

The boundaries of the self: The sense of agency across different sensorimotor aspects

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The sense of agency (SoA) is the sensation of control over our actions. SoA is thought to rely mainly upon the comparison of predictions regarding the sensory outcomes of one's actions and the actual sensory outcomes. Previous studies have shown that when a discrepancy is introduced between one's actions and the sensory feedback, the reported SoA is reduced. Experimental manipulations of SoA are typically induced by introducing a discrepancy between a motor action and visual feedback of a specific sensorimotor aspect. For example, introducing a delay or a spatial deviation between the action and its sensory feedback reduces SoA. However, it is yet unclear whether the sensorimotor prediction processes underlying SoA are related between different aspects. Here in one exploratory and one preregistered experiment we tested the sense of agency across temporal, spatial, and anatomical aspects in a within-subject design. Using a novel virtual-reality task allowing the manipulation of the visual feedback of a motor action across different aspects, we show that the sensitivity of agency is different across aspects, agency judgments are correlated across aspects within subjects and bias toward attributing the viewed action to the self or to an external source is correlated as well. Our results suggest that sensorimotor prediction mechanisms underlying SoA are related between different aspects and that people have a predisposition for the directionality of agency judgments. These findings reveal the psychophysical attributes of SoA across sensorimotor aspects. Data and preregistration are available at <https://goo.gl/SkbGrb>.

limb they wish to act with. While we lack awareness of the complexities of the sensorimotor computations of such actions, we possess an unambiguous sense of authorship for voluntary actions that is termed the *sense of agency* (SoA; Gallagher, 2007; Haggard, 2008; Salomon, 2017). SoA is typically unnoticed and has been suggested to have a “thin phenomenology”; however, violations of SoA are usually quite salient (Haggard, 2017). For example, if a motion deviates from its predicted course, it is likely that an external event (e.g., snagged my sleeve) has occurred. It has been suggested that SoA is primarily based on an internal comparator mechanism (Wolpert, Ghahramani, & Jordan, 1995; Wolpert & Kawato, 1998). This sensorimotor comparator model evaluates the congruency of the predicted sensory consequences of the action (forward models) and the actual afferent signals. If the predicted and afferent signals are congruent, one has SoA over the action, whereas incongruence leads to a loss of SoA (Engbert, Wohlschläger, & Haggard, 2008; Jeannerod, 2009).

SoA has been suggested to be a basic mechanism allowing segregation of the self from the environment and conspecifics (Jeannerod, 2003; Salomon, 2017; Salomon, Lim, Kannape, Llobera, & Blanke, 2013; Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005). While volitional changes of self–other boundaries may have positive emotional effects (see, e.g., Colzato et al., 2012), unsolicited and temporally extended loss of SoA over one's actions may cause an unwilling reduction in self–other segregation, resulting in psychosis-like symptoms (Blanke et al., 2014; Salomon, 2017). For example, if actions are not properly attributed to the self, this could generate a sensation of external control as found in passivity symptoms. Indeed, psychiatric conditions such as psychosis, in which there is a deficit

Introduction

Healthy humans effortlessly carry out goal-directed actions by directing the timing and directionality of the

Citation: Krugwasser, A. R., Harel, E. V., & Salomon, R. (2019). The boundaries of the self: The sense of agency across different sensorimotor aspects. *Journal of Vision*, 19(4):14, 1–11, <https://doi.org/10.1167/19.4.14>.

<https://doi.org/10.1167/19.4.14>

Received October 14, 2018; published April 5, 2019

ISSN 1534-7362 Copyright 2019 The Authors



in the delineation of the self (Sass & Parnas, 2003), typically include deficits of SoA (Lindner, Thier, Kircher, Haarmerier, & Leube, 2005; Maeda et al., 2012; Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010). Several studies have shown a positive correlation between disruptions of SoA and such positive symptoms in individuals with schizophrenia or high schizotypy (Asai & Tanno, 2007; Ford et al., 2001; Lindner et al., 2005).

Investigations of SoA use different measures to probe the affinity between one's actions and their consequences. Some studies directly probe the subjective feeling of action authorship (e.g., "Did you conduct the action?"; see Balslev, Cole, & Miall, 2007; Sato, 2009), while others use implicit or explicit judgments of the congruency of one's actions and their consequences (Engbert et al., 2008; Farrer, Franck, Paillard, & Jeannerod, 2003; Franck et al., 2001; Hara et al., 2015). Here we aimed at probing the psychophysics of SoA across the different aspects of action, and we therefore chose to use the explicit detection of a sensorimotor conflict as the basis for SoA.

