EEG recordings. The average age of the remaining 14 participants was 24 years (range: 18 to 28 years, see Figure 20 for an illustration of the selection procedure). Participants provided informed written consent. The experimental protocol conformed to the research ethics guidelines of the Declaration of Helsinki and of the ethics board of the German Association of Psychology ([www.dgps.de/dgps/aufgaben/ethikr12004.pdf](http://www.dgps.de/dgps/aufgaben/ethikr12004.pdf)) and did thus not require any additional ethics approval.



**Figure 20: Schematic illustration of the selection procedure for the EEG experiment**

Fifty participants participated in the behavioral experiment. Participants were divided in three post-hoc groups according to the magnitude of the illusion effect: a “high illusion” group (n = 19) in which the magnitude of the illusion was higher than 40 %, a “moderate illusion” group (n = 15) in which the magnitude of the illusion was between 20 and 40 %, and a “low illusion” group (n = 16) in which the magnitude of the illusion was less than 20 %. The EEG experiment was conducted only with participants of the “high illusion” group of the behavioral experiment. Seventeen of the participants in that group took part in the EEG experiment. Of these, three participants had to be excluded from the analysis due to low signal-to-noise ratio in the EEG recordings. The data of the remaining fourteen participants was further analyzed.

### 3.4.3.1.2 Procedure

The procedure and experimental conditions were the same as in the behavioral experiment. However, no agency judgments were required from the participants. The *delayed-time control condition* and the *deviant-control condition* served to control for two different possible confounding factors in the EEG data. The first factor is the possibility of measuring a MMN response in the *illusion condition*, because the test phases (no temporal delay) deviate from the adaptation phases (200 ms delay) with regard to their button press - sound delay. It is well known that deviations from a standard stimulus elicit a MMN, which may partially overlap

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with the N1 component, and increase its amplitude (Näätänen & Picton, 1987). In the *deviant-control condition*, we expected a deviant response, but no perceptual illusion and thus no ERP components related to the illusion. The additional 200 ms delay in the adaptation and test phases in the *deviant-control condition* abolish the illusion induced by the otherwise identical *illusion condition*. However, this manipulation required a second control condition, because it has been shown that the temporal delay between button press and sound may reduce the N1/P2 attenuation effect (Hazeman et al., 1975). To control for response differences between the *deviant-control condition* and the *illusion-* and *real-time condition* in the test phases, we included the *delayed-time control condition*. In this condition sounds are presented with a 200 ms delay in both the adaptation and test phases. Thus, this manipulation allows us to control for possible temporal delay effects without the deviant response in the *deviant-control condition*.

In order to quantify attenuation effects of brain responses to sounds elicited by button presses relative to brain responses to passive exposure to the same sounds, we added an “auditory-only” condition, in which we measured EEG responses to the sounds alone, without preceding button presses. This was achieved by playing back the auditory stimuli of the active conditions to the passively listening participants. Finally, to account for motor activity in the EEG recordings, we added a “motor-only” condition, where participants pressed the button in response to the cue but no sounds were played. As in the behavioral experiment the conditions were presented in blocks, which included trials from two different conditions, presented randomly with 50 % probability for each condition. Again the *illusion condition* and *deviant-control condition* were presented first in four active and four passive blocks of 18 trials each. This was followed by another four active and passive blocks of 18 trials each, in which the *real-time condition* and the *delayed-time control condition* trials were mixed. Active blocks were always followed by the respective passive auditory-only blocks. The motor-only block was either presented at the beginning or the end of the experiment, counterbalanced across participants. Thus, for the data analysis 72 test trials were collected per experimental condition and task. The experiment took approximately 80 minutes, excluding subject preparation and breaks. Before the main experiment, participants performed a short training session of the active condition and the motor-only condition to refresh the task and get accustomed to the procedures.

### 3.4.3.1.3 Data recording and analysis

EEG activity was recorded continuously with Ag/AgCl electrodes from 61 standard locations according to the international 10-20 electrode system (Chatrian et al., 1985), including the left and right mastoid (M1, M2). In addition, a ground electrode was placed on the forehead, and a reference electrode was placed on the tip of the nose. EOG was measured using the setup described by Schlögl and colleagues (2007) with one electrode at nasion and two electrodes at the outer canthi. EEG signals were sampled at 500 Hz. Automatic eye movement correction was applied on the data according to the procedure described by Schlögl and colleagues (2007), preceded by a 1 to 100 Hz offline band-pass filter. After EOG artifact correction, data were filtered with a 1-25 Hz band-pass filter (Kaiser-window, ripple: 0.017, length: 5653 points). For each trial, an epoch of 600 ms duration was extracted from the continuous EEG. To avoid introducing motor preparation signals present in the baseline period into the post-stimulus waveforms, no baseline correction was applied (Urbach & Kutas, 2006). Epochs with amplitude changes exceeding 75  $\mu\text{V}$  on any channel were rejected from further analysis. ERPs were averaged time-locked to stimulus onsets separately for each participant. In the last pre-processing step, we corrected for motor activity present in responses to self-initiated sounds by subtracting from all conditions the respective motor-only conditions. ERP amplitudes of the N1 and P2 components were calculated from the individual averages as the mean voltage within an 80 to 100 ms latency window for the N1 component and a 150 to 205 ms window for the P2 component. For each component we performed a repeated measurement ANOVA with the factors *condition* (perceiving agency over the sound production vs. illusory lack of agency) and *task* (initiating the sounds with button presses vs. passively listening to the sounds) for the test phases of the *real-time condition* and the *illusion condition* on the mean amplitude of the fronto-central electrodes Fz, FCz and Cz. Post-hoc tests were calculated to clarify the origin of significant interactions. Greenhouse-Geisser correction was applied when appropriate.

### 3.4.3.2 Results

Sensory attenuation effects were compared between test phases of the *real-time condition* (perceiving agency over the sound production) and the *illusion condition* (illusory lack of agency). Importantly, the test phases of both conditions were physically identical and differed only in the judgment of agency. Analysis of the N1 component revealed a significant

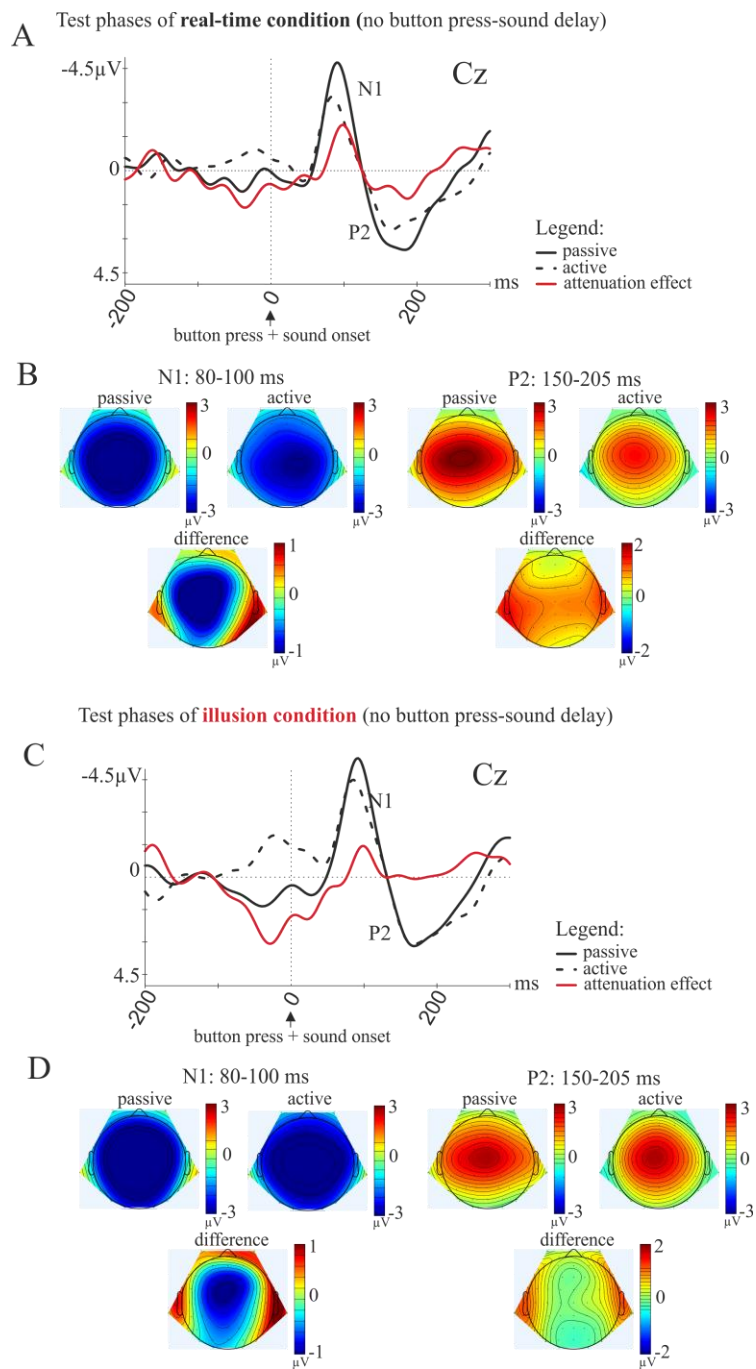
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difference between the sound-evoked responses in the active and the passive condition (significant main effect of *task* on N1 amplitude,  $F_{1,13} = 12.77, p = .003$ ), which was indicated by significant lower N1 amplitudes for self-initiated sounds compared to passive sound exposure in the *real-time control condition* ( $t(13) = -2.81; p = .015$ ) and the *illusion condition* ( $t(13) = -2.44; p = .029$ ). Furthermore, differences between the sound evoked responses of the *real-time condition* and *illusion condition* were observed (significant main effect of *condition* on N1 amplitude,  $F_{1,13} = 11.03, p = .006$ ). This main effect was caused by lower N1 amplitudes in the *real-time condition* compared to the *illusion condition*. However, no interaction between the factors *task* and *condition* was found ( $F_{1,13} = 0.40, ns$ ; Figure 21A and C). The analysis of the P2 component revealed no significant differences between the sound evoked responses of the active and passive sound exposure (no main effect of *task* on P2 amplitude,  $F_{1,13} = 0.60, ns$ ) nor between the *real-time condition* and the *illusion condition* (no main effect of *condition* on P2 amplitude,  $F_{1,13} = 0.19, ns$ ). Additionally, no interaction was found ( $F_{1,13} = 3.77, p = .074$ , Figure 21A and C). The attenuation of the N1 component and the absence of such attenuation effect for the P2 component are also apparent in the topographical scalp distributions of both the N1- and P2 component of each condition (Figure 21B and D). The attenuation effect of the N1 and the absence of this effect for the P2 are also supported by the difference waves (Figure 21A and C).



