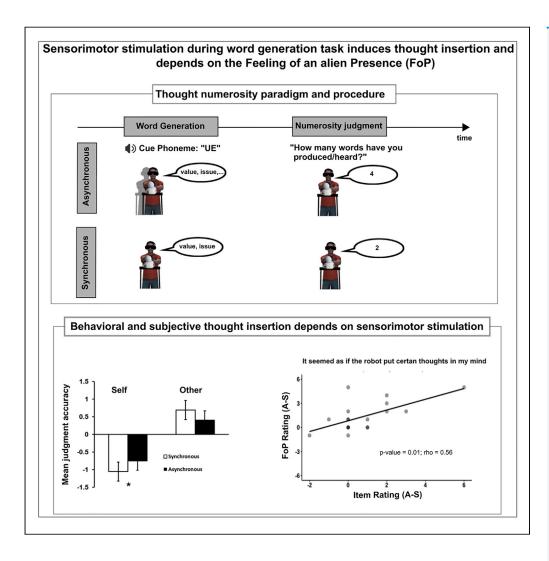
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Thought consciousness and source monitoring depend on robotically controlled sensorimotor conflicts and illusory states



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HIGHLIGHTS

Thought insertion (TI) is an enigmatic and clinically relevant symptom in psychiatry

We report a new roboticsbased approach to study TI experimentally

Sensorimotor conflicts induce feeling of a presence (FoP) in source monitoring tasks

TI depends on source monitoring during sensorimotor processing and FoP

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Thought consciousness and source monitoring depend on robotically controlled sensorimotor conflicts and illusory states

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SUMMARY

Thought insertion (TI) is characterized by the experience that certain thoughts, occurring in one's mind, are not one's own, but the thoughts of somebody else and suggestive of a psychotic disorder. We report a robotics-based method able to investigate the behavioral and subjective mechanisms of TI in healthy participants. We used a robotic device to alter body perception by providing online sensorimotor stimulation, while participants performed cognitive tasks implying source monitoring of mental states attributed to either oneself or another person. Across several experiments, conflicting sensorimotor stimulation reduced the distinction between self- and other-generated thoughts and was, moreover, associated with the experimentally generated feeling of being in the presence of an alien agent and subjective aspects of TI. Introducing a new robotics-based approach that enables the experimental study of the brain mechanisms of TI, these results link TI to predictable self-other shifts in source monitoring and specific sensorimotor processes.

INTRODUCTION

Thought insertion (TI) is one of the most enigmatic psychiatric symptoms and is characterized by the experience that certain thoughts, occurring in one's mind, are not one's own, but rather the thoughts of somebody else. TI violates basic intuitions about consciousness (i.e., Who else than me could possibly have access to my thoughts?) and has fascinated clinicians, scientists, philosophers, and laymen alike. TI is often reported by patients with schizophrenia and other psychotic disorders and may rarely occur in healthy individuals (Johns et al., 2004). TI is classified as the so-called first-rank symptom, implying that a regular occurrence is suggestive of a psychotic disorder (Schneider, 1959).

A long-standing question in psychiatric and cognitive neuroscience has been how the brain generates TI and on which brain mechanisms it depends. One prominent postulation is that first-rank symptoms, including TI, arise from a deficit comparable to those of conscious control for overt actions, that is, a deficit of source monitoring (Feinberg, 1978; Frith, 1987; Ford and Mathalon, 2004) and related sensorimotor mechanisms. This proposal is substantiated by converging behavioral, brain imaging, and electrophysiological evidence in patients with schizophrenia (Ford and Mathalon, 2004; Shergill et al., 2005, 2014) and healthy subjects (Weiskrantz et al., 1971; Shergill et al., 2003; Bays et al., 2005, 2006), but has so far targeted only conscious control of overt actions or auditory verbal hallucinations (i.e., alien voices, Hoffman, 1986). Accordingly, the importance of source monitoring, self-related processes, and the link of TI to conscious monitoring of overt actions, remains poorly understood. Although some authors have investigated the mechanisms related to TI using different cognitive manipulations (Walsh et al., 2015; Sugimori et al., 2011) (see also Stephens and Graham, 2000; Martin and Pacherie, 2013; Gallagher, 2004a; 2004b; Vicente, 2014), research on TI and related cognitive processes has been hampered by the lack of empirical techniques in healthy subjects to probe TI and investigate associated behavioral changes in a more controlled fashion. Accordingly, the mechanisms of TI, and how they potentially depend on conscious control for overt actions and covert mental activity, remain unknown. To provide empirical evidence about the interaction between the sensorimotor control of actions and covert mental activity in potentially generating TI, here

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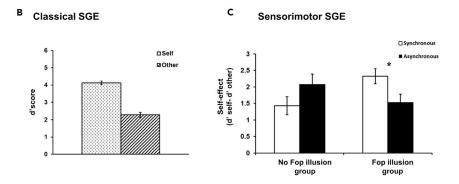
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A Experimental Procedure Familiarization Encoding Recognition (1) Cue word: «Tower» & (1) Target association & distractors "House" Robot Robot Robot



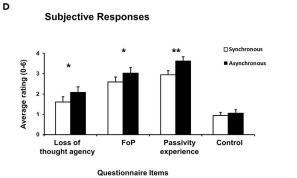


Figure 1. Thought generation (experiment 1)

(A) Experimental procedure for Experiment 1. During encoding, participants operate the robotic system in synchronous or asynchronous mode, followed by the memory recognition phase. Participants answered whether they had generated (active condition) or heard (passive condition) the word.

- (B) Classical SGE (d') was higher in the active versus passive conditions.
- (C) Only individuals experiencing the FoP had significantly less self-advantage (sensorimotor SGE; d'active-d'passive) in the asynchronous when compared with the synchronous condition (error bars standard error of mean).
- (D) Participants reported stronger FoP, passivity experiences, and loss of thought agency during the asynchronous versus synchronous condition. Error bars show standard errors of the mean. *p < 0.05, **p < 0.01.

we applied a robotic device that allowed us to interfere in a specific and controlled way with sensorimotor processing (known to alter source monitoring), while participants performed repetitive cognitive tasks.

Our recently developed robotic system consists of two robots and has previously allowed us to experimentally alter own body perception and, importantly, is able to induce illusory mental states mimicking psychosis-related symptoms, in a controlled manner in healthy subjects (Blanke et al., 2014). During the procedure participants are asked to perform repeated poking movements, through a front robot (i.e., placed in front of participants) (Figure 1) and replicated by a back robot (i.e., placed behind the participants), resulting in controlled tactile stimulation on the participants' back based on their own movements (synchronous stimulation). Blanke et al. (2014) demonstrated that if a temporal delay is introduced between the participants'

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movements and the tactile stimulation delivered on their back (i.e., asynchronous sensorimotor stimulation) healthy participants experience an illusory alteration of their mental state characterized by passivity and loss of agency, as well as being in the presence of somebody else (feeling of an alien presence) (feeling of a presence [FoP]).

In four separate experiments, we investigated whether source monitoring for internal thoughts depends on (1) sensorimotor stimulation and on (2) the level of FoP while exposing our participants to asynchronous and synchronous (i.e., control condition) robotic stimulation. Importantly, for the present experiments, previous work has shown that participants are able to carry out different covert cognitive paradigms while they are also actuating the robotic system and hence receive sensorimotor stimulation (i.e., Salomon et al., 2020; Faivre et al., 2020; Orepic et al., 2020). In the present experiments, in Experiment 1, we tested the effects of robotic stimulation and FoP on source monitoring in a memory task by exploiting the so-called self-generation effect (SGE) and in Experiment 2 in a new task developed to assess thought numerosity (during a verbal fluency task). In Experiment 3, we investigated whether sensorimotor stimulation and the thought numerosity paradigm were associated with explicit changes in subjective thought experience. In a final control experiment, Experiment 4, we excluded that the observed effects were due to a generic reduction of attentional resources during asynchronous stimulation (by using a classical working memory task). Across these four experiments we demonstrate systematic behavioral and subjective changes in source monitoring suggestive of TI while participants performed different mental operations, which depend on online conflicting sensorimotor stimulation and the level of experienced FoP. We discuss the importance of robotics and sensorimotor processes for the understanding of cognitive thought processes, including thought agency as well as abnormal and clinically relevant TI.

RESULTS

Robotically induced sensorimotor conflicts induce FoP and alter source monitoring

In Experiment 1, we used a robotic system (Blanke et al., 2014; Salomon et al., 2020; Faivre et al., 2020; Orepic et al., 2020; Hara et al., 2011) (Figure S1) and exposed a group of healthy participants to repetitive sensorimotor stimulation that induces the FoP in a controlled way (see below) while they simultaneously performed a mental source monitoring task (Experiment 1). In this paradigm, inducing the so-called SGE (Slamecka and Graf, 1978; Transparent methods), the participants were either presented with a list of words (passive condition) or they were asked to generate their own words (active condition) within a given set of rules. During an encoding phase, participants were asked to memorize both the self-generated and the passively heard words. When tested in a subsequent recognition phase, participants typically remember more self-generated than externally presented (heard) items, i.e., SGE. To avoid ceiling and floor effects in the recognition task for self-generated words, only the data of participants who generated more than 50% of expected associations (at least 18 words) and who performed above chance in the recognition task were included to the analysis.

Importantly for the present investigation, our participants additionally performed repetitive tapping movements with both hands to operate the front robot, which was combined with a second robot providing tactile feedback to their back (see Transparent methods, for more detail). In two conditions, tactile feedback was delivered either synchronously with their movement (synchronous control condition) or with a delay (of 500 ms; asynchronous condition) that, critically, we previously showed induces the FoP in healthy participants. In the first part of Experiment 1, while participants were using our robotic system, we asked them to carry out the standard procedure to measure the SGE. Previous work on the sense of agency for overt actions (and its link to self or source monitoring processes) has typically exposed subjects to different sensorimotor conditions, by varying the spatiotemporal contingencies between actions and associated sensory feedback or by measuring consequences in terms of sensory attenuation or motor adaptations (Shergill et al., 2003; Bays et al., 2005, 2006; Blakemore et al., 1998, 2000; Wolpert and Ghahramani, 2020). As indicated above, the SGE is a well-known memory effect, characterized by better recognition for words that are self-generated (active condition) versus words that are only heard and generated by another person (passive condition, Faivre et al., 2020) (Figure 1A; Transparent methods). Here, to study the relation between thought-related source monitoring and sensorimotor processing, we tested whether the magnitude of the SGE (i.e., the difference between recognition for self-generated versus generatedby-another words) was affected by the synchronous-asynchronous manipulation and the associated robotically induced FoP. Participants used the robotic system, either in the synchronous or asynchronous condition, during the word encoding session, i.e., while they were either generating or listening to words. The





SGE for word recognition was tested immediately afterward. We hypothesized that if asynchronous stimulation induces the FoP, it might also decrease source monitoring for self-generated concurrent mental operations, by decreasing a classical self-effect such as the SGE.

