



Sensorimotor conflicts induce somatic passivity and louden quiet voices in healthy listeners

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ABSTRACT

Sensorimotor conflicts are known to alter the perception of accompanying sensory signals, and deficits in sensory attenuation have been observed in schizophrenia. In the auditory domain, self-generated tones or voices (compared to tones or voices presented passively or with temporal delays) have been associated with changes in loudness perception and attenuated neural responses. It has been argued that for sensory signals to be attenuated, predicted and sensory consequences must have a consistent spatiotemporal relationship, between button presses and reafferent signals, via predictive sensory signaling, a process altered in schizophrenia. Here, we investigated auditory sensory attenuation for a series of morphed voices while healthy participants applied sensorimotor stimulations that had no spatiotemporal relationship to the voice stimuli and that have been shown to induce mild psychosis-like phenomena. In two independent groups of participants, we report a loudening of silent voices and found this effect only during maximal sensorimotor conflicts (versus several control conditions). Importantly, conflicting sensorimotor stimulation also induced a mild psychosis-like state in the form of somatic passivity and participants who experienced stronger passivity lacked the sensorimotor loudening effect. We argue that this conflict-related sensorimotor loudness amplification may represent a reduction of auditory self-attenuation that is lacking in participants experiencing a concomitant mild psychosis-like state. We interpret our results within the framework of the comparator model of sensorimotor control, and discuss the implications of our findings regarding passivity experiences and hallucinations in schizophrenia.

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1. Introduction

Our capacity to process motor signals, their reafferent sensory consequences, and sensory prediction signals is crucial for motor control and perception (Jeannerod, 2006) and for updating internal models of the world (Schultz and Dickinson, 2000). Usually, motor and reafferent signals share similar features in the spatial and temporal domains and according to the comparator model (Blakemore et al., 2000b; Miall and Wolpert, 1996), movements are accompanied by prediction signals (of their sensory consequences), which are compared with the actual sensory feedback in a feed-forward manner. Under such conditions, spatiotemporal congruence between predicted and reafferent sensory signals is generally associated with self-attribution of the action (Braun et al., 2018; Gallagher, 2000) and the sense of agency: the feeling

of being in control of one's movement (Gallagher, 2000; Moore and Fletcher, 2012). A wealth of data has shown that incongruences or sensorimotor conflicts between predicted and reafferent sensory signals lead to the loss of agency and control (David et al., 2008; Farrer et al., 2008; Haggard et al., 2002; MacDonald and Paus, 2003; Sato and Yasuda, 2005; Stetson et al., 2006; Tsakiris et al., 2005).

Sensorimotor conflicts are also known to alter the perception of accompanying sensory signals. Processing of self-generated stimuli is known to be attenuated and proposed to result from a prediction-based cancellation of reafferent sensory signals (Bays et al., 2008; Blakemore et al., 2000a, 2000b; Wolpert and Flanagan, 2001). A well-known example is the sensory attenuation of self-generated touch: touches produced by oneself are perceived as weaker compared to externally produced ones, even if applied with the same intensity (Blakemore et al., 1999, 1998; Shergill et al., 2003). Moreover, sensorimotor conflicts accompanying self-generated touches can abolish self-attenuation and thus alter the associated tactile perceptions (Blakemore et al., 2000a, 2000b; Kilteni and Ehrsson, 2017a; Weiskrantz et al., 1971).

Perceptual alterations caused by sensorimotor conflicts of upper-limb movements have also been observed in sensory domains other

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than somatosensation. For instance, studies reported a change in loudness perception of self-generated tones (by a button press), compared to tones presented passively (Sato, 2008; Stenner et al., 2014; Weiss et al., 2011a, 2011b), which was associated with attenuated neural responses (Bansal et al., 2018; Lange, 2011; Martikainen et al., 2005; Mifsud et al., 2016; Schafer and Marcus, 1973). Recent studies have demonstrated that such auditory-motor self-attenuation effects can also be obtained for more complex sounds, such as voices (Knolle et al., 2019; Pinheiro et al., 2018). Together, these studies show that motor activity (e.g. a button press) causally associated with the auditory feedback (e.g. a beep or the sound of one's voice) can cause perceptual alterations of the latter through a manipulation of its spatiotemporal contingencies.

In general, most of the previous work on sensory alterations based on sensorimotor processes has focused on the investigation of sensory cues for upper-limb actions (e.g. pressing a button). However, the concept of agency, sensorimotor processes and the comparator model have also been applied to movements of the body as a whole (e.g. gait; Kannape and Blanke, 2013, 2012; Menzer et al., 2010), thus affecting the full-body sensorimotor system associated with self-consciousness (Blanke and Metzinger, 2009; Park and Blanke, 2019). Extending previous robotic designs (Blakemore et al., 1999; Shergill et al., 2003; Weiskrantz et al., 1971), Hara et al. (2011) associated upper-limb sensory prediction signals with reafferent sensory signals at the participants' torso in order to alter the representation of this global, torso-centered bodily system. Using this robotic device, Blanke et al. (2014) were able to induce in healthy volunteers systematic changes in illusory own body perceptions (i.e. self-touch) and mild psychosis-like phenomena that depended on sensorimotor conflicts. Specifically, while applying asynchronous sensorimotor stimulation between upper-limb movements and tactile feedback on the back, participants reported somatic passivity (i.e. that tactile sensations are being imposed upon their body by somebody else) and felt being in a presence of a non-existing alien entity, phenomenologically resembling passivity experiences (Frith et al., 2000; Sass and Parnas, 2003, 2001) and presence hallucinations (Alderson-Day and Fernyhough, 2016; Critchley, 1955; Jaspers, 1990) observed in schizophrenia.

Here, we investigated whether such robotically-mediated sensorimotor conflicts that are able to induce a mild psychosis-like state (Blanke et al., 2014) can also alter voice perception. Alterations of voice perception are highly prevalent in schizophrenia in the form of auditory verbal hallucinations (AVH) – i.e. hearing voices in the absence of a speaker. Given the importance of the comparator model both for somatic passivity and AVH (Ford et al., 2007, 2001; Swiney and Sousa, 2014), we wanted to explore whether robotically-mediated sensorimotor conflicts (between upper-limb movements and tactile feedback on the back) in healthy participants induce changes in voice perception, resembling the auditory alterations and experiences observed in patients with schizophrenia – specifically loudness alterations (Griffith et al., 1995; Juckel et al., 2008, 2003) and self-other vocal confusion (Frith, 1987; Plaze et al., 2015; Stephane et al., 2018). In two independent experiments, participants were asked to perform repeated upper-limb movements (Blanke et al., 2014), which were conveyed as tactile feedback on their back by the robotic system (Hara et al., 2011). Participants applied sensorimotor stimulation either in a synchronous manner or with a delay while they also performed either the loudness or the self-other voice discrimination task.

2. Methods

2.1. Participants

Each of the two separate experiments involved 30 healthy participants from the general population. In experiment 1, nine participants were male (mean age \pm SD: 21.8 \pm 2.4 years) and in experiment 2, 14 participants were male (23.7 \pm 2.4 years). All participants were

right-handed according to the Edinburgh Handedness Inventory, fluent in French, and without any hearing deficits. Before participating in the experiment, they were screened for eligibility criteria by means of an anamnestic interview investigating medication and substance use, as well as a personal and family history of psychiatric or neurological disorders. Participants were naive to the purpose of the study, gave informed consent in accordance with institutional guidelines (Research project approved by the Comité Cantonal d'Ethique de la Recherche of Geneva) and the Declaration of Helsinki, and received monetary compensation (CHF 20/h).