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**Figure 21: ERP results for the test phases of the real-time- and illusion condition**

Grand-average ERPs at Cz elicited by passive sound exposure (black solid line), self-initiated sounds (black dotted line) and the corresponding difference wave (passive minus self-initiated, red line) as well as the topographical distribution to passive sound exposure, to self-initiation of sounds and the difference wave during the latency ranges of the N1 (80-100ms) and P2 (150-205ms) components are depicted for the test trials of the *real-time condition* (A + B) and the *illusion condition* (C + D).

### 3.4.4 Discussion

The present study aimed to discover the relationship between sensory attenuation effects of cortical brain responses to self-initiated sounds and agency judgments. We recorded ERPs in response to a sound initiated by a button press while participants did or did not perceive agency. To manipulate agency judgments we used a previously reported perceptual illusion (Stetson et al., 2006; Timm, Schönwiesner, et al., under revision) in which participants experienced an illusory lack of agency over the production of a sound. Based on the hypothesis that predictive sensorimotor signals contribute to both sensory attenuation and agency judgments, we expected to find attenuated auditory N1 and/or P2 components only when participants perceived agency but not when participants experienced an illusory lack of agency over the production of the sound.

Our results revealed sensory attenuation effects irrespective of agency judgments. Sensory attenuation was indicated by reduced amplitudes of the auditory N1 component in response to self-initiated sounds (Aliu et al., 2009; Baess et al., 2011; Bässl et al., 2008; Ford et al., 2007; Horváth et al., 2012; Knolle, Schröger, Baess, et al., 2012; Knolle, Schröger, & Kotz, 2012; Martikainen et al., 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973; Timm et al., 2013). Thus, sensory attenuation occurred when participants perceived agency as well as when participants reported an illusory lack of agency. We did not observe a reduction in the amplitude of the P2 component of the auditory ERP. This result fits with previous findings showing that N1 and P2 amplitudes may be modulated independently in attenuation paradigms (Knolle, Schröger, & Kotz, 2012; Minati et al., 2010; Sowman et al., 2012). Importantly, our findings demonstrate that sensory attenuation of brain responses to self-initiated sounds is independent of agency judgments. Thus, our data clearly contradict previous behavioral studies, reporting a direct relationship between agency judgments and sensorimotor processes responsible for self-initiation effects such as intentional binding (Desantis et al., 2011) and sensory attenuation (Desantis, Weiss, et al., 2012). The present results are in agreement with a recent study in the auditory domain suggesting that agency judgments are not based on sensorimotor processes reflected in auditory N1, but might be related to later processes such as the P3a component (Kühn et al., 2011). However, the present results are in contrast to electrophysiological findings in the visual modality reporting decreasing N1 amplitudes to self-initiated visual stimuli for enhanced agency judgments (Gentsch et al., 2012; Gentsch & Schütz-Bosbach, 2011).

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The present results provide evidence that the feeling of agency and judgments of agency represent two different levels of agency representations (Gallagher, 2006; Synofzik et al., 2008). The present data demonstrate that judgments of agency occur independent of sensory attenuation effects, which supports the notion that agency judgments seem to be based more on interpretative and inferential mechanisms than on predictive sensorimotor processes (Synofzik et al., 2008). Our data support results from intentional binding research (Desantis et al., 2011; Haering & Kiesel, 2012; Moore & Haggard, 2008; Moore et al., 2009) and the finding of Sato (2009), reporting that the sense of agency depends on both sensorimotor and contextual information.

Our results can be discussed within the framework of predictive modeling. Our finding of N1 attenuation irrespective of whether participants reported agency or not suggests that N1 attenuation effects depend on whether the action was planned and intended rather than on the comparison of predicted and actual sensory consequences of the action (Timm, SanMiguel, et al., under revision). That is, once the intention to move is formed and the feeling of agency arises during movement preparation, brain responses to self-initiated stimuli are attenuated. This hypothesis is supported by findings in the somatosensory modality (Christensen et al., 2007; Chronicle & Glover, 2003; Haggard & Magno, 1999; Haggard & Whitford, 2004; Moore et al., 2010; Voss et al., 2007, 2006, 2008). In contrast, agency judgments may rely on more perceptual mechanisms that are not related to movement planning and corresponding predictive sensorimotor signals.

Our results also fit with non-predictive accounts of attenuation effects to self-initiated sensory events (Horváth et al., 2012; Horváth, 2013a, 2013b; SanMiguel et al., 2013; Tsakiris & Haggard, 2005). Those models propose that at least a part of the sensory attenuation effect may be the basis for the initial formation of contingent associations between motor and sensory events. In this notion, sensory attenuation effects are unspecific: any sound in the temporal vicinity of the motor act is attenuated. For example, Horváth and colleagues (2012) showed that auditory input is attenuated for a short period after the motor act, even if there is no contingency between button press and sound. Thus, it might be also possible that the observed attenuation effects of the present study reflect mere coincidence detection between button press and sound, which was available irrespective of participants' agency experience over the production of the sound (Horváth et al., 2012; Horváth, 2013a, 2013b).

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In sum, our findings demonstrate sensory attenuation irrespective of agency experience, indicated by reduced amplitudes of the auditory N1 component in response to self-initiated sounds. Thus, our data provides direct evidence that sensory attenuation of brain responses to self-initiated sounds and agency judgments are independent. The present results are in favor of the assumption that the sense of agency represents a combination of predictive and inferential mechanisms.

### 4 General discussion

The present thesis set out to investigate the effects of action-driven predictions in auditory information processing and its connection to the sense of agency. Particularly, the nature of the N1 and/or P2 attenuation effect in response to self-initiated sounds and its specific relation to the sense of agency was examined, using EEG to record ERPs from the human scalp. As it has been pointed out in Chapter 1, it is generally suggested that the attenuation of the auditory N1 and/or P2 component in response to self-initiated sounds relative to externally-generated sounds reflects the cancellation of auditory re-afference, indicating the workings of internal forward model predictions of the acting self (Aliu et al., 2009; Baess et al., 2011; Bäсс et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; Knolle et al., 2013; Knolle, Schröger, & Kotz, 2012; Kühn et al., 2011; Martikainen et al., 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973). Such a predictive mechanism, in turn, allows the correct differentiation between self-generated sensory consequences and sensory input caused by external sources, thereby enabling the attribution of actions to the active agent (Blakemore et al., 2002; Frith et al., 2000). However, the presumption that the N1 and/or P2 attenuation reflects predictive processing is still controversial (Horváth et al., 2012; Horváth, 2013a, 2013b; Hughes et al., 2012; Makeig et al., 1996; SanMiguel et al., 2013; Tsakiris & Haggard, 2005). Furthermore, little is known about how N1 and/or P2 attenuation effects are related to the sense of agency, which is thought to be directly linked to predictive sensorimotor signals processed within internal forward models (Tsakiris & Haggard, 2005; Wolpert & Flanagan, 2001). To shed further light on these issues several research questions have been formulated in the present thesis:

- 1) To which extent can N1 attenuation effects be explained by a differential allocation of attention to self-initiated and externally-initiated sounds? (Experiment 1)
- 2) To which extent do N1 and/or P2 attenuation effects depend on brain activity involved in movement planning (where conscious motor intention and the corresponding feeling of agency are thought to arise)? (Experiment 2)
- 3) To which extent can N1 and/or P2 attenuation effects be related to explicit judgments of agency? (Experiment 3 and 4)

In this chapter the empirical results of all four experiments conducted in the present thesis will be summarized. Afterwards, the findings will be discussed in a framework of predictive modeling and will be related to current models of this field of research. Based on this, a proposal of a model for auditory information processing of the acting self will be made, integrating motor intention, different representations of the sense of agency and auditory N1 and/or P2 attenuation effects, to set the results in a broader context. Finally, open questions and possible further directions will be discussed.

### **4.1 Summary of the empirical results**

The first experiment investigated to which extent the N1 attenuation effect to self-initiated sounds can be explained by a differential allocation of attention to self-initiated and externally-initiated sounds. To overcome possible limitations of the traditional blocked design self-initiated sounds and externally-initiated sounds as well as the motor control were presented within the same block. The allocation of attention was manipulated block-wise in three different attention conditions so that attention was directed to the sounds or was directed away from the sounds towards the own motor behavior or the visual stimulation. It was hypothesized that if attention causes the N1 attenuation effect, then manipulating attention should affect the effect for self-initiated sounds. In contrast, if the N1 attenuation effect reflects the workings of an internal predictive forward model, the attenuation effect to self-initiated sounds was expected to be unaffected by an attentional difference. Moreover, effects of self-initiation were compared with attention effects to determine whether the underlying neural processes affect the same or different structures. The results show that the N1 attenuation was equally large and of equal distribution when participants directed their attention towards the sound and when they directed their attention away from the sounds, towards the button presses or the visual stimuli. Thus, the self-initiation effect can hardly be explained by the differential amount of attention devoted to self- and externally-initiated sounds. Instead, the findings support the notion that the N1 attenuation effect for self-initiated sounds seems to reflect the activity of an internal predictive mechanism. Furthermore, it was found that whereas the effects of voluntary attention affect all N1 components, the self-initiation effect is circumscribed to late N1 components (N1b and N1c).

## General discussion

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The second experiment focused on the specific relationship between N1 and/or P2 attenuation effects to self-initiated sounds and the feeling of agency. Specifically, it was investigated whether attenuation effects of the auditory N1 and P2 component to self-initiated sounds can be explained by brain activity involved in movement planning (where conscious motor intention and the corresponding feeling of agency are thought to arise) rather than movement execution. Therefore, ERPs in response to a sound initiated by a button press were recorded. In one condition, participants moved a finger to press the button voluntarily, whereas, in another condition, a similar, but involuntary, finger movement was initiated by stimulating the corresponding region of the primary motor cortex with transcranial magnetic stimulation (TMS). For involuntary movements no movement intention (and no feeling of agency) could be formed, thus no motor plans were available to the forward model. It was hypothesized that predictive signals involved in the processing of self-initiated sounds are sent during movement planning rather than movement execution. Consequently, an attenuation of the N1 and/or P2 response was expected only for voluntary movements, but not for involuntary movements, because no predictive signals should be available to the predictive forward model during involuntary movements. The results indicate attenuated N1 and P2 amplitudes following voluntary, self-initiated, movements, but not following movements initiated by motor cortex stimulation. Thus, the present findings demonstrate that the origin of the sensory attenuation of brain responses to self-initiated sounds is prior to motor cortex activation. That is, the intention to move and the corresponding feeling of agency rather than the mere movement execution seem to play an essential role for the attenuation of the auditory N1 and P2 component. Taken together, the results support the assumptions of a predictive internal forward-model account operating prior to primary motor cortex activation.

To examine the relation between N1 and/or P2 attenuation effects to self-initiated sounds and explicit judgments of agency, Experiment 3 and 4 were conducted. The idea was to apply a “judgment of agency illusion” to manipulate judgements of agency during self-initiation of sounds in an appropriate way and to study corresponding N1 and/or P2 attenuation effects in conditions where agency was perceived or not (although the sound was always self-initiated, that is, predictive signals were always available to the internal forward model).