SoA can be experimentally manipulated by introducing conflicts between actions and their predicted outcomes (Balslev et al., 2007; David, Newen, & Vogeley, 2008; Engbert et al., 2008; Sato & Yasuda, 2005). Typically, such manipulations use video or virtual reality to manipulate the correspondence between the participants' actions and the visual outcomes (Farrer, Frey, et al., 2008; Kannape, Schwabe, Tadi, & Blanke, 2010; Salomon et al., 2016; Salomon et al., 2013; Tsakiris et al., 2005) along a single aspect (e.g., delay). However, actions comprise multiple properties spanning several aspects. Each action includes information regarding its timing (temporal aspect), spatial properties such as the direction of movement (spatial aspect), and the limb which will perform the action (anatomical aspect). Predicting the sensory consequences of an action must therefore include specific forward models for different aspects of the action (for similar examples in audition, see Aukstulewicz et al., 2018; in motor systems, see Pickering & Clark, 2014; Wolpert & Kawato, 1998). For example, inducing discrepancies in the temporal aspect by shifting the outcome presented to the participants forward with respect to the expected outcome (i.e., delay) has been found to reduce SoA in healthy participants (Farrer, Bouchereau, Jeannerod, & Franck, 2008; Hara et al., 2015; Sato & Yasuda, 2005). In the spatial aspect, when the visual outcome of actions is modified by including angular deviations, SoA is also diminished (Farrer, Franck, Paillard, & Jeannerod, 2003; Fournieret & Jeannerod, 1998; Kannape et al., 2010).

Despite a considerable body of work relating to SoA, it is not yet known whether predictions regarding the

sensory consequences across the different aspects (temporal, spatial, and anatomical) are processed in a similar fashion, possibly by a central neural mechanism (Blakemore, Frith, & Wolpert, 2001; Farrer & Frith, 2002), or are instead processed separately, possibly in more local neural circuits (Friston, 2010; Limanowski & Blankenburg, 2013). While many studies have investigated SoA by inducing sensorimotor conflicts in the temporal or spatial aspects (e.g., Farrer, Frey, et al., 2008; Franck et al., 2001; Salomon et al., 2013; Sato & Yasuda, 2005), and one has compared both temporal and spatial (Farrer, Bouchereau, et al., 2008), to the best of our knowledge none have systematically compared the boundaries of the self across temporal, spatial, and anatomical aspects. Thus, it has not been possible to discern whether sensorimotor predictions underlying SoA across aspects are processed in a similar fashion. In the current study, we investigated in one exploratory experiment—and then confirmed in a preregistered replication—the impact on SoA of modulating sensorimotor conflicts across different prediction aspects. Specifically, we investigated how temporal, spatial, and anatomical deviations affect SoA in a within-subject design, allowing us to compare sensitivity and bias across these aspects. Participants saw a virtual hand moving either similarly to their own movement or with a temporal, spatial, or anatomical alteration. The magnitude of the alterations was manipulated to allow a psychophysical examination of SoA. We expected SoA to decrease with larger alterations and this decrease to be correlated across sensorimotor aspects. Based on the relation between SoA deficits and psychosis, we tested whether sensorimotor conflicts may bias auditory processing (Experiment 1) or be related to schizotypal traits (Experiment 2).

Methods

Experiment 1

Participants

Sixteen healthy, right-handed students (14 women, mean age = 22.2 years, $SD = 2.6$ years) who were unaware of the purpose of the experiment participated. All participants had normal or corrected-to-normal vision and no psychiatric or neurological history (based on self-report). All gave written informed consent and received course credit for their participation. The experiment was performed in accordance with the ethical standards of the Declaration of Helsinki, and the experimental protocols were approved by the ethics committee of Gonda Multidisciplinary Brain Research Center.