2.2. Procedure and materials

We conducted two experiments with the same general procedure and experimental design. Experiment 1 consisted of two and Experiment 2 of three sessions. For the first session of both experiments, participants came with an acquaintance, who also participated in the study, and their voices were recorded. For the second and third sessions (auditory tasks), participants came individually.

2.2.1. Auditory tasks

Participants were recorded saying 10 words in French (Supplementary material). Audacity software was used to filter out the background noise and to normalize the recordings for average intensity (-12 dBFS) and duration (500 milliseconds). The pre-processed voice recordings were then entered into TANDEM-STRAIGHT (Kawahara et al., 2013) to generate voice morphs between two participants (e.g. a voice morph could contain 40% of person A's, 60% of person B's voice). Finally, copies of the voice morphs with different sound intensities were created and the resulting audio files were played to participants through a JBL Control 1 Pro speaker placed 1 m behind them.

During both auditory tasks (loudness, self-other), blindfolded participants repeatedly heard the same word twice, separated by 500 milliseconds. In the loudness task, both words contained the same ratio of the two voices (50% of both participants), but differed in sound intensity. In the self-other task, both words were equally loud, but contained a different ratio of the two voices. In the loudness task, participants reported which of the words they perceived as louder and in the self-other task which of the two words sounded more like their own voice.

Unbeknown to the participants, the first word in each word-pair always sounded the same (50% self-voice, -12 dBFS). The second word varied, either in sound intensity (for the loudness task) or in self-voice percentage (for the self-other task). Six sound intensity levels (dBFS: -14 , -13 , -12.5 , -11.5 , -11 , -10) and six voice ratios (% self-voice: 15, 30, 45, 55, 70, 85) were chosen based on extensive pilot testing.

2.2.2. Robotic system

The robotic system consisted of two integrated units: the front part – a commercial haptic interface (Phantom Omni, SensAble Technologies) – and the back part – a three degree-of-freedom robot (Hara et al., 2011). Participants were seated between the front and back robot and were asked to perform repeated poking movements with their right index finger using the front robot, which was replicated by the movements of the back robot, which applied corresponding touches on their back. This was done either in synchronous (without delay) or asynchronous (with 500 milliseconds delay) fashion, creating different degrees of sensorimotor conflict between the upper limb movement and somatosensory feedback on the back (Blanke et al., 2014).

Experiment 1 and 2 consisted of synchronous and asynchronous sensorimotor conditions. Experiment 2 contained two additional conditions. In the motor-baseline condition, participants performed movements on the front unit, but did not receive the corresponding somatosensory feedback by the back unit. In the touch-baseline condition, the experimenter (not the participant) performed the movements

on the front unit, but the participant received the corresponding somatosensory feedback by the back unit. These two conditions served as baselines, as there was no sensorimotor coupling.

In experiment 2 we also tested whether torso-centered tactile feedback (i.e. back) was necessary for the present effects (Park and Blanke, 2019). For this, we added two more conditions in which the same setup was used as in the synchronous and asynchronous conditions, except that tactile feedback was not applied to the back but to the left hand of the participants – i.e. the back unit was placed in front of the participants and adjusted to point downwards in the vertical axis in order to touch their left hand.

2.2.3. Experimental design

In experiment 1, participants performed two blocks of each auditory task (loudness and self-other) – one block in the synchronous and another block in the asynchronous condition. Each block started with 60 s of robot manipulation, without auditory stimulation, after which an auditory cue indicated the beginning of the actual auditory task. Throughout the auditory tasks, participants continued moving the robot. Importantly, auditory stimuli and participants' movements were not time-locked. Each block contained 60 trials (10 words, each presented with 6 stimulus intensities) presented in a randomized order. The order of tasks (self-other/loudness) and conditions (synchronous/asynchronous) was counterbalanced across participants. An Inter-trial interval of 1 to 1.5 s (randomly jittered), was added to avoid predictability of the stimuli. (Fig. 1). The experimental design was created in MATLAB 2017b with the Psychtoolbox library (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

In experiment 2, participants performed four blocks of the loudness task (synchronous, asynchronous, motor-baseline, touch-baseline) and two additional hand feedback blocks (hand-synchronous, hand-asynchronous). All were equivalent to the loudness-task blocks of experiment 1. The order of blocks was pseudorandomized across participants. In experiment 2, there was no self-other task.

In both experiments, we additionally assessed the subjective experience evoked by the combination of robotically-mediated sensorimotor conflicts and ambiguously-voiced stimuli. Thus, after the auditory tasks, participants performed additional questionnaire blocks in which they passively listened to the same voice morphs while manipulating the robot. For each experimental condition there was an additional block after which they rated several items on a previously used questionnaire (Blanke et al., 2014) (Supplementary material). In experiment 1, we added two blocks (synchronous, asynchronous). In Experiment 2 we added six blocks (synchronous, asynchronous, motor-baseline, touch-baseline, hand-synchronous, hand-asynchronous).

2.3. Statistical analysis

Data of experiment 1 were analyzed with mixed-effects logistic regressions with Response as dependent variable and Condition (synchronous, asynchronous) and Stimulus (levels: 1–6), together with their interaction, as fixed effects. The Response-variable indicates whether participants perceived a stimulus as louder (loudness task) or as sounding more like their own voice (self-other task) compared to the reference stimulus. Random effects included a by-subject random intercept. By-subject random slopes for the main effects were added following model selection based on maximum likelihood. Trials with reaction times greater or smaller than two interquartile ranges from the median for each subject were considered as outliers and excluded.

Analysis for experiment 2 followed a similar approach (two logistic mixed-effects models with Response as a dependent variable). The first model was designed to assess the joint effects of synchrony and location of sensorimotor conflicts, including Condition (synchronous, asynchronous), Location (torso, hand) and Stimulus (levels: 1–6) with interaction terms as fixed effects. The second model extended the first one by investigating the effects of the sensorimotor coupling, regardless of the location. Therefore, it included no main effect of Location and the main effect of Condition had three instead of two levels (synchronous, asynchronous, baseline).

For both experiments, a linear mixed-effects regression was also performed with Reaction Times as a dependent variable, however, as it showed no significant differences between experimental conditions, the results are placed in the Supplementary material.

Questionnaire ratings were assessed by a mixed-effects linear regression and analyzed jointly for experiment 1 and 2, to increase statistical power. As fixed effects, we entered Condition (synchronous, asynchronous) and Question (q1 – q9) with interaction term into the model. As random effects, we had by-subject random intercepts. All analyses were performed with R (R Core Team, 2020), using notably the afex (Singmann et al., 2019), ggplot2 (Wickham, 2016), sjplot (Lüdtke, 2018), lme4 (Bates et al., 2015), and lmerTest (Kuznetsova et al., 2018) packages.