Thus, the third experiment addressed the question whether such an illusory perception of agency for self-initiated sounds can be created experimentally. To this end, a recently reported temporal order illusion of intentional actions and their subsequent sensory effects (Stetson et

al., 2006) was used and its association to judgments of agency was tested. That is, the probability of time intervals between voluntary button presses and sounds was manipulated, such that trials with identical delays between button press and sound prompted different perceptions of temporal order. Participants were asked to rate their sense of agency in these different conditions. Assuming a strong association between temporal order- and agency judgments, it was hypothesized that participants would report no experience of agency in trials in which button press and sound are perceived in reversed order. The results show an absence of the sense of agency in a condition in which sounds were falsely perceived as preceding motor acts relative to the perceived temporal order in the control condition. This finding suggests a strong association between the sense of agency and the temporal order perception of actions and their consequences. Moreover, the results provide further evidence that motor intentions partly determine human time perception.

In the fourth experiment the relationship between N1 and/or P2 attenuation effects to self-initiated sounds and agency judgments was directly tested, making use of the “judgment of agency illusion” demonstrated in the third experiment. To this end, ERPs in response to sounds initiated by button presses were recorded. In one condition, participants perceived agency over the production of the sounds, whereas, in another condition, participants experienced an illusory lack of agency. Importantly, the action-effect sequence was physically identical in both conditions, only the judgment of agency differed between conditions. Based on the hypothesis that predictive sensorimotor signals contribute to both sensory attenuation and agency judgments, it was expected to find attenuated auditory N1 and/or P2 components only when participants perceived agency but not when participants experienced an illusory lack of agency over the production of the sound. The findings demonstrate sensory attenuation irrespective of agency experience. Sensory attenuation was indicated by reduced amplitudes of the auditory N1 component in response to self-initiated sounds. Thus, the present data provide direct evidence that sensory attenuation of brain responses to self-initiated sounds and agency judgments are independent. Taken together, the present results show that N1 attenuation effects depend on whether the action was planned and intended rather than on the comparison of predicted and actual sensory consequences of the action. Furthermore, they are in favor of the assumption that the sense of agency represents a combination of predictive and inferential mechanisms (Synofzik et al., 2008).



### **4.2 I intend to do it: sensory attenuation of brain responses to self-initiated sounds depends on predictive signals involved in movement planning**

As pointed out above, the results of the present thesis support the assumption that sensory attenuation of brain responses to self-initiated sounds depends on functions of predictive internal forward models. The present data strengthen and extend previous findings (Aliu et al., 2009; Baess et al., 2011; Bäss et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; Knolle et al., 2013; Knolle, Schröger, & Kotz, 2012; Kühn et al., 2011; Martikainen et al., 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973) in showing that the predictive signals that are engaged in the processing of self-initiated sounds originate upstream from primary motor cortex where the motor command is executed (Experiment 2). Thus, sensory attenuation effects depend on whether the action was planned and intended rather than on the comparison of predicted and actual sensory consequences of the action (Experiment 2 and 4). That is, once the intention to move is formed, brain responses to self-initiated stimuli are attenuated. Furthermore, the findings of Experiment 1 rule out a possible attentional explanation of auditory attenuation effects to self-initiated sounds reported in previous studies (Baess et al., 2011; Bäss et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; Knolle, Schröger, & Kotz, 2012; Kühn et al., 2011; Martikainen et al., 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973).

The notion that the observed sensory attenuation effects to self-initiated sounds depend on predictive processes involved in movement planning rather than movement execution are in line with previous studies in the somatosensory modality, investigating the processing of voluntary movements and their direct proprioceptive and tactile consequences. For example, no sensory attenuation has been reported for involuntary body movements, irrespective of whether these movements were artificially induced via peripheral (muscle) or central (single pulse TMS to motor cortex) stimulation (Christensen et al., 2007; Haggard & Whitford, 2004; Voss et al., 2007). Moreover, it has been shown that self-generation effects such as sensory attenuation are disrupted when repetitive TMS is applied over areas prior to motor cortex (Haggard & Magno, 1999; Haggard & Whitford, 2004; Moore et al., 2010). Conversely, there is also some evidence that motor planning (Bays, Flanagan, & Wolpert, 2006; Voss et al., 2006) and anticipated movement (Voss et al., 2008), without actual movement execution, may lead to sensory attenuation effects. The findings of Experiment 2 show that the same

mechanism seems to hold in the auditory modality and thus support the assumption of an universal predictive mechanism for sensory processing of voluntary movements that operates prior to movement execution (Crapse & Sommer, 2008a; Wolpert et al., 1995). The results of Experiment 2 and 4 are also in agreement with a recently proposed parietal-premotor network of movement intention (Desmurget et al., 2009). In their model, Desmurget and colleagues (2009) propose that conscious movement intention is independent of movement execution and that parietal areas play a crucial role in generating and monitoring movement intention. Particularly, they assume that predictive motor signals are emitted through forward modeling within the posterior parietal cortex and that these signals form the basis for movement awareness. Thus, intentions and predictions of what will result from carrying out these intentions create our conscious experience that we are moving (Desmurget et al., 2009). In other words, “*What really matters when we initiate an action is the specific goal we have in mind.*” (Desmurget et al., 2009, p. 415).

In line with this, the present data clearly contract the hypothesis that the auditory attenuation effect to self-initiated sounds does not reflect auditory internal forward predictions but rather a dynamic change in the distribution of attentional resources. In particular, this model assumes that performing an action may briefly draw attention away from auditory processing, which results in attenuated auditory responses for sounds close to a button press (Horváth et al., 2012; Hughes et al., 2012; Makeig et al., 1996). According to this assumption, sensory attenuation effects would merely reflect attentional differences between self-initiated and externally-initiated sounds and not sensory predictions resulting from a forward model of the motor command. However, in Experiment 1 of the present thesis it was shown that an attenuation of the auditory N1 for self-initiated compared to externally-initiated sounds was independent from the allocation of attention. Thus, the data provide direct evidence that the N1 attenuation effect cannot be explained by attentional differences between self- and externally-initiated sounds, that is, N1 attenuation cannot be explained by the fact that the motor act draws away attention from auditory processing. Consistent with these results, a recent study reported reduced N1 amplitudes during self-vocalization using a selective attention task to assess the N1 component independent of the attention effect (Kudo et al., 2004). Thus, it can be speculated that the function of an internal forward mechanism, supporting predictions of self-generated speech sounds, also applies to instrumental actions such as self-initiated sounds via button press. That is, shared representations of all auditory predictions can be assumed.

The assumption that self-initiation effects indicate the workings of internal forward predictions is further supported by recent findings of Hughes and colleagues (2012, 2013). In their model, they propose that sensory attenuation effects reported in previous experiments (e.g. Baess et al., 2011; Bäss et al., 2008; Blakemore, Wolpert, et al., 1998; Ford, Mathalon, Kalba, Whitfield, et al., 2001; Knolle, Schröger, Baess, et al., 2012; Schafer & Marcus, 1973) might have been caused by different processes than action prediction mechanisms such as temporal prediction or temporal control. Thus, they systematically investigate the specific role of motor predictions in self-initiation effects. In a recent study they provide direct evidence that the auditory N1 attenuation effect results from motor prediction mechanisms (Hughes et al., 2013). Participants performed one of four voluntary actions on each trial, with each button associated with either predictable or unpredictable action effects. Additionally, actions with each hand could result in action effects that were either congruent or incongruent with the hand-specific prediction (Hughes et al., 2013). Sensory attenuation was only observed for action effects that were congruent with the hand-specific prediction but not for incongruent action effects. Furthermore, no differences in N1 amplitudes between predictable and unpredictable sounds were observed. In agreement with the results of the present thesis, the authors concluded that their findings indicate that accurate motor predictions drive sensory attenuation effects of self-initiated sounds (Hughes et al., 2013). However, the authors pointed out that it is unclear in which way sensory attenuation effects in the auditory modality are linked to causality and the sense of agency (Hughes et al., 2012). Interestingly, the results of the present thesis provide first answers to these questions (see section 4.3).

Another non-predictive model proposes that at least a part of the sensory attenuation effect may be the basis for the initial formation of contingent associations between motor and sensory events. Thus, sensory attenuation effects would be rather unspecific: any sound in the temporal vicinity of the motor act would receive attenuated processing, not indicating a specific motor-sensory prediction. Motor-sensory prediction would only be formed in a later step, once contingency can be extrapolated from repeated pairing (Horváth et al., 2012; Horváth, 2013a, 2013b; Tsakiris & Haggard, 2005). For example, recent findings show that auditory input seems to be attenuated for a short period after the motor act, even if there is no contingency between button press and sound (Horváth et al., 2012; Horváth, 2013a, 2013b). However, the data of Experiment 2 argue against this hypothesis. That is, although button press and sound were coincident for both voluntary and involuntary movements no sensory attenuation in response to self-initiated sounds was observed for involuntary movements.

Thus, only when the intention to move could be formed, sensory attenuation occurred. These findings support the notion that sensory attenuation effects to self-initiated sounds reflect the activity of an internal predictive mechanism involved in movement planning.

However, although the idea that sensory attenuation to self-initiated sounds depends on functions of predictive internal forward models was carried out throughout the whole thesis, it is necessary to mention that the present results also revealed a contribution of the unspecific N1 component to this attenuation effect. Particularly, the data of Experiment 1 show that especially late parts of the auditory N1, that is, the N1b and N1c components are attenuated by self-initiation. The N1b component is known to receive contributions from both the tangentially oriented, sensory-specific component and the unspecific component of the N1 (Näätänen & Picton, 1987). Importantly, only sensory components with sources in auditory cortex are tangentially oriented, showing a fronto-central distribution with polarity inversion at the mastoids. Contrary, the unspecific component, which reflects the orienting response, appears slightly later in time than tangential components and shows no polarity reversal at the mastoids, as it does not originate in auditory cortex (Näätänen & Picton, 1987). However, the data of Experiment 1 did not show self-initiation effects at the mastoids on the polarity-inverted N1 deflection. That is, it seems possible that a part of the N1 attenuation effect may be due to the attenuation of the unspecific N1 component rather than the attenuation of sensory responses in auditory cortex as stipulated from internal predictive models theory. This assumption is supported by a recent finding of SanMiguel and colleagues (2013), suggesting that, in contrast to the P2 attenuation effect, the N1 attenuation effect reflects no stimulus-specific response in auditory cortex but rather mainly represents a reduction of an unspecific component of the auditory N1 outside the auditory cortex. Thus, it could be speculated that attenuation effects of the auditory N1 measured in previous studies (Baess et al., 2011; Bäss et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; Knolle, Schröger, & Kotz, 2012; Kühn et al., 2011; Martikainen et al., 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973) may reflect the fact that self-initiated sounds are less arousing compared to externally-initiated sounds. However, these findings are contradicted by previous MEG studies, which specifically measured the activity of sources in auditory cortex in response to self-initiated and externally-initiated sounds, reporting an attenuated N1 and/or P2 response to self-initiated sounds (Aliu et al., 2009; Horváth et al., 2012; Martikainen et al., 2005). Taken together, it requires further investigation to which extent sensory-specific and unspecific components contribute to the attenuation effect of the auditory N1.