As expected, we found a classical SGE (calculated as a recognition difference in d' between active and passive conditions), with significantly better recognition for actively (self) versus passively (other) generated words (Figure 1B) (self: M = 4.12, SD = 0.45; other: M = 2.28, SD = 0.65; F(1,20) = 180.86, p < 0.0001), confirming that participants better remembered words for which they have been the agents, when compared with words they passively heard. Critically, the SGE was modulated by the sensorimotor conditions (asynchronous versus synchronous), and this depended on the FoP intensity (calculated as the difference between FoP ratings in the synchronous and asynchronous condition) (significant interaction between stimulation condition and FoP intensity scores used as a covariate; F(1,20) = 6.95; p = 0.016) (Figure 1C). To better illustrate how sensorimotor stimulation inducing the FoP effect differently affected recognition in the active and passive conditions, we divided the sample in two groups accordingly to their FoP ratings and directly compared the SGE between participants who did and who did not experience to be in the presence of an alien agent. There was a significant interaction between sensorimotor condition and FoP group (F(1,20) = 7.217, p = 0.014): the SGE (i.e., difference between active and passive conditions) was lower in the FoPinducing asynchronous (versus synchronous) condition, but only in participants experiencing the FoP (FoP group, synchronous: M = 2.33, SD = 0.75; asynchronous: M = 1.53, SD = 0.83) (Figure 1C). This was not the case in the other group of participants (No-FoP group, synchronous: M = 1.43; SD = 0.90; asynchronous: M = 2.07, SD = 1.04). In other words, when the robotically applied sensorimotor conflict induced the experience to be in the presence of an alien agent (FoP), the SGE, an overt behavioral advantage in the ability to remember self-generated (active condition) versus other-generated words (passive condition), was reduced. Importantly this effect was not due to a general interference on memory performance due to the robotic stimulation or to the induced FoP, as there was no main effect of sensorimotor stimulation (p = 0.58) or a Stimulation \times FoP interaction (p = 0.28) on the performance in word recognition in general. This is an important control, excluding that the differences found in the SGE depend on generic differences in distraction or divided attention between the two sensorimotor conditions. Finally, we note that the present results cannot be due to differences in motor patterns spontaneously adopted by participants during the synchronous versus the asynchronous stimulation condition. Indeed, data collected with the same robotic system show that there is no difference in the quantity of poking movements performed in the two conditions, and that there is no link between movement characteristics and the induced FoP (Bernasconi et al., 2020).

To summarize, data from Experiment 1 show that the present sensorimotor conflicts induce selective behavioral changes in the SGE that tap into the brain's source monitoring processes (Figure 1C). Importantly, this SGE decrease in our participants' capacity to better remember self-generated versus othergenerated words depends on the degree of feeling of an alien presence as induced by robotic stimulation (Figure 1D) and only in the conflicting asynchronous condition.

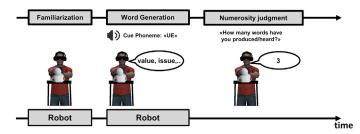
Thought numerosity is associated with source monitoring and the feeling of an alien presence

Blanke et al. (2014) demonstrated that the FoP, induced by the robotic stimulation in the asynchronous condition, was also associated with a change in how many people participants perceived to be close to them during sensorimotor stimulation, such that participants perceived additional people to be present during the FoP-inducing asynchronous condition. Here we asked whether a similar change in numerosity judgments also occurs for the number of concurrent internal thoughts participants hold in their mind. This was also motivated because TI is not only characterized by the experience that certain thoughts, occurring in one's mind, are not one's own thoughts (loss of thought agency), but also by the sensation (or positive symptom) that the thoughts in one's mind are the thoughts of a different, alien and additional, person (i.e., TI proper, Stephens and Graham, 2000; Martin and Pacherie, 2013). A lack of self-other discrimination or decrease in source monitoring as found in Experiment 1 is therefore not sufficient to account for TI that is also characterized by TI proper, because the former does not include a positive mental element characterized by the conscious attribution of one's thoughts to another additional agent. Moreover, the lack of thought agency without TI proper may also occur in healthy subjects, as is the case during unbidden thoughts (Stephens and Graham, 2000; Martin and Pacherie, 2013; Koehler, 1979), whereas TI proper has, to the best of our knowledge, not been reported in healthy subjects.





A Experimental Procedure



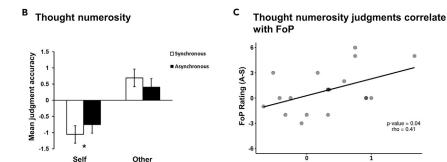


Figure 2. Thought numerosity task (experiment 2)

Source of generation

(A) While operating the robotic system in synchronous or asynchronous mode participants performed the thought numerosity task (either active, self-generating, or passive conditions) (Transparent methods).

(B) Thought numerosity judgments are shown. Participants showed a general suppression of numerosity judgments for self-generated words (active conditions). Crucially, this self-suppression was reduced during asynchronous versus synchronous condition. There was no such change for other-generated words (passive condition).

Judgment accuracy of self-generated words (A-S)

(C) Correlation analysis shows a significant positive correlation between the magnitude of numerosity judgment suppression and the differential FoP score. Error bars show standard errors of the mean. *p < 0.05.

In Experiment 2 we investigated whether we can obtain a behavioral index for alienated thoughts similar to TI proper, which is an index for additional-inserted number of thoughts in healthy participants, and how this depends on the FoP. Blindfolded participants operated the same robotic system, while simultaneously performing a verbal (phonetic) fluency task (Slamecka and Graf, 1978). With the aim to observe changes in overt behavior that are associated with TI proper, we adapted a verbal fluency task and asked a group of participants to estimate the number of words that they have either generated themselves (active condition) or listened to (passive condition), while operating the robotic sensorimotor system in either the synchronous or asynchronous condition. In the active condition, a starting phoneme was played to participants through headphones and they were instructed to generate as many words starting with the specified phoneme as they could in a given time period (phonetic fluency task), which randomly varied between 15 and 30 s. Immediately afterward, each participant estimated how many words he or she had generated. In the passive conditions, the participant listened to a list of words (of 6-10 words, randomized) (Figure 2A; Transparent methods). To prevent participants from simply counting the words in the passive condition, and to avoid strong differences in cognitive load required between the two conditions, they were asked to determine whether each word they heard contained a given phoneme, specified at the beginning of each trial. To obtain a measure of how well subjects are able to estimate the number of "thoughts in their mind" (i.e., thought numerosity), we subtracted the actual number of produced (active condition) or passively heard words (passive condition) from the estimated number of words. We predicted that sensorimotor stimulation should (1) differently impact word numerosity, but specifically in the active self-generating condition (i.e., more thoughts as quantified through word numerosity judgments) and that (2) this should again (as in Experiment 1) be related to the strength of the robotically induced FoP.

We found that participants underestimated the number of self-generated words (M = -0.90, SD = 1.13) when compared with words generated by another agent (M = 0.55, SD = 1.11; main effect active-passive: F(1,18) = 23.306, p < 0.0001). Critically, this self-suppression effect depended on sensorimotor stimulation





(active-passive by sensorimotor condition interaction: F(1,18) = 7.274, p = 0.015), as the number of estimated words in the active conditions differed in the asynchronous (M = -0.75, SD = 1.16) versus synchronous condition (M = -1.05, SD = 1.17; t(18) = 2.192, p = 0.042). This was not observed when words were processed in the passive conditions (synchronous: M = 0.69, SD = 1.20; asynchronous: M = 0.41, SD = 1.14; t(18) = 1.668, p = 0.113) (Figure 2B), showing that these behavioral changes are not related to differences in attentional resources between the sensorimotor conditions or between the passive versus active condition.

We next tested whether this effect, that jointly depends on sensorimotor stimulation (asynchronous-synchronous difference) and source monitoring (active-passive difference), is also associated with the FoP. This was confirmed by the finding that the asynchronous-synchronous difference for the numerosity judgment of actively generated words correlated positively with the FoP intensity (rho = 0.41, p = 0.04) (Figure 2C). That is, the more intense a participant experienced the FoP, the more her self-suppression effect in thought numerosity judgments was reduced in the asynchronous (when compared with the synchronous) condition, that is perceived numerosity of self-generated words became more similar to other-generated words.

Additional analyses excluded that these effects were due to generic differences in attentional resources or cognitive load between experimental conditions. There was neither a difference in the total number of generated words in the active condition (M = 7.95, SD = 2.02) and the number of words where the correct phoneme was identified in the passive condition (M = 8.11, SD = 0.33; F(1,18) = 0.115, p = 0.738), or between both sensorimotor conditions (synchronous: M = 8.18, SD = 1.18; asynchronous: M = 7.88, SD = 0.89; F(1,18) = 3.079, p = 0.096), nor was there an interaction between the source (active-passive) and sensorimotor stimulation (F(1,18) = 0.944, p = 0.344). These effects were also not modulated by the experienced FoP, as when adding FoP ratings as a covariate, no main effects or interactions emerged (all p values >0.35; see also Transparent methods). This is an important control and, extending the results obtained for Experiment 1, excludes that the differences in the estimated number of words depended on general differences in distraction, divided attention, or task difficulty between the two sensorimotor conditions.