3. Results

3.1. Auditory task

3.1.1. Experiment 1 (loudness, self-other)

A mixed-effects logistic regression on loudness judgment revealed higher intercepts in the asynchronous compared to the synchronous condition (estimate = -0.39 , $Z = -2.14$, $p = 0.03$). The model had a

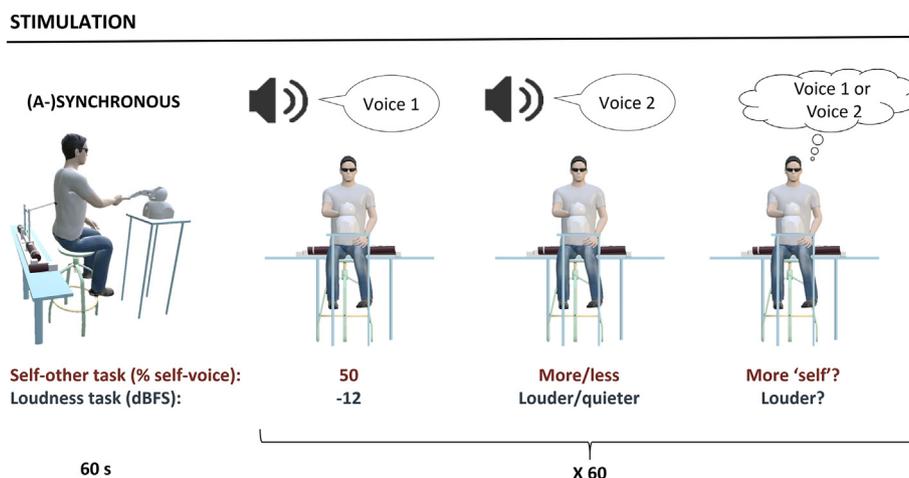


Fig. 1. Experimental block design.

main effect of Stimulus (estimate = 0.59, $Z = 9.50$, $p < 0.001$) and showed no interaction between the Condition and Stimulus (estimate = 0.08, $Z = 0.05$, $p = 0.12$). Following the visual inspection of the results, we performed the same mixed effects logistic regression for each Stimulus level. Results showed that voices were perceived significantly louder in the asynchronous condition only for the lowest sound intensity level (estimate = -0.5 , $Z = -2.49$, $p = 0.01$) (Fig. 2, left), whereas none of the other stimulus levels differed between conditions (Supplementary material).

Concerning the self-other discrimination task, a mixed-effects logistic regression indicated a main effect of Stimulus (estimate = -2.36 , $Z = -6.46$, $p < 0.001$). Intercepts of the synchronous and asynchronous conditions did not differ in the self-other task (estimate = -0.07 , $Z = -0.36$, $p = 0.72$), nor was there a significant interaction between the Condition and Stimulus (estimate = 0.02 , $Z = 0.36$, $p = 0.72$).

3.1.2. Experiment 2 (loudness, hand vs torso)

Experiment 2 replicated the loudness effect observed in experiment 1. In the model assessing both the synchrony and location of sensorimotor conflicts, the intercepts were again significantly higher in the asynchronous compared to synchronous condition (estimate = -0.49 , $Z = -2.92$, $p < 0.01$). The responses differed across stimuli (estimate = 0.36 , $Z = 11.22$, $p < 0.001$), and there was a significant interaction between the effects of Condition and Stimulus (estimate = 0.12 , $Z = 2.51$, $p = 0.01$). Analogously to experiment 1, we performed the same mixed effects logistic regression for each Stimulus level, confirming that the difference in loudness perception between the conditions occurred only for the lowest sound intensity level (estimate = -0.35 , $Z = -2.66$, $p < 0.01$, for other levels see Supplementary material). There was no significant effect of Location (hand vs. torso) nor a significant interaction with other effects (Supplementary material).

We next addressed the effects of the sensorimotor stimulation, regardless of feedback location. In this model the intercept in the asynchronous condition was higher than the synchronous (estimate = -0.29 , $Z = -2.23$, $p = 0.03$) and the baseline (estimate = -0.51 , $Z = -3.34$, $p < 0.001$), whereas there was

no difference between the synchronous and baseline conditions (estimate = -0.17 , $Z = -1.29$, $p = 0.2$) (Fig. 3).

3.2. Subjective experience

As the linear mixed-model analysis revealed a significant interaction between the effects Question and Condition ($F(8, 1091.6) = 2.03$, $p = 0.04$), we ran a separate analysis for each Question. It revealed that participants experienced stronger somatic passivity in the asynchronous versus synchronous condition (Fig. 4, left) (estimate = -0.83 , $t(66.94) = -2.88$, $p < 0.01$) and rated illusory self-touch significantly stronger in the synchronous versus asynchronous condition (Fig. 4, right) (estimate = 0.64 , $t(67.54) = 2.56$, $p = 0.01$), without any significant differences between conditions in other questionnaire items (all $p > 0.05$).

3.3. Loudness task and subjective experience

To assess the relationship between significant questionnaire items and changes in loudness perception, we added a binary variable – Passivity and Self-touch – to the mixed-effects logistic regression assessing loudness task performance, with an interaction term. The variables indicated whether individual participants experienced the illusion assessed by the corresponding question. Thus, participants were divided in two groups – those with a positive asynchronous-synchronous rating difference (e.g. Passivity+) and those with a negative or zero difference (e.g. Passivity-). The analysis revealed a significant interaction between Passivity and Condition (estimate = 0.39 , $Z = 2.04$, $p = 0.04$), showing that loudness perception was altered only in Passivity- group, with no difference between conditions in Passivity+ group (Fig. 5) (Supplementary material). There were no significant interactions between Self-touch and Condition (Supplementary material).

Finally, we ran monotonic (Spearman) correlation analyses between the asynchronous-synchronous difference in loudness perception (named self-attenuation) and in questionnaire ratings (Passivity, Self-touch). We observed a significant negative relationship between

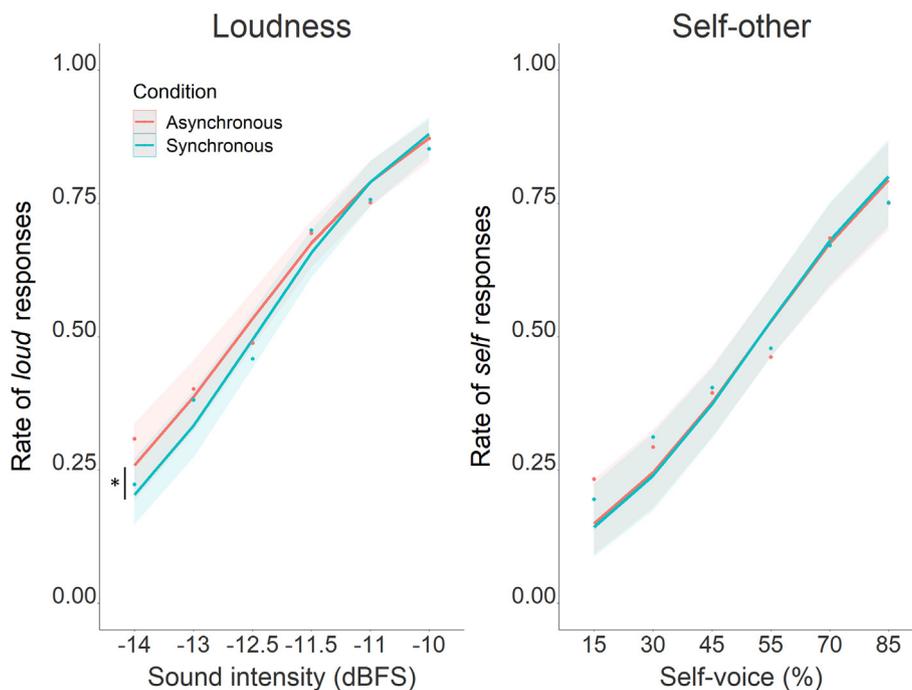


Fig. 2. Psychometric curves fitted for the two auditory tasks of experiment 1. The points indicate the rate at which the corresponding voice was perceived as louder (Loudness task) or more resembling own voice (Self-other task) than the baseline. The shaded areas around each curve represent the 95% confidence intervals. Intercept was significantly higher in the asynchronous condition and for the loudness task only, indicating that the quieter voices were perceived as louder. *: $p < 0.05$.