Furthermore, it is necessary to mention that the data of the present thesis revealed an inconsistent pattern of the P2 attenuation effect in response to self-initiated sounds. That is, whereas in Experiment 2 an attenuated P2 response was observed, the findings of Experiment 4 did not show a reduction in the amplitude of the P2 component of the auditory ERP. These results fit with previous findings showing that N1 and P2 amplitudes may be modulated independently in attenuation paradigms (Knolle, Schröger, & Kotz, 2012; Minati et al., 2010; Sowman et al., 2012). For example, Knolle and colleagues (2012) investigated the specific role of the cerebellum in generating auditory forward predictions in response to self-initiated sounds. They tested a group of patients with focal cerebellar lesions and a healthy control group using the N1 and/or P2 attenuation paradigm. Cerebellar patients, in contrast to healthy controls, did not show a significant N1 attenuation in response to self-initiated sounds, confirming that the cerebellum is involved in the generation of auditory forward predictions (Knolle, Schröger, & Kotz, 2012). However, both patients and controls showed a reduced P2 attenuation effect in response to self-initiated sounds. The authors concluded that the N1 attenuation may reflect an automatic prediction, generated to prepare the auditory cortex to receive an expected sensory input (Creutzfeldt, Ojemann, & Lettich, 1989) whereas the P2 reduction may indicate an additional, presumably more cognitively controlled mechanism involved in identifying self-initiated sounds. However, there exists also evidence that effects on the N1 and P2 in common attenuation paradigms mostly go along with each other (Horváth et al., 2012; Schafer & Marcus, 1973). Thus, it still needs further exploration to which extent N1 and P2 amplitudes in response to self-initiated sounds are modulated independently.

### **4.3 Sensory attenuation effects to self-initiated sounds are associated with the feeling of agency but are independent of agency judgments**

As highlighted above, predictive motor signals involved in movement planning play an essential role for the sensory attenuation of brain responses to self-initiated sounds. Importantly, in the present thesis attenuated N1 and P2 components were only found for intended movements, that is, when participants felt as the agent of the movement (Experiment 2). Thus, the present findings provide evidence for a direct relationship between the N1 and P2 attenuation effect for self-initiated sounds and the feeling of agency. That is, the N1 and P2 attenuation effect seems to reflect a sense of self in action, which allows us to recognize

whether an external event was linked to our own movement or not. These results are consistent with previous findings in the auditory modality, showing that phenomenological sensory attenuation effects indicate a sense of agency (Sato, 2008, 2009; Weiss et al., 2011a, 2011b; Weiss & Schütz-Bosbach, 2012). Furthermore, the present findings are in line with recent predictive modeling accounts, assuming that auditory attenuation effects might be modulated by the sense of agency (Hughes et al., 2012). However, the data of the present thesis further demonstrate that sensory attenuation effects to self-initiated sounds are independent of explicit agency judgments (Experiment 3 and 4). That is, sensory attenuation occurred irrespective of whether participants reported agency or not. Thus, once an action is planned or intended, sensory responses to self-initiated sounds are attenuated. The present data clearly contradict previous behavioral studies, reporting a direct relationship between agency judgments and sensorimotor processes responsible for self-initiation effects such as intentional binding (Desantis et al., 2011) and sensory attenuation (Desantis, Weiss, et al., 2012). Furthermore, they strengthen and extend the electrophysiological findings of a recent study in the auditory domain suggesting that agency judgments are not based on sensorimotor processes reflected in auditory N1, but might be related to later processes such as the P3a component (Kühn et al., 2011). However, the present results are in contrast to findings in the visual modality reporting decreasing N1 amplitudes to self-initiated visual stimuli for enhanced agency judgments (Gentsch et al., 2012; Gentsch & Schütz-Bosbach, 2011).

The results of Experiment 2 and 4 are in agreement with a previously proposed model of agency, suggesting two different levels of agency representations (Gallagher, 2006; Synofzik et al., 2008). Specifically, this theoretical model integrates previously suggested predictive and inferential/interpretative explanations of the sense of agency in a two-step account of agency representations. The predictive account of agency assumes that the sense of agency originates in neural processes responsible for the motor aspects of intentional actions (Haggard, 2005). That is, the sense of agency is generated by or at least linked to the motor commands sent to the muscles and the accompanying efference copy that is internally processed within predictive internal forward models (Tsakiris & Haggard, 2005; Wolpert & Flanagan, 2001). In contrast, the inferential account of agency downplays the specific contributions of the motor system (Wegner, 2002). Wegner (2002) proposes that movement intention and the corresponding sense of agency arise from interpreting our thoughts as the cause of our actions, irrespective of whether or not this inference is appropriate. According to Wegner (2002, 2003) we experience agency when a thought 1) appears prior to an action, 2)

is consistent with the action and 3) is not accompanied by other plausible causes of the action. Thus, Wegner suggests that the sense of agency is determined by the conceptual match between preview information and subsequent sensory consequences. Integrating the predictive and inferential account of agency, the two-step account of agency representations (Synofzik et al., 2008) assumes the following: On a first level the feeling of agency is experienced, which represents an immediate feeling of being the agent of an action. The authors argue that it mainly depends on the automatic processing of sensorimotor signals generated by the acting self. On a second level the feeling of agency is further processed and judgments of agency are formed, reflecting the belief of being the agent of an action. This belief formation represents an interpretative and inferential process looking for the best explanation of the cause of the action. Thus, according to the authors the sense of agency represents a combination of predictive and inferential mechanisms (Synofzik et al., 2008). Recent findings on intentional binding, i.e. the finding that sensory consequences are perceived closer in time to a voluntary movement (Desantis et al., 2011; Haering & Kiesel, 2012; Moore & Haggard, 2008; Moore et al., 2009; Sato, 2009), are consistent with these assumptions. These studies showed that the intentional binding effect, as an implicit measure of agency, depends on both predictive and interpretative mechanisms. In agreement with these findings the present results on sensory attenuation also support the notion of a two-step account of agency representations (Synofzik et al., 2008). Specifically, it was found that judgments of agency occur independent of sensory attenuation effects (Experiment 4), which have been shown to depend on sensorimotor signals involved in movement planning (Experiment 2). Thus, explicit agency judgments seem to be based more on interpretative and inferential mechanisms than on predictive sensorimotor processes.

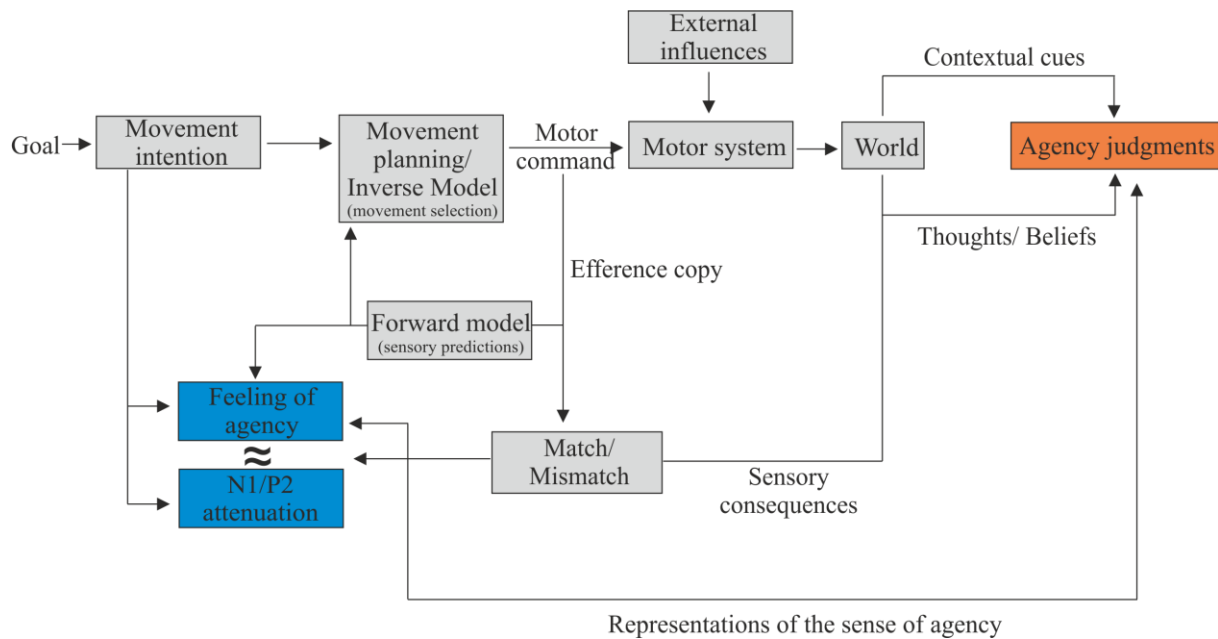
The finding of a direct relationship between the feeling of agency and sensory attenuation effects to self-initiated sounds (Experiment 2) is also in line with results showing that movement intention and the feeling of agency mainly arise from motor preparation processes in premotor and parietal cortex (Haggard, 2005). For example, there exists evidence that cortical electrical stimulation of parietal brain regions can generate feelings of intending to move and even the conviction of having executed the movement (Desmurget & Sirigu, 2009). This perfectly fits with the assumptions of Desmurget and colleagues (2009) discussed in the previous section (see section 4.2). Proposing a parietal-premotor network of movement intention, they argue that predictive motor signals are emitted through forward modeling within the parietal cortex, and that these signals form the basis of a feeling of agency. In

agreement with the model of Desmurget and colleagues (2009) the sensory attenuation to self-initiated sounds, indicating the feeling of agency, reflects a correlate of preparatory neural activity, supporting predictive model accounts of the N1 and/or P2 attenuation effect.

### **4.4 Predictive model of auditory information processing of the acting self**

Based on the literature and the findings of the present thesis a first attempt of a predictive model of auditory information processing of the acting self can be proposed, integrating movement intention, different representations of the sense of agency and auditory N1 and/or P2 attenuation effects (see Figure 22). Initially, the intention to move arises due to a specific goal we have in mind. Presumably, this intention is generated in parietal areas (Desmurget et al., 2009) and initiates processes involved in movement planning. During movement planning inverse models select appropriate motor commands to achieve the desired goal in the external world. The specific motor command is sent to the muscles. At the same time an efference copy triggered by the motor command is implemented in a forward model, generating predictions about the sensory consequences of our actions. These predictive signals seem to form the basis of the feeling of agency and the associated sensory attenuation of brain responses to self-initiated sounds. The feeling of agency can be affected by the match or mismatch between predictions made by forward model and actual sensory consequences. If predicted and actual sensory consequences match, we experience a coherent sense of action processing, indicated by sensory response attenuation. If the comparison process indicated a mismatch, the feeling of agency is reduced or even absent, indicated by the absence of an attenuation effect to self-initiated stimuli. In contrast, explicit agency judgments seem to be mainly affected by inferential/interpretative processes such as prior thoughts or beliefs and contextual information. Both the feeling of agency and explicit judgments of agency contribute to the overall sense of agency.