To summarize, these data reveal a robotically induced reduction of thought-related source monitoring characterized by a reduced ability to discriminate mental processes representing self-generated thoughts from those generated by others, making thought numerosity judgments more similar for words that were either actively generated or passively heard, independently of differences in cognitive load between the present experimental conditions. Importantly, the direction of the self-suppression effect suggests that perceived thought numerosity in the asynchronous active condition (when compared with the synchronous active condition) is shifted toward performance in the passive conditions, i.e., in conditions during which participants judge items generated by another person. This was further corroborated by linking this shift in performance to the experimental induction of being in the presence of an alien agent (FoP), because self-generated words were perceived as more similar to other-generated words in the FoP-inducing asynchronous condition and because the self-suppression effect correlated positively with FoP intensity. Accordingly, the number of self-generated words were perceived as higher and more similar to the number of other-generated words, selectively in the FoP-inducing asynchronous condition, suggesting that under these conditions additional and alien-like thoughts were inserted into the minds of our participants (TI proper), compatible with previous findings on the perceived number of alien people (Blanke et al., 2014).

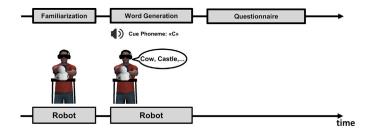
Subjective mental state related to TI depends on the feeling of an alien presence and sensorimotor stimulation

We finally sought to provide additional evidence whether the experimental conditions leading to the changes in overt behavior in Experiment 2 are associated with changes in subjective TI and whether this depends on processes of source monitoring and the FoP. To this aim in Experiment 3, we asked a new group of participants to perform the verbal fluency task (active condition as in Experiment 2), while operating the robotic system in either the synchronous or asynchronous condition (see Transparent methods). At the beginning of each condition, they heard a French phoneme through headphones, and were then asked to generate as many words as they could, starting with the specified phoneme within 3 min (phonetic fluency task, Lezak et al., 1995). At the end of each condition, they were asked to rate the items on a questionnaire referring to their thought process during the task (Figure 3A). The questionnaire was based on previous TI literature (Miller et al., 1999; Schultze-Lutter et al., 2007) and contained a total of twelve items, with six items assessing TI and other aspects of thought consciousness, as well as six control items (Table

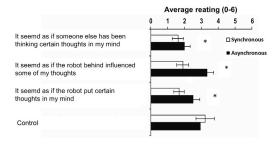




A Experimental Procedure



B Subjective Responses



C Subjective thought insertion correlates with FoP

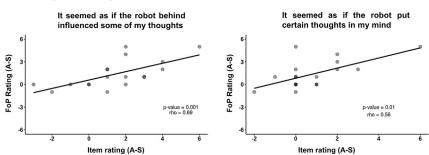


Figure 3. Thought insertion (experiment 3)

(A) At the beginning of each condition, participants heard a phoneme and then had 3 minutes to generate as many words starting with the specified phoneme as they could (Transparent methods).

(B) Subjective responses show that during the FoP-inducing asynchronous condition, participants agreed more with statements about TI and influencing.

(C) Correlation between FoP scores and thought-related experience ratings revealed a significant positive correlation between the differential FoP score and differential ratings of items reflecting TI and thought influencing. Error bars show standard errors of the mean. *p < 0.05.

S1). Both sensorimotor conditions were then repeated in randomized order (without the verbal fluency task) followed by the FoP questionnaire as used in the previous experiments (Transparent methods). We predicted that experimental TI and related aspects of thought consciousness would be stronger during asynchronous versus synchronous sensorimotor stimulation and that it would be associated with the experience of an alien presence (FoP).

Accordingly, results showed that that sensorimotor stimulation affected thought-related items, but not control items, and that this effect depended on the FoP strength as induced by the asynchronous stimulation. Indeed, there was a significant interaction between the type of question (thoughts experience, control), sensorimotor stimulation (synchronous, asynchronous), and FoP score (F(1,17) = 7.49, p = 0.011,





 $\eta^2 = 0.30$). Further analysis, run on thought experience questions only, showed a marginally significant stimulation \times FoP interaction (F(1,14) = 4.32, p = 0.05; η^2 = 0.19), suggesting that the sensorimotor stimulation conditions differently affected subjects responses, as a function of whether they did or did not perceive the FoP. When analyzing individual questions, the sensorimotor X Question (Q1, Q3, Q7, Q8, Q10, and Q11) \times FoP interaction was significant (F(5,85) = 4.60, p < 0.001; η^2 = 0.19), indicating that the effect of sensorimotor stimulation was stronger for some key experimental questions assessing different aspects of thoughts experience. Question-by-question analysis then revealed that, while performing the verbal fluency task, our participants reported mild experiences of thought insertion ("It seemed as if the robot put certain thoughts in my mind") and that their thoughts were manipulated ("It seemed as if the robot influenced some of my thoughts"). Importantly, as predicted, experimental TI and influence were stronger in the asynchronous than in the synchronous condition (thought influence; asynchronous: M = 3.33, SD =1.64, synchronous: M = 1.89, SD = 1.49; Wilcoxon signed-rank test: Z = 2.34, p = 0.01) (TI; asynchronous: M = 2.00, SD = 1.41, synchronous: M = 1.61, SD = 1.38; Wilcoxon signed-rank test: Z = 2.11, p = 0.03; asynchronous: M = 2.5, SD = 1.71, synchronous: M = 1.67, SD = 1.15; Wilcoxon signed-rank test: Z = -1.91, p = 1.67, SD = 1.15; Wilcoxon signed-rank test: SD = 1.71, synchronous: SD = 1.70.03) (Figure 3B; Table S1). As expected, participants also gave higher ratings for the FoP in the asynchronous (M = 3.95; SD = 2.07) versus synchronous condition (M = 2.56; SD = 2.06) (Wilcoxon signed-rank test: Z = -2.69, p = 0.005) and for passivity experiences (asynchronous: M = 4.5, SD = 1.61; synchronous: M = 4.5, M2.77, SD = 1.69; Wilcoxon signed-rank test: Z = -2.57, p = 0.007; Transparent methods). Further analysis revealed that the strength of thought insertion and thought influencing positively correlated with the intensity of the FoP (thought insertion: rho = 0.56, p = 0.01; thought influencing: rho = 0.69, p = 0.001) (Figure 3C). These selective effects were absent for control questions. We only observed a significant effect of question $(F(5,80) = 5.41, p < 0.001, \eta^2 = 0.25)$, showing that participants gave different ratings to the different items; however, these ratings did not differ as a function of sensorimotor stimulation and were not influenced by the FoP effect, as no other main effect or interaction was significant (all p values>.13). These results rule out a possible effect of suggestibility on the questionnaire items and further highlight the selectivity of the effects of sensorimotor stimulation and associated FoP on thought experience.

To summarize, the results from Experiment 3 demonstrate that repetitive spatiotemporal sensorimotor conflicts, while performing a verbal fluency task, induce sensations of thought alienation in healthy subjects. These sensations are weaker in intensity, but mimic aspects of the phenomenology of TI and thought influence as reported by psychiatric patients with delusions. We again induced the FoP in the same (asynchronous) experimental condition and we, importantly, show that the stronger our participants felt to be in the presence of an alien agent (FoP), the stronger they felt that somebody else was thinking or influencing thoughts in their mind, showing that subjective and behavioral TI can be induced and modulated experimentally using sensorimotor stimulation during a repetitive verbal fluency task (Experiments 2 and 3). More work is needed to follow-up on the results of Experiment 3. Thus, two main TI items ("It seemed as if someone else has been thinking certain thoughts in my mind"; "It seemed as if the robot put certain thoughts in my mind") showed higher ratings in the asynchronous FoP-inducing condition, whereas this was not the case for another TI item ("It seems as if some outside force or person is putting thoughts into my mind"). Future work should determine key phenomenological characteristics of TI in healthy participants when exposed to the present robotic system, focusing on the source of inserted thoughts and how thought ownership and thought agency are involved. This work should also determine how subjective aspects of TI potentially differ among individuals along the schizophrenia spectrum, how subjective TI relates to the implicit behavioral changes we observed, and how this depends on the involved cognitive task and sensorimotor stimulation.

Robotic-induced differences in thought-related source monitoring does not depend on differences in attentional demands

Results from Experiment 1 and Experiment 2 showed that the induced differences in self-monitoring during word memory and thought numerosity were specific for the asynchronous condition, were related to the experience of the alien agent (FoP), and did not manifest as a generic decrease in tasks performance; they were characterized by a specific reduction thought-related source monitoring (difference between active/self and passive/other processes). However, it could be argued that the higher level of sensorimotor incongruency in FoP-inducing asynchronous stimulation condition (compared with the synchronous condition) may have caused the described differences. Such an additional factor may have distracted participants, in turn more strongly affecting their SGE and thought numerosity judgments. To exclude this possibility, we tested the effects of robotic stimulation in the synchronous and asynchronous condition on a

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classic working memory 2-back task, chosen to tap into different mechanisms than source monitoring, while being well-known to require high-level attentional resources. If the effects of asynchronous stimulation depend on differences in attentional load between both conditions, then a reduction of working memory performance is expected specifically in the asynchronous condition. Conversely, the absence of a performance difference would rule out an attentional account, further corroborating our previous control analyses and supporting the conclusion that the robotic stimulation specifically affects source monitoring processes for internal thoughts, and not generically any cognitive process.