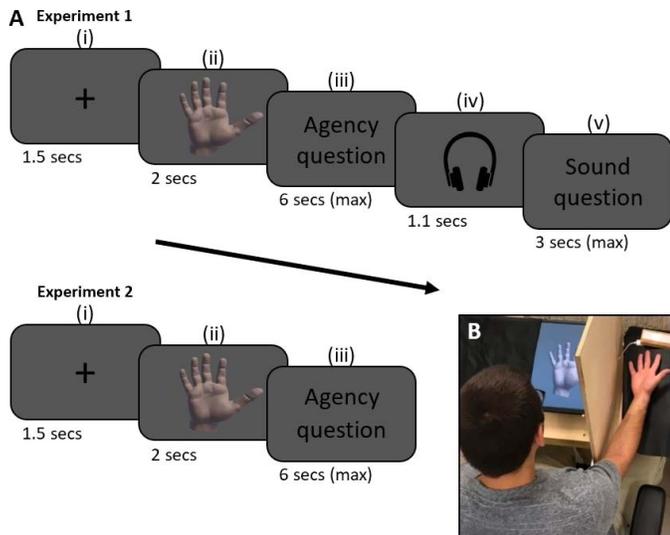


Figure 1. Trial flow for Experiments 1 and 2 and experimental setup. (A) Trial flow. Experiment 1: Each trial started by presenting (i) a fixation cross, then (ii) the modeled virtual hand (in which the participants conducted a movement and saw it on-screen, either altered or unaltered), followed by (iii) an agency question regarding the movement they conducted and saw. Afterward, (iv) a sound consisting of pink noise and non-word syllables was played. The participants were then asked (v) whether they did or did not hear a word. Experiment 2: Similar to Experiment 1, excluding the played sound (iv) and the sound question (v). (B) Experimental setup. Participants sat in front of the monitor, laying their right hand on the right plate (covered by a black cloth) directly beneath the Leap Motion controller and saw their modeled, virtual hand on the right side of the monitor (picture from Experiment 2).

Setup

The experiment was run on a computer (Intel core i7 processor and 16 GB of RAM) running custom-made software (SLabVR, built using Unity 5.6.1). The experiment was displayed on a 24-in. Dell P2417H monitor, at a resolution of $1,920 \times 1,080$ (refresh rate = 60 Hz). On-ear headphones (Philips shb8850nc) with active noise canceling were used to mask sounds from the environment and to present auditory stimuli. Participants wore the headphones for the entire session (apart from the training). Motion tracking and virtual modeling of each participant's right hand was realized by a Leap Motion controller (Leap Motion Inc., San Francisco, CA), creating a virtual-reality model of the hand in real time. Responses were given with a numeric keyboard, with all the keys blocked except three: left, right, and Enter. The left key had a left red arrow on it, the right key had a right green arrow on it, and the Enter key had a black circle on it and a slightly different texture (to allow easy identification). Intrinsic delay of the system was 80 ms.

The physical setup included two wooden plates (40×54 cm) positioned 32° relative to the table. The computer monitor was placed on the left plate, and the participants positioned their right hand, facing upward, directly beneath the Leap Motion controller on the right plate. These plates were separated by another wooden plate (height = 55 cm) to occlude the participants' real hand from view. The Leap Motion controller was fixed to a parallel pole (its center positioned 17 cm right to the separator plate), facing downward (Figure 1B).

The background color of all the screens in this experiment was gray—RGB = (127, 127, 127)—the text color was black (except the message indicating breaks, which was white), and the text font was Segoe UI (size 48). The left half of the screen was covered with a black cloth in order to focus participants' attention to the right of the screen (where the stimuli and questions were displayed); this was done so that the displayed virtual hand was 18 cm from the participants' real hand (Riemer, Kleinböhl, Hölzl, & Trojan, 2013).

Experimental procedure

The experiment consisted of 240 trials, divided into five blocks of 48 (with self-timed breaks of no less than 30 s between blocks). Each trial began with a fixation cross presented on-screen (visual angle = 2.4° , located in the middle of the display: 430 pixels from the right edge of the screen and 515 pixels from the bottom), indicating a new trial beginning (1,500 ms). Immediately afterward, the virtual hand (VH) was displayed (2,000 ms). The participants were instructed to conduct a single bending movement with their index finger as soon as they saw the VH on-screen. In 25% of the trials, the VH made an identical movement to the participant's. In 75% of the trials, the VH performed an altered movement which deviated from the participant's. There were three types of sensorimotor alterations, and each had four levels of magnitude. In the temporal aspect, we introduced delays between the participant's movement and the movement of the VH. Four magnitudes of delay (0, 100, 200, 300 ms) were used (for similar manipulations, see Franck et al., 2001; Salomon et al., 2013; Sato & Yasuda, 2005; Shimada, Qi, & Hiraki, 2009). In the spatial aspect, we introduced a conflict between the sensorimotor predictions and the observed movement by introducing angular deviation of the observed finger movement with respect to actual movement. There were four levels of angular deviation (0° , 6° , 10° , 14°) in which the finger movement occurred with an angular shift (Farrer, Franck, Paillard, & Jeannerod 2003; Franck et al., 2001; Kannape et al., 2010). Finally, we manipulated the anatomical congruence, in which a comparable bending movement was displayed but in a different

finger (index, middle, ring, little finger; see Caspar, Cleeremans, & Haggard, 2015; Salomon et al., 2016). Each alteration magnitude occurred 20 times, and there was a maximum of one alteration per trial (i.e., no combinations). The trials with different alterations were randomly shuffled for each session, such that the participants could not anticipate either the type of alteration that occurred or its magnitude.