**Figure 22: Predictive model of auditory information processing of the acting self**

The feeling of agency and the corresponding N1 and/or P2 attenuation effect seem to mainly depend on movement intention and predictive internal forward signals involved in movement planning. However, they can be also affected by the match or mismatch between predicted and actual sensory feedback. Agency judgments seem to be mainly affected by inferential processes and are not related to auditory attenuation effects. The feeling of agency and agency judgments contribute to the overall sense of agency.

## 4.5 Open questions and further directions

The present thesis provides evidence that movement intention and predictive internal motor signals involved in movement planning play an essential role for the feeling of agency and the corresponding N1 and/or P2 attenuation effect to self-initiated sounds, which is important to differentiate the self as an agent from the external world. However, research on the relation between the sense of agency and its neurophysiological correlates in audition is still at its beginning stages. Based on the present findings several future directions seem to be fruitful for follow up.

First, one might investigate whether the experience of agency and corresponding N1 and/or P2 attenuation effects to self-initiated sounds represent a unique and private experience of the acting self. Interestingly, there exists evidence that self-generation effects such as the intentional binding effect also occur during action observation (Wohlschläger, Engbert, et al.,

2003; Wohlschläger, Haggard, Gesierich, & Prinz, 2003). For example, Wohlschläger and colleagues (2003) showed that the perceived onset times of one's own actions are comparable to the perceived onset times of other people's observed actions. However, both are substantially later than the perceived onset times of physically comparable machine movements. The authors concluded that the attribution of agency, reflected in the intentional binding effect, depends on whether a movement involves a voluntary agent, that is, an intention to move is present. In contrast, Engbert and colleagues (2008) reported no intentional binding effect for observed movements, suggesting that the experience of agency is not socially shared. Moreover, ambiguous results have also been found for phenomenological sensory attenuation effects to self-initiated sounds. For instance, Sato (2009) revealed attenuated sensations both when participants themselves initiated a sound and when they observed the experimenter performing the same action. In the same vein, Weiss and colleagues (2011b) showed that sensory attenuation effects are strongly modulated by social interactions between self and other. They reported that sensory attenuation effects of self- and other-initiated sounds were increased in interactive action contexts, proposing that the feeling of agency can be extended to and is shaped by interactions between individuals (Weiss et al., 2011b). Contrary, Weiss and colleagues (2011a) found sensory attenuation effects specifically related to self-initiation of sounds, assuming that the feeling of agency reflects a private experience, which depends on the privileged access to internally-generated information. Thus, up to now it remains unclear whether action observation indeed modulates the perception of action effects in a similar way as self-initiated actions do. Moreover, it seems that no study has yet examined whether N1 and/or P2 attenuation effects can also be obtained for observed actions or social interactions. As shown in the present thesis, the N1 and/or P2 attenuation effect reflects a neurophysiological correlate of the feeling of agency. Thus, if the feeling of agency represents no private experience, N1 and/or P2 attenuation effects should be affected by action observation and social interactions. The verification of such speculation poses great potential for future research.

Second, it could be interesting to examine the reported relationship between the feeling of agency and N1 and/or P2 attenuation effects to self-initiated sounds in clinical populations such as schizophrenic patients or experts such as musicians. It is well known that schizophrenic patients show abnormal attributions of agency, which has been associated with a failure in monitoring movement intentions (Frith, 2005). There exists evidence that these misattributions originate in dysfunctions in pre-motor areas (Singh et al., 1992). Furthermore,

patients with positive symptoms such as auditory hallucinations do not show N1 and/or P2 attenuation effects to self-generated auditory stimuli, which is normally interpreted as a dysfunction in the predictive internal forward mechanism (Ford et al., 2007). However, the exact mechanisms are still not well understood. The experimental designs presented in Experiment 2 and 4 of the current thesis may provide fruitful tools to further investigate the dysfunctional neurophysiological mechanisms of internal forward processes in patients suffering from schizophrenia. Moreover, one might even think of examining the relationship between sensory attenuation effects to self-initiated sounds and their relation to the sense of agency in musicians. There exists evidence that the processing of self-initiated auditory stimuli is different in musicians, indicated by differences in the auditory N1 compared to non-musicians (Ott & Jäncke, 2013; Ott, Langer, Oechslin, Meyer, & Jäncke, 2011). For example, it could be investigated to which degree altered auditory feedback during music performance influences the feeling of agency and the corresponding neurophysiological correlates in musicians and non-musicians.

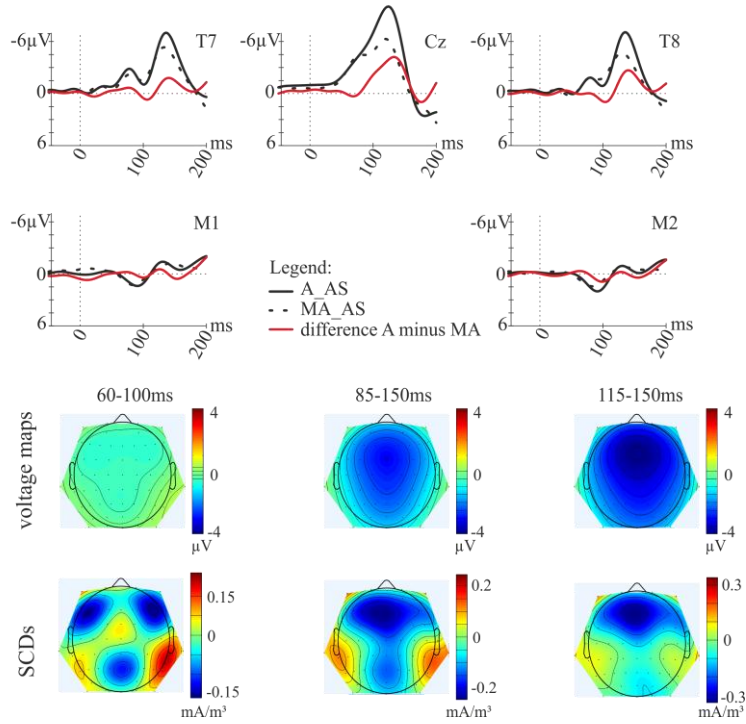
### **4.6 Concluding remarks**

The primary aim of the present thesis was to further investigate the effects of action-driven predictions on the processing of self-initiated sounds and its relation to different representations of the sense of agency. The findings provide evidence that N1 and/or P2 attenuation effects to self-initiated sounds are mainly determined by movement intention and predictive internal motor signals involved in movement planning. Furthermore, it was shown that sensory attenuation effects in audition are directly related to the feeling of agency but occur independent of agency judgments. Based on the literature and the present results, the current thesis proposes a predictive model of auditory information processing of the acting self, integrating movement intention, different representations of the sense of agency and N1 and/or P2 attenuation effects to self-initiated sounds. In conclusion, the present thesis offers new insights in how action-driven predictions of the self in action influence auditory information processing.