As expected, at the subjective level, questionnaire responses showed that participants reported higher scores in the questions assessing the FoP ("I felt as if someone was standing behind my body") (Z = 20, p < 0.03, one-tailed; Wilcoxon) and passivity experiences ("I felt as if someone else was touching my body"; Z = 12; p < 0.01, one-tailed; Wilcoxon). However, the pattern of stimulation did not affect the performance in the working memory task, as there was no difference between conditions in task accuracy (t(1,19) = 0.26, p = 0.54; Cohen's d = -0.14; synchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition, mean accuracy = 92.1%; SD = 5.4; asynchronous condition = 92.1%; SD = 92.chronous condition: mean = 91.7; SD = 5.8). Differently from the previous tasks aimed at measuring the effects of the robot on internal thought processes—i.e., the SGE, Experiment 1, and the thoughts numerosity task, Experiment 2—the performance in the working memory (WM) task was unrelated to the FoP effect. Indeed, when we added the FoP score (i.e., the asynchronous-synchronous difference in the FoP questionnaire) as a covariate, we did not find any difference in performance between conditions (F(1,19) = 1.83, p =0.19, $\eta^2 = 0.86$), or any interaction with the FoP score (F(1,19) = 0.63, p = 0.44, $\eta^2 = 0.29$). Thus, the robotic sensorimotor stimulation did induce a FoP in the asynchronous condition during a working memory task, but this did not alter participants' performance in such a demanding cognitive task. To provide further support to this conclusion, we also run Bayesian statistics allowing us to measure how confidently we can accept the null hypothesis of no difference between conditions. The Bayesian factor was 0.41 (error 0.0002), suggesting a moderate evidence for the null hypothesis. Data from Experiment 4, therefore, suggest that asynchronous sensorimotor stimulation and related FoP do no induce a generic reduction of attentional resources affecting cognitive performance in general, supporting the conclusions from Experiments 1-3 about a specific effect on source monitoring of one's own internal thoughts.

DISCUSSION

Taken together, the behavioral data from Experiments 1–4 show that sensorimotor conflicts, applied during mental operations, reliably induce behavioral changes in thought-related source monitoring (SGE, perceived word numerosity), accompanied by alterations in thought consciousness that are compatible with some aspects of TI that are usually only seen in clinical populations. Importantly, these behavioral changes in conditions with increased TI are characterized by a reduced ability to discriminate mental processes representing self-generated thoughts from those generated by others, reducing the SGE for self-generated versus other-generated words (Experiment 1) and making thought numerosity judgments more similar for words that were either actively generated or passively heard (and generated by another person) (Experiment 3). These effects were especially observed in individuals experiencing an alien presence that we induced by asynchronous sensorimotor stimulation, showing that our robotic manipulation of thought-related source monitoring is not just associated with the loss of thought agency and TI but also with the feeling of the presence of an alien agent. Control analyses and the data from the control Experiment 4 further show that these effects cannot be explained by general differences in cognitive load between the two sensorimotor conditions.

Previous work has shown that the robot-induced FoP results from the manipulation of sensory and motor stimuli, which involve tactile stimulation on the back, as well as proprioceptive, tactile, and motor cues (from the upper limb), the congruency of which in the spatial and temporal domains are controlled via the robot. In the current and our previous research (Blanke et al., 2014; Salomon et al., 2020; Bernasconi et al., 2020), two main experimental conditions were used (synchronous and asynchronous sensorimotor stimulation). Both conditions contain a spatial conflict (between the spatial position of the moving hand and the spatial position of the touch cue delivered on the back of the participants), whereas the asynchronous condition also contains an additional spatiotemporal conflict (i.e., movement performed by the hand is delivered to the back of the participants with a delay of 500 ms). The present FoP setup was motivated by models of sensorimotor processing and the forward model of motor control (Wolpert and Ghahramani, 2020) that have been applied to bodily illusions and hallucinations (Fletcher and Frith, 2009). Previous reports have tested the effects of systematically varied sensorimotor conflicts (i.e., delays) on different





hand-related bodily sensations (Weiskrantz et al., 1971; Blakemore et al., 1998, 2000) and the sense of agency (i.e., Farrer and Frith, 2002). However, there is an important additional element, compared with this previous research that is crucial for FoP induction: the interference with full-body processing (feedback at the back) that represents the body of the subject more globally and is a distinct sensorimotor and multisensory cortical system, when compared with the more local hand-related body representation system that has been studied by most previous investigators (for reviews see Blanke and Metzinger, 2009; Blanke et al., 2015). Thus, based on electrically induced FoP in a neurological patient (Arzy et al., 2006) and previous data using the same robotic system in healthy participants, Blanke et al. (2014) proposed that the FoP results from conflicting sensorimotor full-body signals that lead to the generation of a second self-representation (see self-location data in Blanke et al., 2014, and clinical data in Arzy et al., 2006) behind the participant that is misperceived as another person. Importantly, interference with this full-body system has been shown not only to lead to FoP but also to be related to global body illusions, such as out-of-body illusions and full-body illusions (i.e., Ehrsson, 2007; Lenggenhager et al., 2007).

The present data on TI demonstrate that the same asynchronous sensorimotor stimulation, when applied during mental operations, induces behavioral changes in thought-related source monitoring and in thought consciousness that depend on the FoP. For example, in Experiment 2, we showed that the intensity of the experimentally induced FoP was associated with changes in source monitoring characterized by self-generated words being perceived as more similar to other-generated words in the FoP-inducing asynchronous condition. As the number of self-generated words was perceived as higher and more similar to the number of other-generated words, selectively in the FoP-inducing asynchronous condition, we argue that under these conditions additional and alien-like thoughts were inserted into the minds of our healthy participants. In other words, if participants, while experiencing the FoP, are concurrently engaged in a cognitive task that implies implicit monitoring about the source of internal thoughts, the second self-representation behind the participant that is misperceived as another person (FoP), impacts such cognitive operations by inducing a misattribution of own inner thoughts. Accordingly, we argue that the present conflicting asynchronous sensorimotor stimulation in active, self-generating, conditions induces, in those participants experiencing the FoP, a mental state that is comparable to (albeit to a lesser degree and of short duration) to TI and thought alienation that is usually only reported by psychotic patients.

By defining a novel procedure that links robotics and cognitive science for the investigation of thought consciousness and its aberrations, the present approach offers, in healthy participants, novel insights into an enigmatic and clinically relevant psychotic symptom by firmly linking it to source monitoring and the FoP. Abnormal source monitoring has been shown to elegantly explain certain psychotic bodily experiences (i.e., somatic passivity, Frith, 1987) and has been proposed to account for other first-rank symptoms (Feinberg, 1978; Frith, 1987; Ford and Mathalon, 2004; Shergill et al., 2005) (i.e., delusions of control; auditory verbal hallucinations), but had only limited success in explaining TI (Frith, 1987, 2005). Importantly, previous research was not able to manipulate TI experimentally and especially not able to induce TI-related mental states repeatedly and in controlled fashion (e.g., based on reaction time or accuracy measures) (Walsh et al., 2015; Sugimori et al., 2011). Central to our report is the experimental induction and manipulation of behavioral and subjective aspects of TI in healthy subjects, providing implicit-behavioural (SGE; thought numerosity) and explicit-subjective (questionnaires) data that conflicting sensorimotor stimulation is sufficient to induce alterations in thought consciousness when participants perform active mental operations. Behaviorally, we demonstrate that the present robotically induced TI is characterized by reduced source monitoring, a reduced ability to discriminate mental processes representing one's own mental operations from those representing mental operations of others, resembling passive thoughts and thoughts generated by another person, rather than one's own thoughts. Importantly, by manipulating specific sensorimotor processes that alter body representation (Blanke et al., 2014), we show that these changes were especially prominent in individuals experiencing an illusory and experimentally induced alien presence, as if the illusory alien presence (FoP) inserted alien thoughts into the mind of our healthy participants. We conclude that the present asynchronous sensorimotor stimulation induces in healthy participants, who tend to experience the illusory FoP, a mild and short-lasting behavioral and mental state that is reminiscent of symptomatic TI, an enigmatic and key symptom in psychosis.

Limitations of the study

The current study has some limitations. First, although the behavioral responses related to TI we report are robust and based on many repeated trials, the induction of subjective TI in study 3 was of mild to moderate

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intensity and thus differs from more prolonged and intense symptomatic TI in psychotic patients. Future work should strive to induce mental states of subjective TI of stronger intensity and also test the present robotic procedure and paradigms in psychotic patients with symptomatic TI. Second, in the present study only one condition of asynchronous stimulation was tested to induce the FoP. Thus, no specific indications can be provided about the critical delay between movement and feedback generating the effect. Other data available as pre-print (Bernasconi et al., 2020) show that the intensity of FoP rises depending on the delay between the moving hand and tactile feedback on the back (i.e., from 0 to 500 ms), with a plateau at 500-ms delay. Third, we did not investigate the involved neural correlates of TI or the FoP, which was outside the scope of the present study. Future work should target FoP and TI, jointly with brain imaging methods, in healthy participants and different patient populations, to unravel the brain mechanisms of robot-induced TI and FoP.

Finally, the present data do not allow us to indicate why some healthy participants are more prone to experience the FoP via our robotic sensorimotor stimulation. Individual differences in proneness to perceptual illusions (see, i.e., Marotta et al., 2016) and to bodily illusions (e.g., the rubber hand illusion; Asai et al., 2011; Tsakiris et al., 2011) have been extensively reported. However, different explanations have been proposed and will also apply to FoP. These range from differences in personality traits (e.g., hypnotizability: Lush et al., 2020; schizotypal and empathic traits: Tsakiris et al., 2011; sensory suggestibility: Marotta et al., 2016; perceptual priors within a Bayesian framework: Tulver et al., 2019) to neural differences such as differences in gray matter and in structural and functional connectivity (i.e., Kanai and Rees, 2011). It is possible that these non-mutually exclusive factors also contribute to individual differences in susceptibility to the FoP, but future research is needed to identify their specific roles.

Resource availability

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Materials availability

This study did not generate new unique materials.

Data and code availability

The datasets generated during this study are available at Serino, Andrea (2020), "Thought consciousness and source monitoring depend on robotically-controlled sensorimotor conflicts and illusory states," Mendeley Data, V1, https://doi.org/10.17632/n2k4tjxzg8.1.

METHODS

All methods can be found in the accompanying Transparent methods supplemental file.

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.isci.2020.101955.

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AUTHORS CONTRIBUTION

A.S., F.B., P.P. designed the study, carried out the experiments, analyzed data, and wrote the paper, M.S. carried out the experiments and analyzed data, M.H. and H.B designed and built the robotic device, P.P., K.D., J.P., and P.C. carried out clinical work, M.M., G.S., and H.D. carried out the experiments, A.G. and R.S. analyzed data, G.R. designed the study, built the robotic device, collected data, analyzed data, and wrote the paper; O.B. designed the study, analyzed the data, and wrote the paper.