In order to measure participants' sense of agency, a single question was presented (in Hebrew in both experiments): "Was the movement I've seen congruent with the movement I've made in space and time?" (see Franck et al., 2001). Participants were instructed to answer by pressing a single key: left for no and right for yes (trials in which no answer was chosen during the predefined period of 6 s were counted as "no answer").

Auditory task

Based on previous work linking deficits of agency and positive symptoms of psychosis (Asai & Tanno, 2007; Franck et al., 2001), we tested whether sensorimotor conflicts affecting the sense of agency would cause a bias toward hearing words in ambiguous auditory stimuli (a version of the "babble test"; see Hoffman et al., 2007). To this end, a short auditory stimulus, containing one or two prerecorded Hebrew non-word syllables embedded within pink noise, was played to the participants. There were 24 different sound stimuli, each of which occurred 10 times during the experiment in a pseudorandom fashion. Although none of the stimuli contained a word, the participants were told that a word would be present in 50% of the trials. After the sound was played, participants were presented with a single question, "Did I hear a word?", to which they replied in the same manner as to the agency question. A short training session was held before the experiment. It comprised 24 trials: two of each alteration type, keeping the same altered-to-unaltered ratio as the actual experiment (3:1). This was done for the participants to get familiar with the VH display and response method. The training session did not contain the auditory part of the experiment.

Data analysis

SoA was calculated for each participant, for each level in each aspect, by averaging responses to the agency question. Participants' movements were analyzed, and trials with deviant or no movement were removed from the analysis (~7% of the trials). The proportion of trials in which the participant reported hearing a word was quantified in the same manner. To test for differences in SoA across different aspects, we employed a 3×4 repeated-measures analysis of variance (ANOVA) with aspect and alteration magni-

tude as within-subject factors (when required, Greenhouse–Geisser corrections were applied). Null effects were assessed by aspect-pairwise Bayesian repeated-measures ANOVA and Bayesian paired t test: $BF_{10} < 0.33$ implies substantial evidence for the null hypothesis, $0.33 < BF_{10} < 3$ suggests insensitivity of the data, and $BF_{10} > 3$ implies substantial evidence for the alternative hypothesis (see Quintana & Williams, 2018). We applied the same methods to investigate a possible relation between hearing words and sensorimotor alterations of the different aspects.

To test participants' performance across aspects, we used signal-detection theory (SDT; Stanislaw & Todorov, 1999; Swets, 1964) and quantified the sensitivity and criterion of each aspect. We used nonparametric measures of sensitivity (A') and bias (B'' ; Macmillan & Creelman, 1996) due to violations of assumptions of SDT (that the two conditional probability density functions are Gaussian and have equal variance; see Pastore & Scheirer, 1974). To test for correlations, we used Pearson's r correlation measure. Statistical significance was calculated using permutation testing in which the scores were permuted 10,000 times and the true correlation was compared to this distribution (Salomon et al., 2011).

Experiment 2

Experiment 2 was a preregistered replication of Experiment 1. The preregistration can be viewed at <https://goo.gl/SkbGrb>. As no substantial results were obtained for the auditory task in Experiment 1, it was excluded from Experiment 2.

Participants

A power calculation based on the results of Experiment 1 (G*Power 3.1.9.2; see Faul, Erdfelder, Buchner, & Lang, 2009) indicated that 19 participants were needed to achieve a power of 0.95; we therefore decided to acquire 20 valid results data sets (see preregistration). Twenty-seven healthy, right-handed participants who were unaware of the purpose of the experiment were recruited. Seven participants were excluded based on criteria defined in the preregistration (four due to technical difficulties, two who did not comply with the task, and one who had a negative d' ; see Methods section in Supplementary File S1). Data from the remaining 20 participants (14 women, mean age = 22.7 years, $SD = 2.8$ years) were included in the analysis. All participants had normal or corrected-to-normal vision and no psychiatric or neurological history (based on self-report). All gave written informed consent and received credit coupons or monetary recompense (~50 Shekels) for their partici-

pation. The experiment was performed in accordance with the ethical standards of the Declaration of Helsinki, and experimental protocols were approved by the ethics committee of Gonda Multidisciplinary Brain Research Center.

Setup

The setup was identical to the setup of Experiment 1, except that no headphones were used in this experiment.