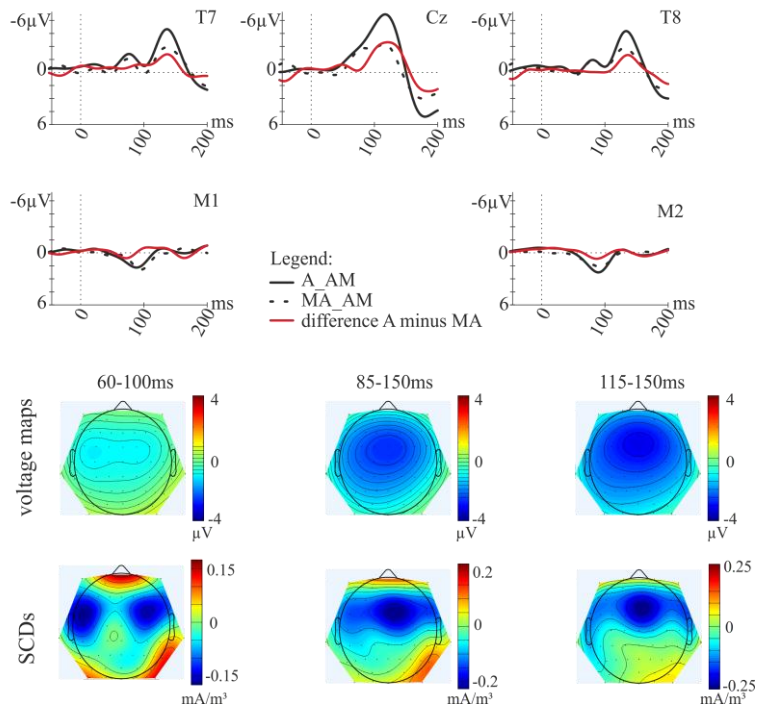


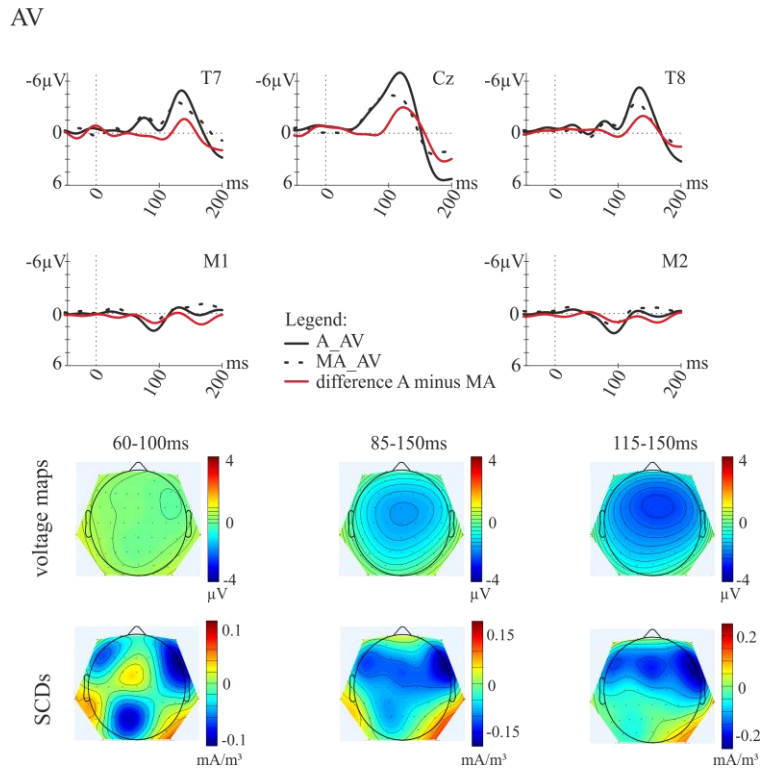
Additional file 1

AS



AM

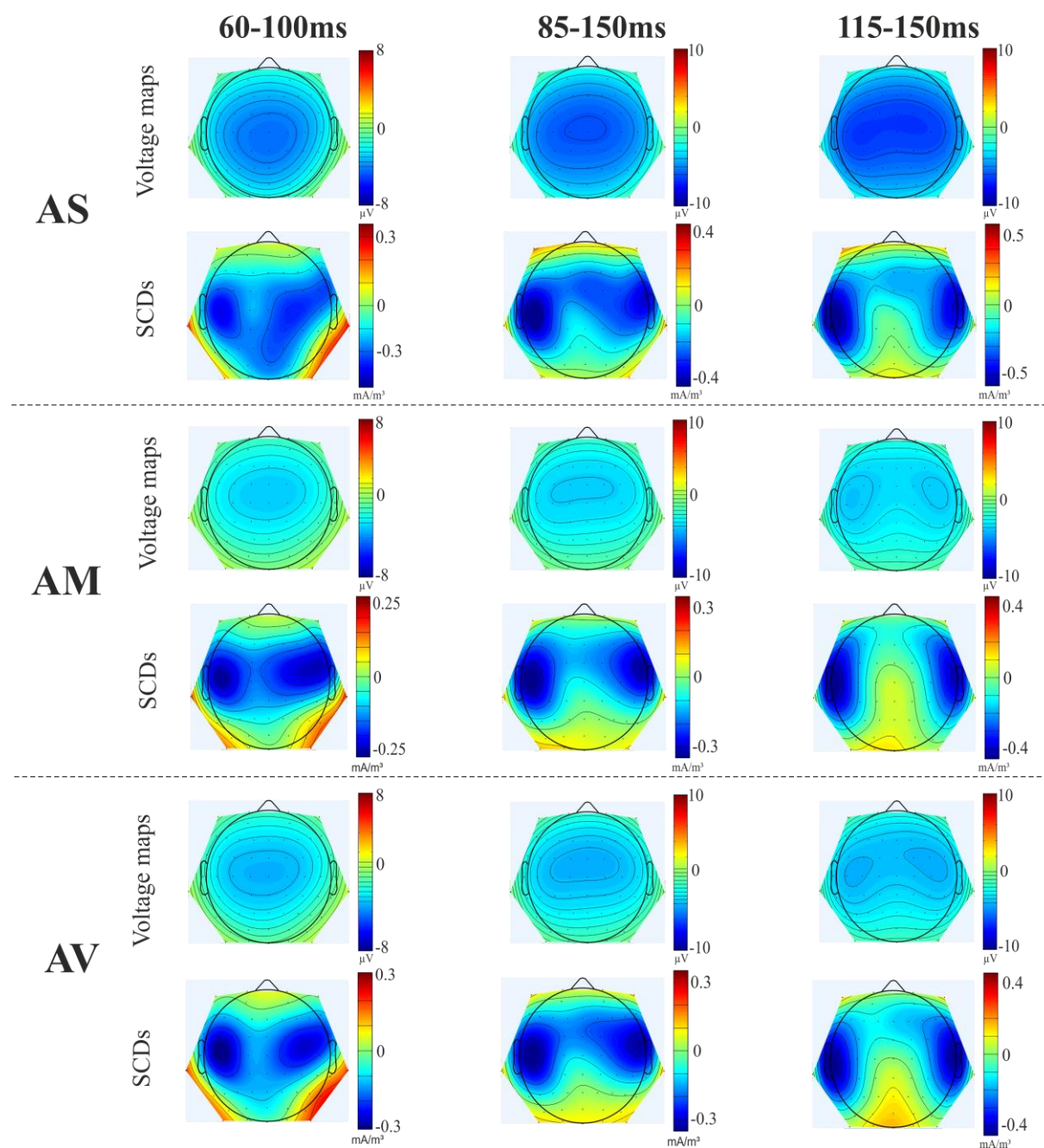




**Figure 23: Grand-average ERPs of single attention conditions**

Grand-average ERP waves elicited by externally-initiated sounds (black solid line) and self-initiated sounds (black dotted line), separately for the single attention conditions *Attention Sounds* (AS), *Attention Motor* (AM) and *Attention Visual* (AV) at temporal and central electrodes and the mastoids. The corresponding difference waves (externally-initiated minus self-initiated) are depicted in red. Voltage maps and scalp current densities (SCDs) of the difference wave during the latency ranges of the N1a (60-100 ms), N1b (85-150 ms) and N1c (115-150 ms) time window are also depicted.

## Additional file 2

**Figure 24: Attention effect for single attention conditions**

Voltage maps and scalp current densities (SCDs) of the attention effects for the single attention conditions *Attention Sounds (AS)*, *Attention Motor (AM)* and *Attention Visual (AV)* during the latency ranges of the N1a (60-100 ms), N1b (85-150 ms) and N1c (115-150 ms) time window are depicted.





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### List of Abbreviations

°	Degree
μV	Microvolt
Ag-AgCl	Silver-silverchlorid
ANOVA	Analysis of Variance
CNS	Central nervous system
dB	Decibel
EEG	Electroencephalography
EOG	Electrooculography
ERP	Event-Related Potential
fMRI	functional Magnetic Resonance Imaging
HEOG	Horizontal Electrooculography
Hz	Hertz
MEG	Magnetoencephalogram
ms	Milliseconds
PET	Positron Emission Tomography
PSS	Point of Subjective Simultaneity
RT	Reaction Time
s	Seconds
SCD	Scalp Current Densities
SD	Standard Deviation
SOA	Stimulus Onset Asynchrony
TMS	Transcranial Magnetic Stimulation
VEOG	Vertical Electrooculography

### Summary

One of the fundamental functions of the human brain is to predict sensory consequences of our own voluntary actions. In auditory information processing, self-initiated sounds evoke a smaller N1 and/or P2 component of the auditory event-related brain potential (ERP) than passive sound exposure of the same sound sequence (Schafer & Marcus, 1973). It has been proposed that such sensory attenuation effects in response to self-initiated sounds indicate the functions of internal forward models, an idea that relates to the refference principle (von Holst & Mittelstaedt, 1950) and the concept of corollary discharge (Sperry, 1950) in physiological literature. Specifically, those models assume that whenever a voluntary action is performed, a forward model receives a copy of the current motor command and predicts the expected sensory consequences. Actual sensory consequences that match the prediction are attenuated (Tsakiris & Haggard, 2005). The prediction also enables differentiating the sensory consequences of one's own actions from other sensory input. Thus, it has been argued that forward model predictions allow the mind to attribute actions to agents and particularly to the self (Blakemore et al., 2002; Frith et al., 2000). This so-called sense of agency is normally understood as the experience that we are the cause of our own actions and their sensory consequences (Gallagher, 2000).

The assumption that N1 and/or P2 attenuation effects to self-initiated sounds depend on internal forward model predictions is supported by numerous studies (Aliu et al., 2009; Baess et al., 2011; Bäсс et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; Knolle et al., 2013; Knolle, Schröger, & Kotz, 2012; Kühn et al., 2011; Martikainen et al., 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973). However, less complex and non-predictive explanations such as attentional influences or mere temporal contiguity between motor action and sound have been proposed recently to explain auditory attenuation effects to self-initiated sounds (Horváth et al., 2012; Horváth, 2013a, 2013b; Hughes et al., 2012; Makeig et al., 1996; SanMiguel et al., 2013; Tsakiris & Haggard, 2005). Furthermore, little is known about how N1 and/or P2 attenuation effects are related to the sense of agency, which is thought to be directly linked to predictive sensorimotor signals processed within internal forward models (Haggard, 2005). Thus, the aim of the present thesis was to further investigate the nature of the N1 and/or P2 attenuation effect to self-initiated sounds and to examine its specific relationship to the sense of agency.

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In the first experiment, it was investigated to which extent the N1 attenuation effect to self-initiated sounds can be explained by a differential allocation of attention to self-initiated and externally-initiated sounds. To test this, the allocation of attention to the sounds was varied over several levels and its influence on the N1 attenuation effect was determined. That is, attention was either directed to the sounds or was directed away from the sounds towards the own motor behavior or visual stimulation. It was hypothesized that if attention causes the N1 attenuation effect, then manipulating attention should affect the effect for self-initiated sounds. In contrast, if the N1 attenuation effect reflects the workings of an internal predictive forward model, the attenuation effect to self-initiated sounds was expected to be unaffected by an attentional difference. The results show that the N1 attenuation was equally large and of equal distribution when participants directed their attention towards the sound and when they directed their attention away from the sounds, towards the button presses or the visual stimuli. Thus, the self-initiation effect can hardly be explained by the differential amount of attention devoted to self- and externally-initiated sounds. Instead, the findings support the notion that the N1 attenuation effect for self-initiated sounds seems to reflect the activity of an internal predictive mechanism.

The second experiment focused on the specific relationship between N1 and/or P2 attenuation effects to self-initiated sounds and the feeling of agency. Specifically, it was investigated whether attenuation effects of the auditory N1 and P2 component to self-initiated sounds can be explained by brain activity involved in movement planning (where conscious motor intention and the corresponding feeling of agency are thought to arise) rather than movement execution. Therefore, ERPs in response to a sound initiated by a button press were recorded. In one condition, participants moved a finger to press the button voluntarily, whereas, in another condition, a similar, but involuntary, finger movement was initiated by stimulating the corresponding region of the primary motor cortex with transcranial magnetic stimulation (TMS). For involuntary movements no movement intention (and no feeling of agency) could be formed, thus no motor plans were available to the forward model. It was hypothesized that predictive signals involved in the processing of self-initiated sounds are sent during movement planning rather than movement execution. Consequently, an attenuation of the N1 and/or P2 response was expected only for voluntary movements, but not for involuntary movements, because no predictive signals should be available to the predictive forward model during involuntary movements. The results indicate attenuated N1 and P2 amplitudes following voluntary, self-initiated, movements, but not following movements initiated by

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motor cortex stimulation. Thus, the present findings demonstrate that the origin of the sensory attenuation of brain responses to self-initiated sounds is prior to motor cortex activation. That is, the intention to move and the corresponding feeling of agency rather than the mere movement execution seem to play an essential role for the attenuation of the auditory N1 and P2 component. Taken together, the results support the assumptions of a predictive internal forward-model account operating prior to primary motor cortex activation.

To examine the relation between N1 and/or P2 attenuation effects to self-initiated sounds and explicit judgments of agency, Experiment 3 and 4 were conducted. The idea was to apply a “judgment of agency illusion” to manipulate judgements of agency during self-initiation of sounds in an appropriate way and to study corresponding N1 and/or P2 attenuation effects in conditions where agency was perceived or not (although the sound was always self-initiated, that is, predictive signals were always available to the internal forward model).