DECLARATION OF INTERESTS

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., G.R., and M.H. 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 Metaphysiks 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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REFERENCES

Arzy, S., Seeck, M., Ortigue, S., Spinelli, L., and Blanke, O. (2006). Induction of an illusory shadow person. Nature 443, 287.

Asai, T., Mao, Z., Sugimori, E., and Tanno, Y. (2011). Rubber hand illusion, empathy, and schizotypal experiences in terms of self-other representations. Conscious. Cogn. 20, 1744–1750.

Bays, P.M., Flanagan, J.R., and Wolpert, D.M. (2006). Attenuation of self-generated tactile sensations is predictive, not postdictive. PLoS Biol. 4, e28.

Bays, P.M., Wolpert, D.M., and Flanagan, J.R. (2005). Perception of the consequences of selfaction is temporally tuned and event driven. Curr. Biol. 15, 1125–1128.

Bernasconi, F., Blondiaux, E., Potheegadoo, J., Stripeikyte, G., Pagonabarraga, J., Bejr-Kasem, H., Bassolino, M., Akselrod, M., Martinez-Horta, S., Sampedro, F., et al. (2020). Neuroscience robotics reveals fronto-temporal brain mechanisms of sensorimotor hallucinations in patients with Parkinson's disease. Sci. Transl. Med. https://doi.org/10.1101/2020.05.11.054619.

Blakemore, S.J., Wolpert, D.M., and Frith, C.D. (1998). Central cancellation of self-produced tickle sensation. Nat. Neurosci. *1*, 635–640.

Blakemore, S.J., Wolpert, D.M., and Frith, C.D. (2000). Why can't you tickle yourself? Neuroreport 11, R11–R16.

Blanke, O., Pozeg, P., Hara, M., Heydrich, L., Serino, A., Yamamoto, A., Higuchi, T., Salomon, R., Seeck, M., Landis, T., et al. (2014). Neurological and robot-controlled induction of an apparition. Curr. Biol. 24, 2681–2686.

Blanke, O., and Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. Trends Cogn. Sci. 13, 7–13.

Blanke, O., Slater, M., and Serino, A. (2015). Behavioral, neural, and computational principles of bodily self-consciousness. Neuron 88, 145–166.

Ehrsson, H.H. (2007). The experimental induction of out-of-body experiences. Science 317, 1048.

Faivre, N., Vuillaume, L., Bernasconi, F., Salomon, R., Blanke, O., and Cleeremans, A. (2020). Sensorimotor conflicts alter metacognitive and action monitoring. Cortex 124, 224–234.

Farrer, C., and Frith, C.D. (2002). Experiencing oneself vs another person as being the cause of an action: the neural correlates of the experience of agency. Neuroimage 15, 596–603.

Feinberg, I. (1978). Efference copy and corollary discharge: implications for thinking and its disorders. Schizophrenia Bull. 4, 636.

Fletcher, P.C., and Frith, C.D. (2009). Perceiving is believing: a Bayesian approach to explaining the positive symptoms of schizophrenia. Nat. Rev. Neurosci. 10, 48–58.

Ford, J.M., and Mathalon, D.H. (2004). Electrophysiological evidence of corollary discharge dysfunction in schizophrenia during talking and thinking. J. Psychiatr. Res. 38, 37–46.

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.

Frith, C.D. (2005). The self in action: lessons from delusions of control. Conscious. Cogn. 14, 752–770.

Gallagher, S. (2004a). Agency, ownership, and alien control in schizophrenia. Adv. Consciosuness *59*, 89–104.

Gallagher, S. (2004b). Neurocognitive models of schizophrenia: a neurophenomenological critique. Psychopathology *37*, 8–19.

Hara, M., Rognini, G., Evans, N., Blanke, O., Yamamoto, A., Bleuler, H., and Higuchi, T. (2011). A novel approach to the manipulation of bodyparts ownership using a bilateral master-slave system. IEEE/RSJ Int. Conf. Intell. Robots Syst. 4664–4669.

Hoffman, R.E. (1986). Verbal hallucinations and language production processes in schizophrenia. Behav. Brain Sci. 9, 503–517.

Johns, L.C., Cannon, M., Singleton, N., Murray, R.M., Farrell, M., Brugha, T., Bebbington, P., Jenkins, R., and Meltzer, H. (2004). Prevalence and correlates of self-reported psychotic symptoms in the British population. Br. J. Psychiatry 185, 298–305.

Kanai, R., and Rees, G. (2011). The structural basis of inter-individual differences in human behaviour and cognition. Nat. Rev. Neurosci. 12, 231–242.

Koehler, K. (1979). First rank symptoms of schizophrenia: questions concerning clinical boundaries. Br. J. Psychiatry 134, 236–248.

Lenggenhager, B., Tadi, T., Metzinger, T., and Blanke, O. (2007). Video ergo sum: manipulating bodily self-consciousness. Science 317, 1096–1099.

Lezak, M., Howieson, D., and Loring, D. (1995). Executive functions and motor performance. Neuropsychol. Assess. *3*, 650–685.

Lush, P., Botan, V., Scott, R.B., Seth, A.K., Ward, J., and Dienes, Z. (2020). Trait phenomenological control predicts experience of mirror synaesthesia and the rubber hand illusion. Nat. Commun. 11, 1–10.

Marotta, A., Tinazzi, M., Cavedini, C., Zampini, M., and Fiorio, M. (2016). Individual differences in the rubber hand illusion are related to sensory suggestibility. PLoS One 11, e0168489.

Martin, J.R., and Pacherie, E. (2013). Out of nowhere: thought insertion, ownership and

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context-integration. Conscious. Cogn. 22, 111–122.

Miller, T.J., McGlashan, T.H., Woods, S.W., Stein, K., Driesen, N., Corcoran, C.M., Hoffman, R., and Davidson, L. (1999). Symptom assessment in schizophrenic prodromal states. Psychiatr. Q. 70, 273–287.

Orepic, P., Rognini, G., Kannape, O.A., Faivre, N., and Blanke, O. (2020). Sensorimotor Conflicts Induce Somatic Passivity and Louden Quiet Voices in Healthy Listeners. https://doi.org/10.1101/2020.03.26.005843.

Salomon, R., Progin, P., Griffa, A., Rognini, G., Do, K.Q., Conus, P., Marchesotti, S., Bernasconi, F., Hagmann, P., Serino, A., and Blanke, O. (2020). Sensorimotor induction of auditory misattribution in early psychosis. Schizophr Bull. 8, 947–954.

Schneider, K. (1959). Clinical Psychopathology (Grune and Stratton).

Schultze-Lutter, F., Addington, J., Ruhrmann, S., and Klosterkötter, J. (2007). Schizophrenia Proneness Instrument, Adult Version (SPI-A) (Giovanni Fioriti).

Shergill, S.S., Bays, P.M., Frith, C.D., and Wolpert, D.M. (2003). Two eyes for an eye: the neuroscience of force escalation. Science 301, 187.

Shergill, S.S., Samson, G., Bays, P.M., Frith, C.D., and Wolpert, D.M. (2005). Evidence for sensory prediction deficits in schizophrenia. Am. J. Psychiatry *162*, 2384–2386.

Shergill, S.S., White, T.P., Joyce, D.W., Bays, P.M., Wolpert, D.M., and Frith, C.D. (2014). Functional magnetic resonance imaging of impaired sensory prediction in schizophrenia. JAMA Psychiatry 71, 28–35

Slamecka, N.J., and Graf, P. (1978). The generation effect: delineation of a phenomenon. J. Exp. Psychol. Hum. Learn. Mem. 4, 592.

Stephens, G.L., and Graham, G. (2000). When Self-Consciousness Breaks: Alien Voices and Inserted Thoughts (The MIT press).

Sugimori, E., Asai, T., and Tanno, Y. (2011). Sense of agency over thought: external misattribution of thought in a memory task and proneness to auditory hallucination. Conscious. Cogn. 20, 688–695.

Tsakiris, M., Jiménez, A.T., and Costantini, M. (2011). Just a heartbeat away from one's body: interoceptive sensitivity predicts malleability of body-representations. Proc. R. Soc. B Biol. Sci. 278, 2470–2476.

Tulver, K., Aru, J., Rutiku, R., and Bachmann, T. (2019). Individual differences in the effects of priors on perception: a multi-paradigm approach. Cognition 187, 167–177.

Vicente, A. (2014). The comparator account on thought insertion, alien voices and inner speech: some open questions. Phenomenol. Cogn. Sci. 13, 335–353.

Walsh, E., Oakley, D.A., Halligan, P.W., Mehta, M.A., and Deeley, Q. (2015). The functional anatomy and connectivity of thought insertion and alien control of movement. Cortex *64*, 380–393.

Weiskrantz, L., Elliott, J., and Darlington, C. (1971). Preliminary observations on tickling oneself. Nature *230*, 598–599.

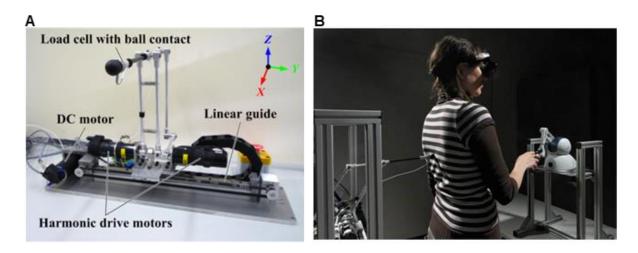
Wolpert, D.M., and Ghahramani, Z. (2020). Computational principles of movement neuroscience. Nat. Neurosci. 3, 1212–1217.