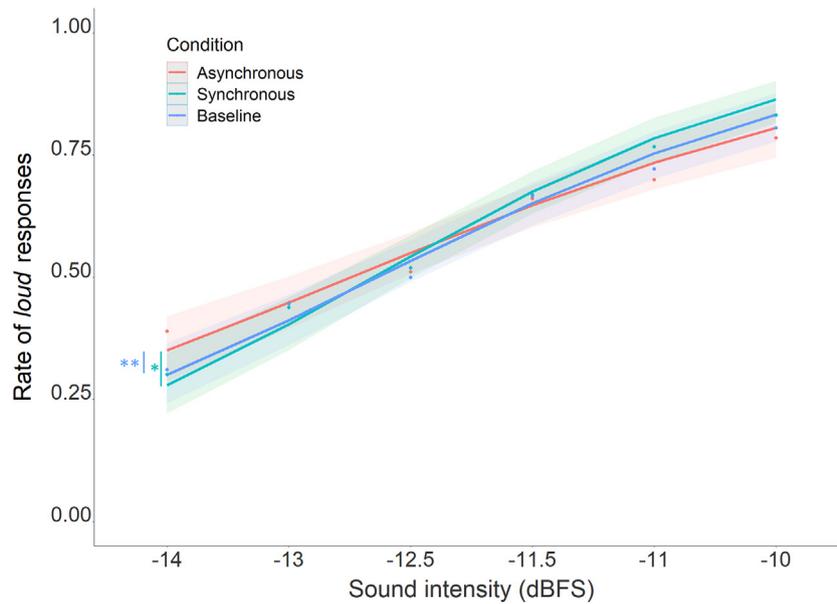


Fig. 3. In experiment 2, the intercept in the asynchronous condition was significantly higher than in the synchronous and the baseline conditions, whereas there was no difference between the synchronous and the baseline conditions. *: $p < 0.05$, **: $p < 0.01$.

self-attenuation and Passivity ($\rho = -0.3$, $p = 0.03$), and no significant relationship with Self-touch ($\rho = 0.2$, $p = 0.14$).

4. Discussion

Replicating the induction of somatic passivity based on sensorimotor stimulation in a healthy population using a robotic procedure (Blanke et al., 2014; Hara et al., 2014; Salomon et al., 2020) we investigated potential links with voice perception and clinical phenomenology (i.e. AVHs) and demonstrate that voice perception is modulated by sensorimotor stimulation with somatosensory feedback. We confirmed this somatosensory-motor effect on auditory perception in two independent cohorts in two studies. Specifically, quiet voices were perceived as louder in the asynchronous condition, differing from voices heard in synchronous and baseline conditions. This effect was reduced in participants experiencing somatic passivity.

Changes in perception during actions are usually interpreted within the comparator model framework: self-generated movements are accompanied by sensory predictions, which cause an attenuation of the

reafferent sensory signals, especially if they are received in spatiotemporal congruency (Blakemore et al., 2000a, 2000b; Miall and Wolpert, 1996). Thus, in order for the sensory signal to be attenuated, predicted and reafferent sensory consequences must have a consistent spatiotemporal relationship, such as pushing a response button with one's right index finger attenuating processing of tactile (Blakemore et al., 2000a, 2000b; Shergill et al., 2003) or auditory (Knolle et al., 2019; Martikainen et al., 2005) stimuli. Lack of predictive mechanisms is associated with decreases in sensory attenuation and perceived as amplification of the sensory stimuli accompanying actions (i.e. stronger touches (Kilteni and Ehrsson, 2017b; Shergill et al., 2003; Teufel et al., 2010) or louder sounds (Sato, 2008; Stenner et al., 2014; Weiss et al., 2011a, 2011b)).

The present findings extend sensory attenuation research in two ways. First, there was no time-locking between our participants' movements and the auditory stimuli they were asked to judge. Participants manipulated the robot independently from the sounds and the auditory task – ruling out the possibility that classical trial-by-trial sensory comparisons between an action and its sensory consequences account for the present loudness alterations, thereby suggesting a state-dependent

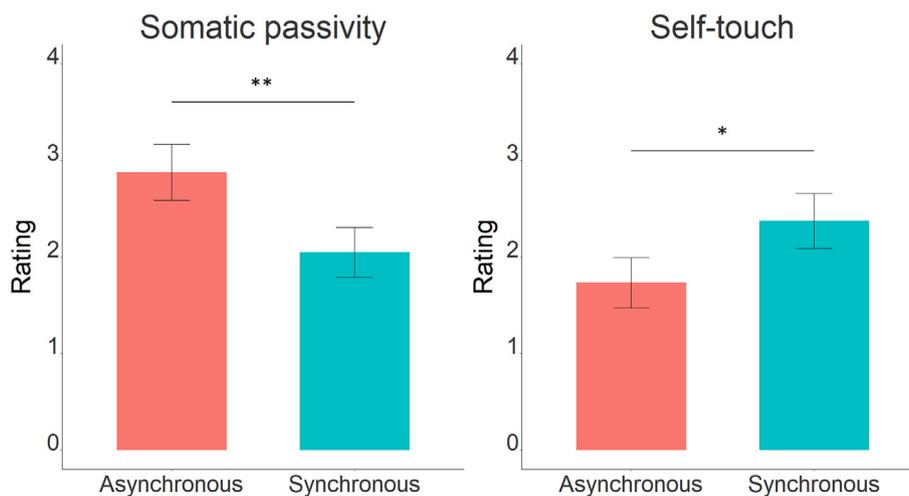


Fig. 4. Significant questionnaire items. Reported somatic passivity sensations were significantly higher in the asynchronous (left) and self-touch impressions in the synchronous condition (right). Abscissa of bar plots indicates the two experimental conditions and ordinate the corresponding Likert-scale ratings. The height of a bar plot indicates the mean rating and error bars its standard error. *: $p < 0.05$, **: $p < 0.01$.