Thus, the third experiment addressed the question whether such an illusory perception of agency for self-initiated sounds can be created experimentally. To this end, a recently reported temporal order illusion of intentional actions and their subsequent sensory effects (Stetson et al., 2006) was used and its association to judgments of agency was tested. That is, the probability of time intervals between voluntary button presses and sounds was manipulated, such that trials with identical delays between button press and sound prompted different perceptions of temporal order. Participants were asked to rate their sense of agency in these different conditions. Assuming a strong association between temporal order- and agency judgments, it was hypothesized that participants would report no experience of agency in trials in which button press and sound are perceived in reversed order. The results show an absence of the sense of agency in a condition in which sounds were falsely perceived as preceding motor acts relative to the perceived temporal order in the control condition. This finding suggests a strong association between the sense of agency and the temporal order perception of actions and their consequences. Moreover, the results provide further evidence that motor intentions partly determine human time perception.

In the fourth experiment the relationship between N1 and/or P2 attenuation effects to self-initiated sounds and agency judgments was directly tested, making use of the “judgment of agency illusion” demonstrated in the third experiment. To this end, ERPs in response to sounds initiated by button presses were recorded. In one condition, participants perceived

agency over the production of the sounds, whereas, in another condition, participants experienced an illusory lack of agency. Importantly, the action-effect sequence was physically identical in both conditions, only the judgment of agency differed between conditions. Based on the hypothesis that predictive sensorimotor signals contribute to both sensory attenuation and agency judgments, it was expected to find attenuated auditory N1 and/or P2 components only when participants perceived agency but not when participants experienced an illusory lack of agency over the production of the sound. The findings demonstrate sensory attenuation irrespective of agency experience. Sensory attenuation was indicated by reduced amplitudes of the auditory N1 component in response to self-initiated sounds. Thus, the present data provide direct evidence that sensory attenuation of brain responses to self-initiated sounds and agency judgments are independent. Taken together, the present results show that N1 attenuation effects depend on whether the action was planned and intended rather than on the comparison of predicted and actual sensory consequences of the action. Furthermore, they are in favor of the assumption that the sense of agency represents a combination of predictive and inferential mechanisms (Synofzik et al., 2008).

Taken together, the findings of the present thesis provide evidence that N1 and/or P2 attenuation effects to self-initiated sounds are mainly determined by movement intention and predictive internal motor signals involved in movement planning, supporting the assumptions of the internal forward model theory. The present data further rule out an attentional explanation of the previously reported attenuation effects to self-initiated sounds (Aliu et al., 2009; Baess et al., 2011; Bässl et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; Knolle et al., 2013; Knolle, Schröger, & Kotz, 2012; Kühn et al., 2011; Martikainen et al., 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973). Importantly, it was shown that sensory attenuation effects in audition are directly related to the feeling of agency, but occur independent of agency judgments. Based on the literature and the present results, the current thesis proposes a predictive model of auditory information processing of the acting self, integrating movement intention, different representations of the sense of agency and N1 and/or P2 attenuation effects to self-initiated sounds. In conclusion, the present thesis offers new insights in how action-driven predictions of the self in action influence auditory information processing.



### Zusammenfassung

Eine der grundlegenden Funktionen des menschlichen Gehirns ist es, die sensorischen Konsequenzen unserer eigenen Handlungen vorherzusagen. Es wurde gezeigt, dass bei der Verarbeitung auditiver Informationen selbst-initiierte Töne eine kleinere N1 und/oder P2 Komponente des auditorischen Ereignis-korrelierten Potentials (EKP) evozieren als physikalisch identische extern-initiierte Töne (Schafer & Marcus, 1973). Es wird angenommen, dass diese sensorischen Abschwächungseffekte für selbst-initiierte Töne das Wirken von internalen, prädiktiven Vorwärts-Mechanismen anzeigen, eine Idee, welche auf früheren physiologischen Konzepten wie denen des Reafferenzprinzips (von Holst & Mittelstaedt, 1950) oder des ‘Corollary Discharge‘ Mechanismus (Sperry, 1950) beruht. Dabei gehen solche kognitiven Modelle davon aus, dass bei jeder selbst-initiierten Handlung eine ‘Efferenzkopie‘ des motorischen Kommandos in ein Vorwärts-Modell eingespeist wird, welches dann Vorhersagen (d.h. Prädiktionen) der erwarteten sensorischen Konsequenzen der Handlung generiert. Diese Prädiktionen werden dann an die entsprechenden sensorischen Areale gesendet und mit den tatsächlich eintreffenden sensorischen Konsequenzen verglichen. Im Falle einer Übereinstimmung werden die eintreffenden sensorischen Konsequenzen abgeschwächt (Tsakiris & Haggard, 2005). Die erfolgreiche Prädiktion sensorischer Konsequenzen ermöglicht somit die Differenzierung des sensorischen Inputs unserer eigenen Handlungen von anderem sensorischen Input. Folglich wird angenommen, dass Vorwärts-Prädiktionen es uns erlauben, Handlungen zu Handelnden und insbesondere uns selbst zuzuordnen (Blakemore et al, 2002; Frith et al, 2000). Dieses sogenannte Erleben der eigenen Urheberschaft (‘sense of agency‘) beschreibt daher die Erkenntnis, dass wir selbst unsere Handlungen und die daraus resultierenden sensorischen Konsequenzen erzeugen (Gallagher, 2000).

Die Annahme, dass N1 und/oder P2 Abschwächungseffekte bei selbst-initiierten Tönen das Wirken von internalen, prädiktiven Vorwärts-Mechanismen anzeigen, wird durch zahlreiche Studien unterstützt (Aliu et al., 2009; Baess et al., 2011; Bäss et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; Knolle et al., 2013; Knolle, Schröger, & Kotz, 2012; Kühn et al., 2011; Martikainen et al., 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973). Jedoch wurden kürzlich weniger komplexe und nicht-prädiktive Modelle vorgeschlagen, um die auditiven Abschwächungseffekte für selbst-initiierte Töne zu erklären

(Horváth et al., 2012; Horváth, 2013a, 2013b; Hughes et al., 2012; Makeig et al., 1996; SanMiguel et al., 2013; Tsakiris & Haggard, 2005). So wurde beispielsweise postuliert, dass aufmerksamkeitsbedingte Einflüsse oder aber die bloße zeitliche Nähe zwischen motorischer Handlung und Ton die berichteten Effekte erklären könnten (Horvath et al., 2012). Darüber hinaus ist wenig bekannt, in welcher Weise N1 und/oder P2 Abschwächungseffekte bei selbst-initiierten Tönen mit dem Erleben der eigenen Urheberschaft verbunden sind, von welchem angenommen wird, dass es direkt an prädiktive sensomotorische Signale internaler Vorwärts-Mechanismen gebunden ist (Haggard, 2005). Folglich ist das primäre Ziel der vorliegenden Arbeit, die Erforschung der zugrundeliegenden Mechanismen der N1 und/oder P2 Abschwächungseffekte für selbst-initiierte Töne und deren spezifische Beziehung zu dem Erleben der eigenen Urheberschaft weiter voranzutreiben.

Im ersten Experiment wurde untersucht, in welchem Maß die berichteten N1 Abschwächungseffekte für selbst-initiierte Töne durch die unterschiedliche Verteilung von Aufmerksamkeit auf selbst-initiierte und extern-initiierte Töne erklärt werden können. Um dies zu testen, wurde die Verteilung der Aufmerksamkeit auf die Töne über mehrere Ebenen variiert und deren Einfluss auf die Abschwächung der N1 Komponente bestimmt. Das heißt, die Aufmerksamkeit wurde entweder auf die Töne gerichtet oder aber wurde von den Tönen weg, in Richtung der eigenen motorischen Handlung oder einer visuellen Stimulation gerichtet. Im Falle, dass Aufmerksamkeit die Abschwächung der N1 Komponente bewirkt, sollte die Manipulation der Aufmerksamkeit den Effekt für selbst-initiierte Töne beeinflussen. Wenn hingegen die Abschwächung der N1 Komponente das Wirken eines internalen, prädiktiven Vorwärts-Mechanismus widerspiegelt, sollten N1 Abschwächungseffekte unabhängig von der Aufmerksamkeitsmanipulation auftreten. Die Ergebnisse zeigen gleichgroße und gleichverteilte N1 Abschwächungseffekte für selbst-initiierte Töne, wenn Probanden ihre Aufmerksamkeit entweder auf Töne, eine motorische Handlung oder eine visuelle Stimulation richteten. Somit kann der Selbst-Initiierungseffekt nicht durch eine unterschiedliche Verteilung der Aufmerksamkeit auf selbst-initiierte und extern-initiierte Töne erklärt werden. Stattdessen unterstützen die Ergebnisse die Annahme, dass N1 Abschwächungseffekte für selbst-initiierte Töne das Wirken eines internalen, prädiktiven Vorwärts-Mechanismus reflektieren.

Im zweiten Experiment wurde die spezifische Beziehung zwischen N1 und/oder P2 Abschwächungseffekten für selbst-initiierte Töne und dem prä-reflexiven Erleben der eigenen

Urheberschaft untersucht. Genauer gesagt wurde getestet, ob Abschwächungseffekte der auditorischen N1 und P2 Komponenten für selbst-initiierte Töne durch Hirnaktivität erklärt werden können, welche in der Planung und nicht der Ausführung einer Bewegung involviert ist. Es wird angenommen, dass die Bewegungsplanung eng mit einer Bewegungsintention verbunden ist und dass während dieser Prozesse das prä-reflexive Erleben der eigenen Urheberschaft entsteht. Um dies zu testen, wurden EKPs in Reaktion auf einen Ton, welcher mit einem Tastendruck initiiert wurde, aufgezeichnet. In einer Bedingung drückte der Proband den Knopf freiwillig, während in einer zweiten Bedingung eine ähnliche, aber unfreiwillige Fingerbewegung durch die Stimulierung des entsprechenden Bereichs des primären motorischen Kortex mit transkranieller Magnetstimulation (TMS) initiiert wurde. Für unfreiwillige Bewegungen konnte somit keine Bewegungsintention (und kein prä-reflexives Erleben der eigenen Urheberschaft) gebildet werden, sodass keine motorischen Handlungspläne für den Vorwärts-Mechanismus verfügbar waren. Es wurde vermutet, dass prädiktive Signale, welche in die Verarbeitung selbst-initiiertes Töne involviert sind, während der Bewegungsplanung und nicht während der Bewegungsausführung gesendet werden. Folglich wurde eine Abschwächung der N1 und P2 Komponenten nur für willkürliche Bewegungen, jedoch nicht für unwillkürliche Bewegungen erwartet, da dem Vorwärts-Mechanismus keine prädiktiven Signale für unwillkürliche Bewegungen zur Verfügung standen. Die Ergebnisse zeigen eine Abschwächung der N1 und P2 Amplituden nur für freiwillige, selbst-initiierte Bewegungen, aber nicht für Bewegungen, welche von einer Stimulation des motorischen Kortex initiiert wurden. Somit demonstrieren die vorliegenden Ergebnisse, dass N1 und P2 Abschwächungseffekte für selbst-initiierte Töne vor der Aktivierung der primären motorischen Kortex entstehen. Das heißt, eine Bewegungsintention und das begleitende prä-reflexive Erleben der eigenen Urheberschaft - und nicht die Bewegungsausführung - spielen eine entscheidende Rolle für die Abschwächungseffekte der auditorischen N1 und P2 Komponenten. Zusammenfassend unterstützen die Ergebnisse die Annahmen eines prädiktiven, internalen Vorwärts-Mechanismus, welcher vor der Aktivierung des primären motorischen Kortex agiert.