Supplemental Information

Thought consciousness and source monitoring depend on robotically controlled sensorimotor conflicts and illusory states

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Supplemental Figure and Table



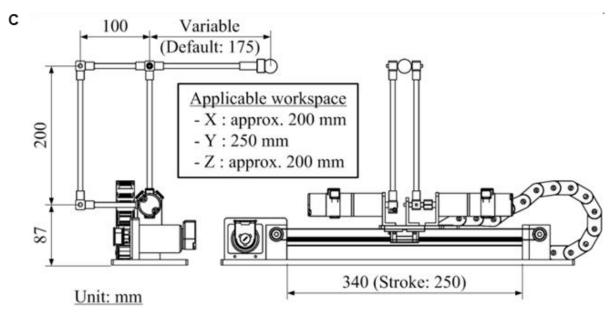


Figure S1. Lead-follow robotic system, related to Figure 1, Figure 2, Figure 3 (Experiment 1-4). This system is composed of a commercial haptic interface, the lead robot (Phantom Omni, SensAble Technologies), and a three degree-of-freedom robot (follow robot). The follow device consists of two mechanisms: a belt-drive mechanism and a parallel-link mechanism. The belt-drive mechanism is made up of a belt linked to a direct-drive DC motor (RE 40, Maxon) moving a carrier on a linear guide allowing movements in the y (forward-backward) direction. The parallel-link mechanism is actuated through two harmonic drive motors (RH-8D 6006, Harmonic Drive Systems) and enables both tapping and stroking in x (right-left) and z (up-down) directions. These three motors equipped with optical encoders for positions sensing are connected to motor drivers (4-Q-DC Servoamplifier LSC 30/2 & ADS 50/5, Maxon) that receive the command voltages from a computer via PCI data acquisition cards (NI PCI-6221 & NI PCI-6014, National Instruments). The overall workspace of the follow device is 200mm in the x direction, 250mm in the y direction and 200mm in the z direction. A load cell (ELPFTIM-50N, Measurement Specialties) is attached on the tip of the follow device in order to measure contact force.

| | М | | SEM | | | |
|--|-------|-------|------|-------|------|------|
| Questionnaire item | Sync | Async | Sync | Async | Z | р |
| Thought influencing | | | | | | |
| Q7: It seemed as if the robot behind | | | | | | |
| influenced some of my thoughts. | 1.89 | 3.33 | 0.35 | 0.39 | 2.34 | 0.01 |
| Q3: It seemed as if some outside force or | | | | | | |
| person has influenced some of my thoughts. | 2.28 | 3.00 | 0.36 | 0.36 | 1.25 | 0.12 |
| Thought insertion | 2.20 | 3.00 | 0.50 | 0.50 | 1.23 | 0.12 |
| Thought insertion | | | | | | |
| Q1: It seemed as if someone else has been | | | | | | |
| thinking certain thoughts in my mind. | 1.61 | 2.00 | 0.32 | 0.33 | 2.11 | 0.03 |
| Q11: It seemed as if the robot put certain | | | | | | |
| thoughts in my mind. | 1.67 | 2.50 | 0.31 | 0.41 | 1.91 | 0.03 |
| Q8: It seemed as if some outside force or | | | | | | |
| person has put certain thoughts into my | 2.44 | 244 | 0.24 | 0.43 | 0.26 | 0.20 |
| mind. Q10: It seemed as if some thoughts (that | 2.44 | 2.44 | 0.34 | 0.42 | 0.36 | 0.38 |
| were not my own) intruded my mind. | 2.28 | 2.06 | 0.40 | 0.38 | 0.21 | 0.45 |
| Thought ownership | | | | | | |
| Q5: It seemed as if certain thoughts I had | | | | | | |
| belonged to someone else. | 1.61 | 2.00 | 0.33 | 0.39 | 0.98 | 0.19 |
| Thought withdrawal | | | | | | |
| Q2: It seemed as if some of my thoughts | | | | | | |
| have been removed from my mind. | 4.00 | 4.39 | 0.40 | 0.26 | 0.80 | 0.23 |
| Parasite thoughts | | | | | | |
| Q12: It seemed as if the train of my | | | | | | |
| thoughts have been interrupted by some | 4 4 7 | 4.20 | 0.24 | 0.24 | 0.44 | 0.24 |
| unimportant "parasite" thoughts. | 4.17 | 4.28 | 0.34 | 0.31 | 0.41 | 0.34 |
| Thought echoing Q4: It seemed as if some of my thoughts | | | | | | |
| were echoed back to me. | 2.72 | 2.89 | 0.52 | 0.40 | 0.05 | 0.49 |
| Voice distortion | 2.72 | 2.05 | 0.02 | | 0.00 | 0.15 |
| Total distortion | | | | | | |
| Q6: It seemed as if my voice became | | | | | | |
| distorted. | 2.33 | 2.61 | 0.59 | 0.54 | 0.88 | 0.21 |
| | | | | | | |
| Q9: It seemed as if my speech became | 2.22 | | | 0.55 | | 0.40 |
| hard to understand. | 3.22 | 2.94 | 0.55 | 0.56 | 0.94 | 0.19 |

Table S1. Subjective response results, related to Figure 3 (Experiment 3). All items from the Thought insertion questionnaire with average item ratings, standard errors of the mean for synchronous and asynchronous conditions, and Z and 2-tailed p-values of Wilcoxon signed rank tests for the differences between the ratings of synchronous and asynchronous conditions. TI related questions are: Q1, Q3, Q7, Q8, Q10 and Q11. Control Questions are: Q2, Q4, Q5, Q6, Q9, Q12.

Transparent Methods

Participants

A total of 93 healthy participants took part in four separate behavioural experiments. Experiment 1 consisted of 35 participants (11 female; mean age: M=20.5 years, SD=2.5 years), Experiment 2 of 19 participants (9 female; mean age: M=20.3 years, SD=2.4 years), and Experiment 3 of 19 participants (6 female; mean age M=20.9 years, SD=2.0 years), and Experiment 4 of 20 participants (10 female; mean age M = 28.4 years, SD = 6.29 years). All participants for Experiments were recruited by an advertisement at the EPFL campus (École Polytechnique Fédérale de Lausanne, Lausanne, Switzerland) and at Campus Biotech (Geneva, Switzerland). All participants had normal touch perception and no psychiatric or neurologic history as assessed by self-report. All participants were native French speakers. Each participant only took part in one experiment only. All participants were naive to the purpose of the experiments and gave written informed consent to take part in the experiment. Experiments were approved by the EPFL ethics committee (Comité d'éthique de la recherche humaine) and were conducted according to the ethical standards laid down in the Declaration of Helsinki. Participants gave written informed consent after the experimental procedures were explained to them and were reimbursed for their participation with 20 Swiss Francs.

Apparatus

Robotic sensorimotor system. To experimentally create sensorimotor mismatch we adapted a bilateral master-slave robotic system that has been previously used to manipulate changes in bodily self-consciousness (Blanke et al., 2014; Hara et al., 2011). This system is composed of a commercial master haptic interface, the Phantom Omni (Sens Able Technologies), and a three degree-of-freedom slave robot. The slave device consists of two mechanisms: a belt-drive mechanism and a parallel-link mechanism. The belt-drive mechanism is made up of a belt linked to a direct-drive DC motor (RE 40, Maxon) moving a carrier on a linear guide allowing movements in the y (forward-backward) direction. The parallel-link mechanism is actuated through two harmonic drive motors (RH-8D 6006, Harmonic Drive Systems) and enables both tapping and stroking in x (right-left) and z (up-down) directions. These three motors equipped with optical encoders for positions sensing are connected to motor drivers (4-Q-DC Servoamplifier LSC 30/2 & ADS 50/5, Maxon) that receive the command voltages from a computer via PCI data acquisition cards (NI PCI-6221 & NI PCI-6014, National Instruments). The overall workspace of the slave

device is 200mm in the x direction, 250mm in the y direction, and 200mm in the z direction (See Figure S1).

A load cell (ELPFTIM-50N, Measurement Specialties) is attached to the tip of the slave device in order to measure contact force. This allowed us to introduce a compliance factor on the system preventing the slave device from applying instantaneous strong force to the participants, making the interaction safer and more realistic. The system was controlled through an application programmed in Visual C++ (Microsoft) at a sampling rate of 1 kHz. The latency related to information transfer delays and computational processing necessary for mapping the master device movements to the slave device movements (i.e. touching the back of the participants) was equal to 1ms. The system had a bandwidth of approximately 2.5 Hz allowing a good synchrony between the master and the slave even during rapid and abrupt changes in velocity and direction (Hara et al., 2011). This allowed reducing the constraints on participants' movements.

In each experiment, the participants were first explained the task and informed about the general procedure of the experiment. Then they were instructed on how to use the robotic device to apply touch on their back through the tip of the slave device. The experimenter demonstrated the type of movements they were supposed to perform during the experimental blocks. In particular, they were asked to perform tapping movements in front of them by holding the master device with both hands, while receiving the touch on their back by the slave device. They were allowed to tap in different directions (up-down, left-right) resulting in different touches applied on their back within a workspace of 200x200mm. In the training session, the participants used the system in the synchronous mode for about 1 minute without being blindfolded.

General experimental procedure

The robotic sensorimotor system was used to apply sensorimotor stimulation in the different experiments in two different conditions: synchronous sensorimotor stimulation (the participants were asked to move the lead robot via their right index finger, this way actuating the follow robot which provided immediate and congruent touches to the participant's back) and asynchronous sensorimotor stimulation (500 ms delay between the first robot operated via the right index finger and the second robot applying tactile feedback on the participants' back). During the robotic stimulation participants were always blindfolded. In each experiment, the participants were first explained the task and informed about the general procedure of the experiment. Then they were instructed on how to use the robotic device to apply touch on their back through the tip of the follow device. The experimenter demonstrated the type of movements they were supposed to perform during the experimental blocks. In particular, they were asked to perform tapping

movements in front of them by holding the lead device, while receiving the touch on their back by the follow device. They were allowed to tap in different directions (up-down, left-right) resulting in different touches applied on their back within a workspace of 200x200mm. In the training session, the participants used the system in the synchronous mode for about 1 minute without being blindfolded.