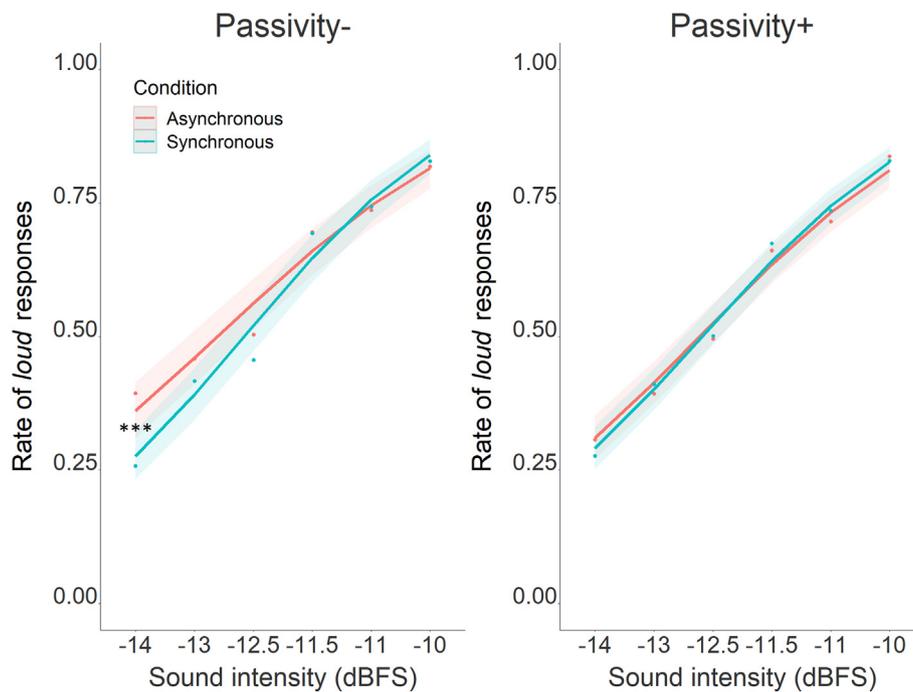


Fig. 5. Amplification of quiet voices was observed only for the participants not experiencing somatic passivity during the experiment (Passivity-, left). With somatic passivity (Passivity+, right), self-attenuation was reduced. ***: $p < 0.001$.

effect on perception. Secondly, perceptual changes in both experiments were only present in the asynchronous condition, accentuating the importance of temporal aspects (between movement and somatosensory feedback) of sensorimotor conflicts. In experiment 1 and 2, we observed a difference in loudness perception between the asynchronous and synchronous conditions. In experiment 2, we additionally observed that perception in the asynchronous condition is the deviating one, as it alone differed from baseline conditions. Crucially, the perception in the spatially-conflicting, yet synchronous condition did not differ from the no-conflict conditions (touch- and motor-baseline), suggesting that mainly the temporal conflict, present only in the asynchronous condition, drives the present perceptual effects. Temporal conflicts have been shown to cause a decrease in the sense of agency and self-attenuation, by manipulating sensory action consequences of upper-limb movements and related losses of hand movement agency (Farrer et al., 2008; Sato and Yasuda, 2005; Tsakiris et al., 2005). When extending such manipulations to a torso-centered bodily system (Blanke and Metzinger, 2009; Park and Blanke, 2019), more than just a decrease in the sense of agency, alterations in bodily self-consciousness manifested as other-agency sensations were introduced (Blanke et al., 2014; Salomon et al., 2020), together with an altered state of bodily self-consciousness (Blanke et al., 2014; Salomon et al., 2020). We argue that loudness amplification, observed solely in the asynchronous condition, may represent a state-dependent reduction of auditory self-attenuation, resulting from such other-agency-related alterations in bodily self-consciousness.

Deficits in self-attenuation have been observed in schizophrenia. While healthy participants overestimate the externally-applied stimulation, arguably due to sensory attenuation for actively produced movements, individuals with schizophrenia perform differently, suggesting a reduction of self-attenuation (Blakemore et al., 2000a, 2000b; Shergill et al., 2005), compatible with reduced differences in neural responses between self- and externally-generated sounds (Ford et al., 2007, 2001). Our results in healthy participants support this inverse relationship by demonstrating a reduction of auditory self-attenuation only in the hallucinating group. Specifically, we observed that the loudness effect, induced by concomitant asynchronous sensorimotor conflicts, was reduced in participants prone to experiencing somatic passivity,

thereby mimicking a reduction of self-attenuation commonly reported in schizophrenia. Moreover, the magnitude of the loudness effect negatively correlated with the strength of somatic passivity and this relationship was lacking for illusory self-touch, a sensation not involving an external agent. We propose that (1) torso-centered sensorimotor conflicts induce a state characterized by a self-to-other shift (Alderson-Day and Fernyhough, 2016; Krugwasser et al., 2019; Leptourgos and Corlett, 2020; Seghezzi et al., 2019) and speculate that this may (2) impose top-down effects (Corlett et al., 2019; Powers et al., 2017; Schmack et al., 2013; Sterzer et al., 2018; Teufel et al., 2010) on voice perception which resemble auditory self-attenuation. Similar to schizophrenia, (3) such effects on self-attenuation are reduced in participants experiencing a mild psychosis-like state in the form of somatic passivity. Further experimental, neuroimaging, and modeling work is needed to describe the underlying mechanisms in greater detail.

Differences in divided attention between asynchronous vs. synchronous conditions cannot account for these effects, because (1) both sensorimotor conditions contained a strong conflict and both induced an altered mental state (asynchronous: somatic passivity; synchronous: self-touch), because (2) reaction times revealed no differences between both sensorimotor conditions, and because (3) the effect was only observed in one auditory task. Although it is further known that auditory perception is altered during movement (Reznik and Mukamel, 2019), movements in the synchronous and motor-only conditions were not accompanied by changes in auditory perception, suggesting the necessity of a temporal conflict for the present loudness effect.

It remains unclear why the effect was bound to temporal sensorimotor conflicts (i.e. the delay between the movement and the corresponding touches), but did not depend on the tested spatial conflicts (i.e. hand versus back feedback). Previous research investigating spatiotemporal aspects in sensorimotor perception have used a large variety of paradigms, stimuli, and behavioral read-outs, hampering any direct comparison (e.g. Farrer et al., 2008; Kannape et al., 2010; Krugwasser et al., 2019). More work with several temporal sensorimotor delays and several spatial feedback locations and conflicts is necessary to investigate this issue.

The present sensorimotor conflicts did not affect self-other voice discriminability. A similar finding was observed in a previous study in psychotic patients (Salomon et al., 2020), where robotic-sensorimotor

stimulation did not induce errors in auditory-verbal self-monitoring in both healthy controls and in psychotic patients without passivity experiences, but only in psychotic patients with passivity. It might therefore be argued that self-other discrimination changes for auditory stimuli, as induced by the robot under the present experimental conditions, are not sufficient to induce similar auditory-verbal effects in individuals without inherent self-monitoring deficits, such as passivity sensations. Compared to the study of Salomon and colleagues, our study involved an auditory task employing voice-morphing technology, which is why we expected that it would be more susceptible to capturing such an effect in an adequately powered sample of healthy volunteers. Moreover, the presence of auditory-verbal effects in self-other voice discrimination might also depend on other methodological aspects that we did not test here (e.g. habituation effects, number of repetitions, different delays, etc.). Finally, it is possible that a motor component involving speech production is necessary to observe stronger misattribution of one's own voice in healthy individuals, as is argued to occur in AVHs (Frith, 1987; Moseley et al., 2013; Nazimek et al., 2012; Stephan et al., 2009). In the present study, we assessed differences in passive self-voice perception, thus involving predictive mechanisms related to the sensorimotor stroking, but not predictive mechanisms for speech itself. The orthogonal sensorimotor stimulation, as tested in the present experiments, changes loudness, but not identity of the heard voice.