Um die Beziehung zwischen N1 und P2 Abschwächungseffekten für selbst-initiierte Töne und expliziten Urteilen der eigenen Urheberschaft zu untersuchen, wurden zwei weitere Experimente durchgeführt. Die Idee war, eine Illusion über eigene Urheberschafts-Urteile zu erzeugen. Somit sollten die Urteile der eigenen Urheberschaft während der Selbst-Initiierung von Tönen in angemessener Weise manipuliert werden und begleitende N1 und/oder P2

Abschwächungseffekte in Situationen unterschiedlicher Urheberschafts-Urteile analysiert werden. Tatsächlich jedoch wurden die Töne immer selbst-initiiert, sodass dem Vorwärts-Mechanismus immer prädiktive Signale zur Verfügung standen. Demzufolge befasste sich das dritte Experiment mit der Frage, ob eine solche illusorische Wahrnehmung der eigenen Urheberschaft für selbst-initiierte Töne experimentell erzeugt werden kann. Zu diesem Zweck wurde eine kürzlich berichtete Illusion der zeitlichen Reihenfolge von intentionalen Handlungen und sensorischen Konsequenzen (Stetson et al., 2006) verwendet und ihre Verbindung zu expliziten Urheberschafts-Urteilen getestet. Das heißt, die Wahrscheinlichkeit von zeitlichen Intervallen zwischen freiwilligen Tastendrücken und Tönen wurde dahingehend manipuliert, dass Durchgänge mit identischen zeitlichen Verzögerungen zwischen Tastendruck und Ton eine unterschiedliche Wahrnehmung der zeitlichen Reihenfolge der Ereignisse bei den Probanden hervorriefen. Die Probanden wurden in diesen unterschiedlichen Bedingungen gebeten, ein Urteil über die eigene Urheberschaft abzugeben. Unter der Annahme, dass Urteile über die zeitliche Reihenfolge von Ereignissen und Urteile über die eigene Urheberschaft unmittelbar miteinander verbunden sind, wurde vermutet, dass die Probanden keine eigene Urheberschaft berichten würden, wenn Tastendruck und Ton in umgekehrter zeitlicher Reihenfolge wahrgenommen wurden. Die Ergebnisse zeigen ein Fehlen des Urteils der eigenen Urheberschaft für eine fälschlicherweise umgekehrt wahrgenommene zeitliche Reihenfolge von Tastendruck und Ton. Dieser Befund deutet auf eine starke Assoziation zwischen Urheberschafts-Urteilen und der Wahrnehmung der zeitlichen Reihenfolge von Handlungen und ihren sensorischen Konsequenzen hin. Darüber hinaus liefern die Ergebnisse einen weiteren Beweis dafür, dass Bewegungsintentionen zumindest teilweise die menschliche Zeitwahrnehmung bestimmen.

Im vierten Experiment wurde die Beziehung zwischen N1 und/oder P2 Abschwächungseffekten für selbst-initiierte Töne und expliziten Urteilen der eigenen Urheberschaft unter Anwendung der im dritten Experiment berichteten 'eigenen Urheberschafts-Illusion' direkt getestet. Zu diesem Zweck wurden EKPs in Reaktion auf Töne, welche durch Tastendrücke ausgelöst wurden, aufgezeichnet. In einer Bedingung nahmen die Probanden die eigene Urheberschaft wahr, während in einer anderen Bedingung aufgrund einer perzeptuellen Illusion keine eigene Urheberschaft wahrgenommen wurde. Wichtig ist hierbei, dass die Sequenz von Handlung und sensorischer Konsequenz in beiden Bedingungen physikalisch identisch war und sich die Bedingungen lediglich durch die unterschiedlichen Wahrnehmungen über die eigene Urheberschaft unterschieden. Basierend

auf der Hypothese, dass prädiktive sensomotorische Signale sowohl zu N1 und/oder P2 Abschwächungseffekten für selbst-initiierte Töne als auch zu eigenen Urheberschafts-Urteilen beitragen, wurden abgeschwächte N1 und/oder P2 Komponenten lediglich dann erwartet, wenn Probanden eine eigene Urheberschaft wahrnahmen, jedoch nicht, wenn keine eigene Urheberschaft berichtet wurde. Die Ergebnisse zeigen N1 Abschwächungseffekte für selbst-initiierte Töne unabhängig von eigenen Urheberschafts-Urteilen. Die Daten beweisen somit, dass sensorische Abschwächungseffekte von Hirnantworten auf selbst-initiierte Töne und explizite Urheberschafts-Urteile unabhängig voneinander auftreten. Zusammenfassend verdeutlichen die vorliegenden Befunde, dass N1 Abschwächungseffekte hauptsächlich davon abhängen, ob eine Handlung geplant oder intendiert war und nicht primär von einem Vergleich der vorhergesagten und tatsächlichen sensorischen Konsequenzen der Handlung. Weiterhin sprechen die Ergebnisse für die Annahme, dass das Erleben der eigenen Urheberschaft eine Kombination aus prädiktiven und schlussfolgernden Mechanismen darstellt (Synofzik et al., 2008).

Zusammenfassend liefern die Ergebnisse der vorliegenden Arbeit Hinweise darauf, dass N1 und/oder P2 Abschwächungseffekte für selbst-initiierte Töne hauptsächlich durch Bewegungsintentionen und internale, prädiktive motorische Signale, welche in die Bewegungsplanung involviert sind, bestimmt wird. Somit unterstützen die präsentierten Ergebnisse die Annahmen eines internalen, prädiktiven Vorwärts-Mechanismus. Weiterhin schließen die vorliegenden Daten eine aufmerksamkeitsbasierte Erklärung bisher beschriebener N1 und/oder P2 Abschwächungseffekte für selbst-initiierte Töne aus (Aliu et al., 2009; Baess et al., 2011; Bäss et al., 2008; Ford et al., 2007; Knolle, Schröger, Baess, et al., 2012; Knolle et al., 2013; Knolle, Schröger, & Kotz, 2012; Kühn et al., 2011; Martikainen et al., 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973). Es konnte weiterhin gezeigt werden, dass auditorische Abschwächungseffekte direkt mit dem prä-reflexiven Erleben der eigenen Urheberschaft verbunden sind, jedoch unabhängig von expliziten Urheberschafts-Urteilen auftreten. Basierend auf der vorhandenen Literatur und den vorliegenden Ergebnissen wird ein prädiktives Modell der auditiven Informationsverarbeitung des handelnden Selbst vorgeschlagen, welches die Konzepte der Bewegungsintention, verschiedene Repräsentationen des Erlebens der eigenen Urheberschaft und N1 und/oder P2 Abschwächungseffekte für selbst-initiierte Töne integriert. Zusammenfassend leistet die vorliegende Arbeit einen Beitrag zum Verständnis handlungsgetriebener Prädiktionen des handelnden Selbst und deren Einfluss auf die Verarbeitung auditiver Informationen.



# Curriculum Vitae

## Personal Information

Name                      Jana Timm  
Date of birth             July 9<sup>th</sup>, 1986  
Place of birth            Zeulenroda, Germany

## Academic Education and Career

11/2011-07/2012      Research visit at the International Laboratory for Brain, Music and Sound Research (BRAMS), Montréal, Canada (Prof. Dr. Marc Schönwiesner), Erasmus Mundus Auditory Cognitive Neuroscience (ACN) exchange stipend

07/2011                 Summer School on Auditory Cognition, Groningen, Netherlands (ACG)

since 10/2010         Research assistant and PhD student working on the Reinhart Koselleck project “Predictive modeling in audition” at the Institute of Psychology, Cognitive including Biological Psychology, University of Leipzig (Prof. Dr. Erich Schröger)

04/2009-09/2010      Student assistant working on the DFG project “Temporal window for auditory object representation (WAO): the role of segmentation for long sounds” and the Reinhart Koselleck project “Predictive modeling in audition” at the Institute of Psychology, Cognitive including Biological Psychology, University of Leipzig (Prof. Dr. Erich Schröger)

10/2006-09/2010      Studies of Psychology at the University of Leipzig, Diploma in Psychology

08/2001-06/2006      Grammar school (Schwalm-Gymnasium), Schwalmstadt-Treysa, Hessen, Germany, Degree: A-Level

08/1998-06/2001      Grammar school (Friedrich-Schiller-Gymnasium), Zeulenroda, Thüringen, Germany

## Awards:

12/2012                 Awardee of the “Nachwuchspreis” at the 11<sup>th</sup> Research Festival Leipzig

06/2011                 Erasmus Mundus Auditory Cognitive Neuroscience (ACN) research stipend





## **Publications and submitted work**

- Timm, J., Schönwiesner, M., SanMiguel, I., & Schröger, E. (under revision II). Sensation of agency and perception of temporal order.
- Timm, J., SanMiguel, I., Keil, J., Schröger, E., & Schönwiesner, M. (under revision II). Motor intention determines sensory attenuation of brain responses to self-initiated sounds.
- Keil, J., Timm, J., SanMiguel, I., Schulz, H., Obleser, J., & Schönwiesner, M. (under revision II). Cortical Brain States and Corticospinal Synchronization Influence TMS-evoked motor potentials.
- Timm, J., SanMiguel, I., Saupe, K., & Schröger, E. (2013). The N1-suppression effect for self-initiated sounds is independent of attention. *BMC Neuroscience*, 14, 2.
- Timm, J., Weise, A., Grimm, S., & Schröger, E. (2011). An Asymmetry in the Automatic Detection of the Presence or Absence of a Frequency Modulation within a Tone: A Mismatch Negativity Study. *Frontiers in Psychology*, 2, 189.

## **Publications in preparation**

- Timm, J., SanMiguel, I., Schönwiesner, M., & Schröger, E. (in prep). Agency judgments are independent of sensory attenuation of brain responses to self-initiated sounds.



## **Selbstständigkeitserklärung**

Hiermit erkläre ich, dass die vorliegende Arbeit ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt wurde und dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind. Die Arbeit ist in keinem früheren Promotionsverfahren angenommen oder abgelehnt worden.

Jana Timm

Leipzig, 12.09.2013