Experiment 1 – self generation effect: design, procedure and analyses

Experiment 1 was designed to assess the so-called self-generation effect (SGE, Slamecka et al., 1978), originally described by Slamecka and Graf, while performing robotic stimulation. In this paradigm, the participants are either presented with a list of words (passive condition; participants only heard the words) or they were asked to generate their own words (active condition; participants produced and heard the words) within a given set of rules (see next two paragraphs for more detail). During the encoding session, we asked participants to memorize both the heard and the self-generated words. In the recognition session, participants were presented with a list of words (pre-recorded and played back), containing either the words they had generated or heard and other semantically related words, that were never presented and used as distractor (50% of target and 50% of distractor words were presented in random order). Participants were asked to determine for each word whether it is a word he or she had generated or heard during the encoding session or not. Participants typically remember the self-generated items (active condition) better than the heard items (passive condition). This phenomenon, termed selfgenerated effect, SGE, has been shown to be very robust and has been described in recognition and recall tasks and with a variety of materials, generation rules, and retention intervals (Hirshman et al., 1988).

Active condition. In the active conditions, participants heard 35 cue words, each followed by a cue letter. Participants were instructed to generate an associated word, which had to start with the specified letter, and utter it out loud. If the participant's generated word matched the predicted word (target word), the experimenter registered it, and the word was later used in the recognition task during the test recognition phase. The time interval between the cue word and cue letter presentation was 1s, and participants' performance was self-paced in the encoding as well as in the recognition session.

Passive Condition. In the encoding session of the passive conditions, participants merely listened to 35 audio-played word pairs, and were instructed that they would be later tested for recognition of the second word in a pair.

Design and procedure. We performed a 2 x 2 factorial repeated measures design with the factor Sensorimotor stimulation (synchronous and asynchronous sensorimotor stimulation) and the factor Source (active, passive). Each participant therefore completed four experimental conditions, given in randomized order. At the beginning of each condition and before the encoding session started, we asked participants to move the robot for 60 seconds. During the encoding session, depending on the condition, they listened to either pairs of words (passive conditions) or they generated their own words after hearing a cue word and a cue letter (active conditions), while continuing to operate the robotic device. Participants wore headphones and were blindfolded throughout the encoding phase. After the encoding session, participants were asked to stop operating the robot and to remove the blindfolding and commenced the recognition task. At the end of the task and after each condition, participants were administered the questionnaire (see below).

Effect size estimation. We estimated the effect size for the self-effect for Experiment 1 based on the Experiment reported in Blanke et al., 2014 (study 4), where by participants were asked to estimated how many people there were close to them. Participants reported on average 0.74 (SD=0.30) and 0.99 (SD=0.34) persons, resulting in an effect size of 0.73 resulting on a suggested sample size of N = 28. We initially recruited 35 participants and we only included in the present analysis those participants, who produced enough word associations and whose performance was above chance (Slamecka et al., 1978). This sample size is in line with the original report of the Generation effect by (Slamecka et al., 1978) (N = 24).

Data analysis. In order to avoid ceiling effects in the recognition task for self-generated words, only the data of participants who generated more than 50% of expected associations (at least 18 words) were included into analysis. Also, participants who performed below chance level in the recognition task were excluded from analysis, leaving data from 22 remaining participants for further analysis. Task performance was defined by d-prime scores, which were then analyzed with repeated measures ANOVA, with Source and Sensorimotor stimulation as the two within-subjects factors and the feeling of a presence (FoP) score as a covariate. Based on the recent finding that the FoP can be experimentally induced in healthy participants due to a specific spatial and temporal sensorimotor mismatch (Blanke et al., 2014), we calculated the FoP score by subtracting the ratings of the FoP questionnaire item in the asynchronous from the ratings in the synchronous condition. Thus, higher FoP scores indicate a stronger FoP illusion due to the robotically induced sensorimotor mismatch.

Acquisition and preparation of auditory word stimuli. For Experiment 1, 250 word association pairs were first selected from the database of word association norms containing a collection of French

words (Ferrand et al., 1998). In order to balance the strength of association between the cue word and its associated target word across conditions, we have recruited 10 native French speakers (2 females; 18 – 23 years, M=20.1, SD=1.66). They were given the selected 250 cue words and cue letters (first letter of the predefined target word) to generate associations. The strength of the association was defined as the frequency with which participants chose the target word. 70 association pairs with higher association strength (0.7 - 1) were then selected for the selfgenerated conditions to increase the probability of participant generating the target word. 70 association pairs with lower association strength (0.3 - 0.6) were used for the other-generated conditions. Another 140 words were selected from the database to be used as distractor words during recognition task. The association pairs were then sorted into 4 alternative word lists (2 for self-generated and 2 for other-generated conditions), each consisting of 35 word pairs, with balanced association strength. Similarly, the distractor words were divided into 4 lists, each containing 35 distractor words. We verified, using the multivariate analysis of variance (MANOVA), that there was no significant difference in terms of frequency of use (www.lexique.org) and word length between the alternative lists (F(6, 544)=0.494, p=0.813) or between the target and distractor words (F(2, 271)=0.001, p=0.999). The word set was then recorded by two male and two female native French speakers and registered in wav format with 11025 Hz sampling frequency. In both Experiment 1 and Experiment 2, as well as during the pilot experiment (see below, Supplementary Results), the auditory word stimuli were played to participant in a gender-matched voice. In Experiment 1, two gender-matched voices were alternating between the encoding and testing phase in a balanced manner throughout the experiment.

Experiment 2 - Thought numerosity: design, procedure and analyses

Experiment 2 was designed to estimate the number of thoughts in the participants' mind while performing robotic stimulation (in analogy to perceptual numerosity tasks; Krueger, 1972). To this aim, we implemented a fluency task, whereby, we asked participants to estimate the number of words that they have either generated themselves (active condition) or have listened to (passive condition), while operating the robotic sensorimotor system.

Design. We used a 2 x 2 factorial repeated-measures design, whereby we manipulated the Sensorimotor stimulation (synchronous and asynchronous sensorimotor stimulation) and the Source of the words to be estimated (active, passive). In the active conditions, a starting phoneme was played to participants through the headphones and they were instructed to generate as many words as possible starting with the specified phoneme, in a given time period (phonetic fluency

task). This time period randomly varied between 15 and 30s, in order to avoid participants always producing and estimating a similar number of words. The experimenter counted and registered the words and, immediately afterwards, the participant had to estimate how many words she or he had generated. In the passive conditions the participants listened to a list of words, consisting of between 6 and 10 words (based on the number of words another group of participants generated in the active condition; see *Pilot experiment* in Supplementary Results). The number of words randomly varied throughout the trials. The words were played to participants with an inter-stimuli interval of 2.5s. All words and phoneme cues were presented to participants as auditory stimuli using MATLAB software (MathWorks, Inc.). In the passive condition, in order to prevent participants from counting the words, they were asked to determine whether each word they heard contains a phoneme, specified at the beginning of a trial. Each condition was repeated three times, and each repetition consisted of 4 trials, resulting in total of 12 numerosity judgments per condition. The order of repetitions of the different experimental conditions was counterbalanced across the participants. The dependent variable was the numerosity judgement accuracy, calculated by subtracting the actual number of played or produced words from the number of judged number of words. Prior to the beginning of the experimental session, participants went through a training session, comprising one repetition of each condition. Before or after the experiment in a counterbalanced manner, participants were asked to operate the robot for 60s in the synchronous and asynchronous mode (run in counterbalanced order), being blindfolded and instructed to only focus on their movements and tactile feedback. After the synchronous and asynchronous blocks, they were given the FoP illusion questionnaire in order to measure the degree of the illusion induced by the sensorimotor stimulation.

Effect size estimation. Data from Experiment 1 were used to estimate the minimum sample size for Experiment 2 (self-effect part). In the group who experienced the FoP, the self-effect for asynchronous and synchronous stimulation was 1.53 (SD=0.83) and 2.33 (SD=0.75), resulting in an effect size of 1.008 and suggesting a minimum sample size of 15. We recruited 19 participants. For the questionnaire part, we estimated the required sample to replicate the FoP effect based on Study 3 from Blanke et al., 2014. The average ratings for the FoP question were 4 (SD=1.9) and 2.14 (SD=1.65) in the asynchronous and synchronous conditions respectively, resulting in a size effect of 1.30 and suggesting a sample size of 15 participants. We tested 19 participants via questionnaires assessing subjective thought insertion.

Data analysis. Two trials from two participants were discarded from analysis, because they failed to generate any word within the given time limit. The differences between the numerosity judgment and actual number of words (judgment accuracy) were averaged within each condition

for each participant and then analyzed with repeated measures ANOVA where *Sensorimotor stimulation* (synchronous and asynchronous sensorimotor stimulation) and *Source* (active, passive) were used as within-subject factors.

Experiment 3 – changes in thoughts subjective experience: design, procedure and analyses Experiment 3 was designed to measure whether robotic sensorimotor stimulation induced explicit changes in the subjective experience associated to internal thoughts. To this aim, a new group of participants again operated the robotic lead-follow system (as in Experiment 1 and 2), while simultaneously performing a phonetic fluency task. In a repeated-measures design, we manipulated the factor Sensorimotor stimulation (synchronous vs asynchronous). Participants manipulated the robotic system in synchronous and asynchronous mode for 3 minutes. At the start of each condition, they heard a French phoneme through headphones, and were then given three minutes to generate as many words as possible that started with the specified phoneme. At the end of each condition, they were asked to answer several questions referring to their thinking process during task performance (see below). The order of synchronous and asynchronous conditions was counterbalanced across the subjects. Before or after the experiment in a counterbalanced manner, participants were also asked to operate the robot for 60s in both, synchronous and asynchronous modes while blindfolded and focused on their bodily sensations. After these synchronous and asynchronous blocks, they were given the FoP questionnaire (see below).

In order to evaluate subjective experience during internal thoughts, we designed a detailed, 12-item questionnaire. The items were constructed based on the literature on thought possession disorders (Miller et al., 1999; Schultze-Lutter et al., 2007) and particularly targeted feelings related to thought insertion (ex. "It seemed as if some outside force or person has put certain thoughts in my mind"), thought influence (ex. "It seemed as if some outside force or person has influenced some of my thoughts"), thought ownership (ex. "It seemed as if certain thoughts I had belonged to someone else") and thought withdrawal (ex. "It seems as if some of my thoughts have been removed from my mind"). Other items, which served as control for suggestibility, pertained to positive psychotic symptoms, but not to disorders of thought possession, i.e. parasite thoughts, thought echoing, and voice distortion. The participants were asked to rate how much they agreed with each questionnaire item on a 7-point Likert scale (0 = not at all, 3 = not certain, 6 = very strong) (see Table S2).