To the best of our knowledge, this is the first study to demonstrate that temporal sensorimotor conflicts in the somatosensory domain can affect voice perception even if the auditory stimulus is not systematically linked to the movement. We found that healthy listeners heard quiet voices as louder when exposed to asynchronous sensorimotor stimulation related to somatic passivity experiences. We argue that this amplification represents a reduction in self-attenuation mechanisms, reminiscent of altered voice perception in psychiatric populations. Together, our findings extend the understanding of subjective and perceptual alterations caused by conflicting sensorimotor processing and suggest that passivity experiences and voice perception rely, at least partly, on common sensorimotor brain mechanisms.

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CRedit authorship contribution statement

Study concept and design: PO, GR, NF, OB. Acquisition of data: PO. Analysis and interpretation of data: PO, GR, NF, OK, OB. Drafting of the manuscript: PO, OK, NF, OB. Critical revision of the manuscript for important intellectual content: All authors. Statistical analysis: PO, GR, NF. Obtained funding: OB. Administrative, technical, or material support: All authors. Study supervision: NF, OB.

Declaration of competing interest

O.B. and G.R. are inventors of a granted US patent 10,349,899 B2 (System and method for predicting hallucinations, 2019). O.B. and G.R. are inventors of a granted US patent 10,286,555 B2 (Robot controlled induction of the feeling of a presence, 2019). O.B. and G.R. are founders, shareholders, and members of the board of directors of Metaphysics Engineering SA (Switzerland). O.B. is member of the board of directors of Mindmaze SA (Switzerland). The other authors do not have any competing interests to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.schres.2021.03.014>.

References

- Alderson-Day, B., Fernyhough, C., 2016. Auditory verbal hallucinations: social, but how? *J. Conscious. Stud.* 23, 163–194. https://doi.org/10.1007/978-1-4614-0959-5_9.
- Bansal, S., Ford, J.M., Sperling, M., 2018. The function and failure of sensory predictions. *Ann. N. Y. Acad. Sci.* 1426, 199–220. <https://doi.org/10.1111/nyas.13686>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Bays, P.M., Wolpert, D.M., Haggard, P., Rossetti, Y., Kawato, M., 2008. Predictive attenuation in the perception of touch. *Sensorimotor Foundations of Higher Cognition*. Oxford University Press, USA, pp. 339–358.
- Blakemore, S.J., Wolpert, D.M., Frith, C.D., 1998. Central cancellation of self-produced tickle sensation. *Nat. Neurosci.* 1, 635–640. <https://doi.org/10.1038/2870>.
- Blakemore, S.J., Frith, C.D., Wolpert, D.M., 1999. Spatio-temporal prediction modulates the perception of self-produced stimuli. *J. Cogn. Neurosci.* 11, 551–559. <https://doi.org/10.1162/0899892990563607>.
- Blakemore, S.J., Smith, J., Steel, R., Johnstone, E.C., Frith, C.D., 2000a. The perception of self-produced sensory stimuli in patients with auditory hallucinations and passivity experiences: evidence for a breakdown in self-monitoring. *Psychol. Med.* 30, 1131–1139. <https://doi.org/10.1017/S0033291799002676>.
- Blakemore, S.J., Wolpert, D., Frith, C., 2000b. Why can't you tickle yourself? *Neuroreport* 11, R11–R16. <https://doi.org/10.1586/14737175.7.10.1337>.
- Blanke, O., Metzinger, T., 2009. Full-body illusions and minimal phenomenal selfhood. *Trends Cogn. Sci.* 13, 7–13. <https://doi.org/10.1016/j.tics.2008.10.003>.
- Blanke, O., Pozeg, P., Hara, M., Heydrich, L., Serino, A., Yamamoto, A., Higuchi, T., Salomon, R., Seeck, M., Landis, T., Arzy, S., Herbelin, B., Bleuler, H., Rognini, G., 2014. Neurological and robot-controlled induction of an apparition. *Curr. Biol.* 24, 2681–2686. <https://doi.org/10.1016/j.cub.2014.09.049>.
- Brainard, D.H., 1997. The psychophysics toolbox. *Spat. Vis.* 10, 433–436. <https://doi.org/10.1163/156856897X00357>.
- Braun, N., Debener, S., Spychala, N., Bongartz, E., Sörös, P., Müller, H.H.O., Philippen, A., 2018. The senses of agency and ownership: a review. *Front. Psychol.* 9, 1–17. <https://doi.org/10.3389/fpsyg.2018.00535>.
- Core Team, R., 2020. R: a language and environment for statistical computing. *R Found. Stat. Comput.*
- Corlett, P.R., Horga, G., Fletcher, P.C., Alderson-day, B., Schmack, K., Iii, A.R.P., 2019. Hallucinations and strong priors. *Trends Cogn. Sci.* 23, 114–127. <https://doi.org/10.1016/j.tics.2018.12.001>.
- Critchley, M., 1955. The idea of a presence. *Acta Psychiatr. Scand.* 30, 155–168. <https://doi.org/10.1111/j.1600-0447.1955.tb06055.x>.
- David, N., Newen, A., Vogeley, K., 2008. The “sense of agency” and its underlying cognitive and neural mechanisms. *Conscious. Cogn.* 17, 523–534. <https://doi.org/10.1016/j.concog.2008.03.004>.
- Farrer, C., Bouchereau, M., Jeannerod, M., Franck, N., 2008. Effect of distorted visual feedback on the sense of agency. *Behav. Neurosci.* 19, 53–57. <https://doi.org/10.1155/2008/425267>.
- Ford, J.M., Mathalon, D.H., Heinks, T., Kalba, S., Faustman, W.O., Roth, W.T., 2001. Neurophysiological evidence of corollary discharge dysfunction in schizophrenia. *Am. J. Psychiatry* 158, 2069–2071.
- Ford, J.M., Gray, M., Faustman, W.O., Roach, B.J., Mathalon, D.H., 2007. Dissecting corollary discharge dysfunction in schizophrenia. *Psychophysiology* 44, 522–529. <https://doi.org/10.1111/j.1469-8986.2007.00533.x>.
- Frith, C.D., 1987. The positive and negative symptoms of schizophrenia reflect impairments in the perception and initiation of action. *Psychol. Med.* 17, 631–648. <https://doi.org/10.1017/S0033291700025873>.
- Frith, C.D., Blakemore, S.J., Wolpert, D.M., 2000. Abnormalities in the awareness and control of action. *Philos. Trans. R. Soc. London. Ser. B Biol. Sci.* 355, 1771–1788. <https://doi.org/10.1098/rstb.2000.0734>.
- Gallagher, S., 2000. Philosophical conceptions of the self: implications for cognitive science. *Trends Cogn. Sci.* 4, 14–21. [https://doi.org/10.1016/S1364-6613\(99\)01417-5](https://doi.org/10.1016/S1364-6613(99)01417-5).
- Griffith, J., Hoffer, L.D., Adler, L.E., Zerbe, G.O., Freedman, R., 1995. Effects of sound intensity on a midlatency evoked response to repeated auditory stimuli in schizophrenic and normal subjects. *Psychophysiology* 32, 460–466.
- Haggard, P., Clark, S., Kalogeras, J., 2002. Voluntary action and conscious awareness. *Nat. Neurosci.* 5, 382–385. <https://doi.org/10.1038/nm827>.
- Hara, M., Rognini, G., Evans, N., Blanke, O., Yamamoto, A., Bleuler, H., Higuchi, T., 2011. A novel approach to the manipulation of body-parts ownership using a bilateral master-slave system. *IEEE International Conference on Intelligent Robots and Systems*, pp. 4664–4669. <https://doi.org/10.1109/IRoS.2011.6048519>.
- Hara, M., Salomon, R., van der Zwaag, W., Kober, T., Rognini, G., Nabae, H., Yamamoto, A., Blanke, O., Higuchi, T., 2014. A novel manipulation method of human body ownership using an fMRI-compatible master-slave system. *J. Neurosci. Methods* 235, 25–34. <https://doi.org/10.1016/j.jneumeth.2014.05.038>.
- Jaspers, K., 1990. Über leibhaftige Bewußtheiten (Bewußtheitätsäuschungen), ein psychopathologisches Elementarsymptom. *Gesammelte Schriften Zur Psychopathologie*. Springer, Berlin, Heidelberg, pp. 413–420. https://doi.org/10.1007/978-3-642-62027-0_8.
- Jeannerod, M., 2006. The origin of voluntary action. *History of a physiological concept*. *C. R. Biol.* 329, 354–362. <https://doi.org/10.1016/j.crv.2006.03.017>.
- Juckel, G., Gallinat, J., Riedel, M., Sokullu, S., Schulz, C., Möller, H.J., Müller, N., Hegerl, U., 2003. Serotonergic dysfunction in schizophrenia assessed by the loudness dependence measure of primary auditory cortex evoked activity. *Schizophr. Res.* 64, 115–124. [https://doi.org/10.1016/S0920-9964\(03\)00016-1](https://doi.org/10.1016/S0920-9964(03)00016-1).
- Juckel, G., Gudlowski, Y., Müller, D., Özgürdal, S., Brüne, M., Gallinat, J., Frodl, T., Witthaus, H., Uhl, I., Wutzler, A., Pogarell, O., Mulert, C., Hegerl, U., Meisenzahl, E.M., 2008. Loudness dependence of the auditory evoked N1/P2 component as an indicator of