Experiment 4 - working memory task - design, procedure and analyses

Experiment 4 was designed to assess the effects of robotic stimulation on a working memory task. As in the previous experiments, blindfolded participants operated the robotic lead-follow system, while they were performing a 2-back verbal task, selected as a well-established paradigm and highly demanding in terms of cognitive resources. In a repeated-measures design, we manipulated *Sensorimotor stimulation* (synchronous vs asynchronous). Participants performed 16, 24 or 32 second blocks of sensorimotor stimulation with the robot either in the synchronous or asynchronous conditions, in counterbalanced order. During the stimulation, they were presented with a series of numbers (one every two seconds), which were administered via headphones. Subjects were required to respond (via button press) if the current number in the series was equal to the last but one heard in the series. Each condition consisted of 24 trials. At the end of the task, they were also presented with the BSC questionnaire assessing the FoP and related sensations (see below).

Effect size estimation. Effect size was calculated based on the results of Experiment 2. Given the obtained differences between self-generated and other-generated words and the associated standard deviations, resulting in a significant interaction between stimulation condition and agent (p=0.015), the necessary sample size to replicate the effect with a p<0.05 is N=20.

Subjective changes in BSC.

To measure changes in bodily self-consciousness as induced by the robotic sensorimotor stimulation, for all experiments, we administered the same questionnaire as used previously (4). The questionnaire consists of 8 items, referring to the feeling of presence ("I felt as if someone was standing behind my body"), sensation of passivity ("I felt as if someone else was touching my body"), and other bodily illusions (see Supplementary Information). Two items served as control items for suggestibility (i.e. "I felt as if I had no body" and "I felt as if I had more than one body"). Participants were asked to designate on a 7-point Likert scale, how strongly they felt the sensation described by each item (0 = not at all, 3 = not certain, 6 = very strong).

Statistical Analysis. To assess statistical differences induced by the different experimental conditions on the subjective experiences (thoughts and BSC questionnaires), a one-tailed Wilcoxon signed rank test was applied to each question independently to compare response for the synchronous and asynchronous stimulation condition. One-tailed was decided because of the strong hypothesis that our effects would be always bigger for the asynchronous sensorimotor stimulation.

Supplemental Results

Experiment 1

FoP Questionnaire. Participants experienced stronger sensation to be touched by another person in the asynchronous condition (synchronous: M = 3.20, SD = 1.71; asynchronous: M = 3.84, SD = 1.78; Z = -2.399, p = 0.005) and also reported a stronger feeling of a presence in the same, asynchronous condition (synchronous: M = 2.80, SD = 1.55; asynchronous: M = 3.24, SD = 1.48; Z = -2.361, p = 0.005). Conversely, the participants reported stronger illusory self-touch when they operated the robotic system in the synchronous condition (synchronous: M = 3.18, SD = 1.50; asynchronous: M = 2.24, SD = 1.43; Z = -2.985, p = 0.002). The ratings of the control items were low and not significantly affected by the sensorimotor stimulation (M < 1.5, SD < 1.80, all p < 0.05), except the item: "I felt as if I was behind my body" (synchronous: M = 2.30, SD = 1.77; asynchronous: M = 1.82, SD = 1.47; Z = -2.623, D = 0.005).

Subjective loss of thought agency (Questionnaire). The effect of sensorimotor stimulation modulation was also observed for the sense of agency over self-generated thoughts. The participants reported a reduced sense of agency ("It seemed as if I was not the one who generated the words") for the words they generated in the asynchronous (M = 2.21, SD = 1.728) as compared to the synchronous condition (M = 1.73, SD = 1.625; Z = -1.894, p = 0.029). The sensorimotor stimulation did not modulate the experience of thought insertion proper (synchronous: M = 2.97, SD = 1.610, asynchronous: M = 3.03, SD = 1.794; Z = -.340, p = 0.367) or ownership for self-generated words (synchronous: M = 1.55, SD = 1.348, asynchronous: M = 1.67, SD = 1.407; Z = -0.537, p = 0.296), although in both cases ratings were higher in the asynchronous condition.

Pilot Experiment: Verification of the generation effect with auditory stimuli. To confirm that the generation effect can be also achieved by using selected word stimuli presented in the auditory modality, prior to the main experiment we conducted a pilot experiment without the robotic sensorimotor stimulation. 6 native French speaking participants (3 females, M = 20.6 years, SD = 2.7) were recruited to participate in this experiment. They completed two self-generated and two other-generated conditions in a randomized order. Two-tailed paired-sample t-test showed that the accuracy rate (t(5) = 5.289, p = 0.003), as well as sensitivity (t(5) = 7,264, p = 0.001), in the recognition task was significantly higher for the self-generated words, demonstrating that the generation effect was replicated with the selected auditory word material.

Behavioral paradigm: Self-generation effect. The analysis of performance in the memory task replicates the classical self-generation effect (SGE), as the main effect of source was significant (self: M = 4.12, SD = 0.45; other: M = 2.28, SD = 0.65; F(1,20) = 180.86, P < 0.0001). Importantly, this self-effect was significantly modulated by the manipulation of the sensorimotor stimulation in relation to the experience of FoP (interaction between generation source, sensorimotor stimulation and covariate FoP score: (F(1,20) = 6.95, p = 0.016). To investigate this interaction, we split the sample into two groups according to the experience of FoP (No-FoP group: Fop score ≤ 0; FoP group: FoP score > 0) and tested whether the two groups differed in the modulation of the self-effect due to sensorimotor mismatch. The mixed ANOVA on the strength of the self-effect (calculated as d' for recognition of self-generated - d' for other generated words) showed a significant interaction between sensorimotor stimulation and group (F(1,20) = 7.217, p = 0.014). Post-hoc comparisons further showed a significant decrease of the self-effect in the asynchronous condition, but only in the group, which experienced the FoP (synchronous: M = 2.33, SD = 0.75; asynchronous: M = 1.53, SD = 0.83; one-tailed t-test: t(10) = 2.148, p = 0.029; No-FoP group: synchronous: M = 1.43; SD = 0.90; asynchronous: M = 2.07, SD = 1.04, one-tailed t-test: t(10) =1.660, p = 0.064).

Experiment 2

The number of generated words in the thought numerosity judgment. In Experiment 2 (Numerosity judgment), we used the same auditory verbal stimuli as in Experiment 1 (in total 420 French words and 22 phonemes). To verify that the found differences in numerosity judgment were not due to the differences in the number of generated words between the experimental conditions, we conducted a repeated-measures ANOVA with *source* and *sensorimotor stimulation* as within-subject factors. The analysis showed that the number of generated words did not differ between the active (M = 7.95, SD = 2.02) and passive conditions (M = 8.11, SD = 0.33; F(1,18) = 0.115, p = 0.738), neither it was modulated by the sensorimotor stimulation (synchronous: M = 8.18, SD = 1.18; asynchronous: M = 7.88, SD = 0.89; F(1,18) = 3.079, p = 0.096) or the interaction between the source and sensorimotor stimulation (F(1,18) = 0.944, p = 0.344).

Absolute accuracy in the thought numerosity judgment. To verify whether the difference in the numerosity judgments was not due to differences in cognitive load between the active and passive conditions or between synchronous and asynchronous conditions, we analyzed the absolute accuracy. This was defined as a percentage of trials when the numerosity judgment was correct within each experimental condition. The repeated measures ANOVA showed that the absolute

accuracy was not affected by the *Source* (F(1,18) = 0.833, p = 0.374), *Sensorimotor stimulation* (F(1,18) = 0.810, p = 0.380) or their interaction (F(1,18) = 1.118, p = 0.304).

Experiment 3

Analyses of the questionnaire data revealed that the synchrony between participants' movements and received tactile feedback significantly modulated ratings of the questionnaire items related to thought insertion and thought influencing. In particular, as compared to the synchronous, the asynchronous mode of stimulation resulted in significantly higher ratings of the items assessing thought insertion: "It seemed as if someone else has been thinking certain thoughts in my mind" (synchronous: M = 1.61, SD = 1.38, asynchronous: M = 2.00, SD = 1.41; Z = 2.111, p = 0.03), thought influencing: "It seemed as if the robot behind influenced some of my thoughts" (synchronous: M = 1.89, SD = 1.49, asynchronous: M = 3.33, SD = 1.64; Z = 2.345, p = 0.01) and a significant higher ratings of the item assessing robotically-induced thought insertion: "It seemed as if the robot put certain thoughts in my mind" (synchronous: M = 1.67, SD = 1.33, asynchronous: M = 2.5, SD = 1.76; Z = 1.911, p = 0.03). The ratings of other questionnaire items were not significantly modulated by the sensorimotor mismatch (all p > 0.05). See Table S2.

Supplemental References

- 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., and Rognini, G. (2014). Neurological and robot-controlled induction of an apparition. Current Biology *24*, 2681-2686.
- Ferrand, L., and Alario, F.X. (1998). Normes d'associations verbales pour 366 noms d'objets concrets. L'Année psychologique *98*, 659-709.
- 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/RSJ International Conference on Intelligent Robots and Systems, 4664-4669.
- Hirshman, E. and Bjork, R.A. (1988). The generation effect: Support for a two-factor theory. Journal of Experimental Psychology: Learning, Memory, and Cognition *14*, 484.
- Krueger, L.E. (1972). Perceived numerosity. Perception and Psychophysics 11, 5-9.
- Miller, T.J., McGlashan, T.H., Woods, S.W., Stein, K., Driesen, N., Corcoran, C.M., Hoffman, R., and Davidson, L. (1999). Symptom assessment in schizophrenic prodromal states. Psychiatric Quarterly *70*, 273-287.
- Schultze-Lutter, F., Addington, J., Ruhrmann, S., and Klosterkötter, J. (2007). Schizophrenia proneness instrument, adult version (SPI-A) (Rome: Giovanni Fioriti).
- Slamecka, N.J., and Graf, P. (1978). The generation effect: delineation of a phenomenon. Journal of experimental Psychology: Human learning and Memory *4*, 592.