- serotonergic dysfunction in patients with schizophrenia - a replication study. *Psychiatry Res.* 158, 79–82. <https://doi.org/10.1016/j.psychres.2007.08.013>.
- Kannape, O.A., Blanke, O., 2012. Agency, gait and self-consciousness. *Int. J. Psychophysiol.* 83, 191–199. <https://doi.org/10.1016/j.ijpsycho.2011.12.006>.
- Kannape, O.A., Blanke, O., 2013. Self in motion: sensorimotor and cognitive mechanisms in gait agency. *J. Neurophysiol.* 110, 1837–1847. <https://doi.org/10.1152/jn.01042.2012>.
- Kannape, O.A., Schwabe, L., Tadi, T., Blanke, O., 2010. The limits of agency in walking humans. *Neuropsychologia* 48, 1628–1636. <https://doi.org/10.1016/j.neuropsychologia.2010.02.005>.
- Kawahara, H., Morise, M., Banno, H., Skuk, V.G., 2013. Temporally variable multi-aspect N-way morphing based on interference-free speech representations. 2013 Asia-Pacific Signal and Information Processing Association Annual Summit and Conference, APSIPA 2013. IEEE, pp. 1–10. <https://doi.org/10.1109/APSIPA.2013.6694355>.
- Kilteni, K., Ehrsson, H.H., 2017a. Body ownership determines the attenuation of self-generated tactile sensations. *Proc. Natl. Acad. Sci.* 114, 8426–8431. <https://doi.org/10.1073/pnas.1703347114>.
- Kilteni, K., Ehrsson, H.H., 2017b. Sensorimotor predictions and tool use: hand-held tools attenuate self-touch. *Cognition* 165, 1–9. <https://doi.org/10.1016/j.cognition.2017.04.005>.
- Kleiner, M., Brainard, D.H., Pelli, D.G., Ingling, A., Murray, R., Broussard, A., Ingling, R., Murray, C., 2007. What's new in Psychtoolbox-3? *Perception* 36, 1–16. <https://doi.org/10.1068/v070821>.
- Knolle, F., Schwartze, M., Schröger, E., Kotz, S.A., 2019. Auditory predictions and prediction errors in response to self-initiated vowels. *Front. Neurosci.* 13, 1146.
- Krugwasser, R., Harel, E.V., Salomon, R., 2019. The boundaries of the self: the sense of agency across different sensorimotor aspects. *J. Vis.* 19, 14. <https://doi.org/10.1167/19.4.14>.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2018. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* 82, 1–26. <https://doi.org/10.18637/jss.v082.i13>.
- Lange, K., 2011. The reduced N1 to self-generated tones: an effect of temporal predictability? *Psychophysiology* 48, 1088–1095. <https://doi.org/10.1111/j.1469-8986.2010.01174.x>.
- Leptourgos, P., Corlett, P.R., 2020. Embodied predictions, agency, and psychosis. *Front. Big Data* 3, 27. <https://doi.org/10.3389/FDATA.2020.00027>.
- Lüdtke, D., 2018. sjPlot: Data Visualization for Statistics in Social Science. R Package Version 2.6.2. <https://doi.org/10.5281/zenodo.1308157>.
- MacDonald, P.A., Paus, T., 2003. The role of parietal cortex in awareness of self-generated movements: a transcranial magnetic stimulation study. *Cereb. Cortex* 13, 962–967. <https://doi.org/10.1093/cercor/13.9.962>.
- Martikainen, M.H., Kaneko, K.I., Hari, R., 2005. Suppressed responses to self-triggered sounds in the human auditory cortex. *Cereb. Cortex* 15, 299–302. <https://doi.org/10.1093/cercor/bhh131>.
- Menzer, F., Brooks, A., Halje, P., Faller, C., Vetterli, M., Blanke, O., 2010. Feeling in control of your footsteps: conscious gait monitoring and the auditory consequences of footsteps. *Cogn. Neurosci.* 1, 184–192. <https://doi.org/10.1080/17588921003743581>.
- Miall, R.C., Wolpert, D.M., 1996. Forward models for physiological motor control. *Neural Netw.* 9, 1265–1279.
- Mifsud, N.G., Oestreich, L.K.L., Jack, B.N., Ford, J.M., Roach, B.J., Mathalon, D.H., Whitford, T.J., 2016. Self-initiated actions result in suppressed auditory but amplified visual evoked components in healthy participants. *Psychophysiology*. <https://doi.org/10.1111/psyp.12605>.
- Moore, J.W., Fletcher, P.C., 2012. Sense of agency in health and disease: a review of cue integration approaches. *Conscious. Cogn.* 21, 59–68. <https://doi.org/10.1016/j.concog.2011.08.010>.
- Moseley, P., Fernyhough, C., Ellison, A., 2013. Auditory verbal hallucinations as atypical inner speech monitoring, and the potential of neurostimulation as a treatment option. *Neurosci. Biobehav. Rev.* 37 (10), 2794–2805. <https://doi.org/10.1016/j.neubiorev.2013.10.001>.
- Nazimek, J.M., Hunter, M.D., Woodruff, P.W.R., 2012. Auditory hallucinations: Expectation-perception model. *Med. Hypotheses* 78, 802–810. <https://doi.org/10.1016/j.mehy.2012.03.014>.
- Park, H.D., Blanke, O., 2019. Coupling inner and outer body for self-consciousness. *Trends Cogn. Sci.* 23, 377–388. <https://doi.org/10.1016/j.tics.2019.02.002>.
- Pelli, D.G., 1997. The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat. Vis.* 10, 437–442. <https://doi.org/10.1163/156856897X00366>.
- Pinheiro, A.P., Schwartze, M., Kotz, S.A., 2018. Voice-selective prediction alterations in nonclinical voice hearers. *Sci. Rep.* 8, 1–10. <https://doi.org/10.1038/s41598-018-32614-9>.
- Plaze, M., Mangin, J.F., Paillière-Martinot, M.L., Artiges, E., Olié, J.P., Krebs, M.O., Gaillard, R., Martinot, J.L., Cachia, A., 2015. “Who is talking to me?” - self-other attribution of auditory hallucinations and sulcation of the right temporoparietal junction. *Schizophr. Res.* 169, 95–100. <https://doi.org/10.1016/j.schres.2015.10.011>.
- Powers, A.R., Mathys, C., Corlett, P.R., 2017. Pavlovian conditioning-induced hallucinations result from overweighting of perceptual priors. *Science* 357, 596–600. <https://doi.org/10.1126/science.aan3458> (80-).
- Reznik, D., Mukamel, R., 2019. Motor output, neural states and auditory perception. *Neurosci. Biobehav. Rev.* 96, 116–126. <https://doi.org/10.1016/j.neubiorev.2018.10.021>.
- Salomon, R., Progin, P., Griffa, A., Rognini, G., Do, K.Q., Conus, P., Marchesotti, S., Bernasconi, F., Haggmann, P., Serino, A., Blanke, O., 2020. Sensorimotor induction of auditory misattribution in early psychosis. *Schizophr. Bull.* <https://doi.org/10.1093/schbul/sbz136>.
- Sass, L.A., Parnas, J., 2001. Phenomenology of self-disturbances in schizophrenia: some research findings and directions. *Philos. Psychiatry, Psychol.* 8, 347–356. <https://doi.org/10.1353/ppp.2002.0027>.
- Sass, L.A., Parnas, J., 2003. Schizophrenia, consciousness, and the self. *Schizophr. Bull.* 29, 427–444.
- Sato, A., 2008. Action observation modulates auditory perception of the consequence of others' actions. *Conscious. Cogn.* 17, 1219–1227. <https://doi.org/10.1016/j.concog.2008.01.003>.
- Sato, A., Yasuda, A., 2005. Illusion of sense of self-agency: discrepancy between the predicted and actual sensory consequences of actions modulates the sense of self-agency, but not the sense of self-ownership. *Cognition* 94, 241–255. <https://doi.org/10.1016/j.cognition.2004.04.003>.
- Schafer, E.W.P., Marcus, M.M., 1973. Self-stimulation alters human sensory brain responses. *Science* 181, 175–177 (80-).
- Schmack, K., de Castro, A.G.C., Rothkirch, M., Sekutowicz, M., Rössler, H., Haynes, J.D., Heinz, A., Petrovic, P., Sterzer, P., 2013. Delusions and the role of beliefs in perceptual inference. *J. Neurosci.* 33, 13701–13712. <https://doi.org/10.1523/JNEUROSCI.1778-13.2013>.
- Schultz, W., Dickinson, A., 2000. Neural coding of prediction errors. *Annu. Rev. Neurosci.* 23, 473–500.
- Seghezzi, S., Giannini, G., Zapparoli, L., 2019. Neurofunctional correlates of body-ownership and sense of agency: a meta-analytical account of self-consciousness. *Cortex* 121, 169–178. <https://doi.org/10.1016/j.cortex.2019.08.018>.
- Shergill, S.S., Bays, P.M., Frith, C.D., Wolpert, D.M., 2003. Two eyes for an eye: the neuroscience of force escalation. *Science* 301, 187. <https://doi.org/10.1126/science.1085327> (80-).
- Shergill, S.S., Samson, G., Bays, P.M., Frith, C.D., Wolpert, D.M., 2005. Evidence for sensory prediction deficits in schizophrenia. *Am. J. Psychiatry* 162, 2384–2386. <https://doi.org/10.1176/appi.ajp.162.12.2384>.
- Singmann, H., Bolker, B., Westfall, J., Aust, F., 2019. afex: Analysis of Factorial Experiments. R Package Version 0.23-0.
- Stenner, M.P., Bauer, M., Sidarus, N., Heinze, H.J., Haggard, P., Dolan, R.J., 2014. Subliminal action priming modulates the perceived identity of sensory action consequences. *Cognition* 130, 227–235. <https://doi.org/10.1016/j.cognition.2013.11.008>.
- Stephan, K.E., Friston, K.J., Frith, C.D., 2009. Dysconnection in Schizophrenia: From abnormal synaptic plasticity to failures of self-monitoring. *Schizophr. Bull.* 35, 509–527. <https://doi.org/10.1093/schbul/sbn176>.
- Stephane, M., Burton, P., Meriwether, D., Yoon, G., 2018. “Other” tags for “self”-generated speech in patients with auditory verbal hallucinations, an fMRI study. *Schizophr. Res.* 202, 410–411. <https://doi.org/10.1016/j.schres.2018.06.056>.
- Sterzer, P., Adams, R.A., Fletcher, P., Frith, C., Lawrie, S.M., Muckli, L., Petrovic, P., Uhlhaas, P., Voss, M., Corlett, P.R., 2018. The predictive coding account of psychosis. *Biol. Psychiatry* 84, 634–643. <https://doi.org/10.1016/j.biopsych.2018.05.015>.
- Stetson, C., Cui, X., Montague, P.R., Eagleman, D.M., 2006. Motor-sensory recalibration leads to an illusory reversal of action and sensation. *Neuron* 51, 651–659. <https://doi.org/10.1016/j.neuron.2006.08.006>.
- Swiney, L., Sousa, P., 2014. A new comparator account of auditory verbal hallucinations: how motor prediction can plausibly contribute to the sense of agency for inner speech. *Front. Hum. Neurosci.* 8, 675. <https://doi.org/10.3389/fnhum.2014.00675>.
- Teufel, C., Kingdon, A., Ingram, J.N., Wolpert, D.M., Fletcher, P.C., 2010. Deficits in sensory prediction are related to delusional ideation in healthy individuals. *Neuropsychologia* 48, 4169–4172. <https://doi.org/10.1016/j.neuropsychologia.2010.10.024>.
- Tsakiris, M., Haggard, P., Franck, N., Mainy, N., Sirigu, A., 2005. A specific role for efferent information in self-recognition. *Cognition* 96, 215–231. <https://doi.org/10.1016/j.cognition.2004.08.002>.
- Weiskrantz, L., Elliott, J., Darlington, C., 1971. Preliminary observations on tickling oneself. *Nature* 230, 598–599. <https://doi.org/10.1038/230598a0>.
- Weiss, C., Herwig, A., Schütz-Bosbach, S., 2011a. The self in action effects: selective attenuation of self-generated sounds. *Cognition* 121, 207–218. <https://doi.org/10.1016/j.cognition.2011.06.011>.
- Weiss, C., Herwig, A., Schütz-Bosbach, S., 2011b. The self in social interactions: sensory attenuation of auditory action effects is stronger in interactions with others. *PLoS One* 6, 16–18. <https://doi.org/10.1371/journal.pone.0022723>.
- Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.
- Wolpert, D.M., Flanagan, J.R., 2001. Motor prediction. *Curr. Biol.* 11, R729–R732.