Experimental procedure

The experimental design was similar to that of Experiment 1, with a few differences: It consisted of 360 trials, divided into eight blocks of 45. Each trial consisted of a fixation-cross display then a VH display, followed by an agency question (Figure 1A). In this experiment, each alteration magnitude occurred 30 times, keeping the same altered-to-unaltered ratio as in the first experiment. A training session similar to that of Experiment 1 was held before the beginning of Experiment 2.

After the experiment, participants were given a Schizotypal Personality Questionnaire–Brief (SPQ-B; Raine & Benishay, 1995). High scores on this questionnaire are considered evidence of a schizotypal personality, and we wished to assess putative links between SoA performance and schizotypy (Asai & Tanno, 2007).

Data analysis

Data analysis was identical to that of Experiment 1, apart from the exclusion of the auditory task and the additional analysis of correlations between A' and the SPQ-B score. In this experiment, ~1.5% of the trials were removed from the analysis.

Results

Experiment 1

The ANOVA revealed a main effect of aspect, $F(2, 30) = 65.22$, $p < 0.001$, $\eta^2 = 0.81$, driven by lower SoA ratings in the anatomical aspect ($M_{\text{anatomical}} = 0.21$, $SD_{\text{anatomical}} = 0.36$) compared to the temporal and spatial aspects, which had much higher rates of SoA ($M_{\text{temporal}} = 0.61$, $SD_{\text{temporal}} = 0.29$; $M_{\text{spatial}} = 0.65$, $SD_{\text{spatial}} = 0.3$). As expected, there was also a main effect of alteration, $F(3, 45) = 121.83$, $p < 0.001$, $\eta^2 = 0.89$, driven by a decrease of SoA ratings as alteration magnitude increased ($M_{\text{alt0}} = 0.85$, $SD_{\text{alt0}} = 0.13$; M_{alt1}

	Experiment	Temporal-spatial	Temporal-anatomical	Spatial-anatomical
Sensitivity (A')	1	0.54**	0.56**	0.49*
	2	0.54**	0.64**	0.45*
Bias (B'')	1	0.58**	0.56*	0.48*
	2	0.7***	0.61**	0.59**

Table 1. Pearson's r correlations of sensitivity and bias measures between different aspects. Notes: * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$.

$= 0.52$, $SD_{\text{alt1}} = 0.39$; $M_{\text{alt2}} = 0.35$, $SD_{\text{alt2}} = 0.32$; $M_{\text{alt3}} = 0.23$, $SD_{\text{alt3}} = 0.27$). Critically, an Aspect \times Alteration interaction was also discovered, $F(6, 90) = 33.11$, $p < 0.001$, $\eta^2 = 0.69$. As can be seen in Figure 2, this was driven by differences in SoA decrease between anatomical and temporal aspects, $F(1, 15) = 118.91$, $p < 0.001$, $\eta^2 = 0.89$, and between anatomical and spatial, $F(1, 15) = 108.09$, $p < 0.001$, $\eta^2 = 0.88$; no significant difference was found between the temporal and spatial aspects, $F(1, 15) = 0.67$, $p \approx 0.43$, $\eta^2 = 0.04$, $BF_{10} = 0.13$ (see Figure 2).

SDT results showed that mean A' was highest in the anatomical aspect, where SoA judgments errors were very rare ($\bar{A}'_{\text{temporal}} = 0.76$, $\bar{A}'_{\text{spatial}} = 0.75$, $\bar{A}'_{\text{anatomical}} = 0.95$, see Supplementary Figure S1), likely due to the fact that the anatomical aspect is categorical rather than parametric. The bias measure B'' indicated that participants had a bias toward self-attribution in the temporal and spatial aspects but a tendency to categorize as nonself in the anatomical aspect ($\bar{B}''_{\text{temporal}} = -0.35$, $\bar{B}''_{\text{spatial}} = -0.38$, $\bar{B}''_{\text{anatomical}} = 0.7$). We then examined the correlations of sensitivity and bias scores across the different aspects and tested their significance using permutation testing. As can be seen in Table 1, sensitivity scores showed high, positive, and significant correlations across all aspects: temporal-spatial $r = 0.54$, $p < 0.01$; temporal-anatomical $r = 0.56$, $p < 0.01$; spatial-anatomical $r = 0.49$, $p < 0.05$. Bias also showed high, positive correlations across all aspects: temporal-spatial $r = 0.58$, $p < 0.01$; temporal-anatomical $r = 0.56$, $p < 0.05$; spatial-anatomical $r = 0.48$, $p < 0.05$.

We found no evidence of relationships between SoA and reporting of words in the ambiguous auditory stimuli. Participants did not report hearing more words following altered trials, $t = 1.57$, $p \approx 0.93$, $BF_{10} = 0.11$, nor was there any difference based on the aspect or magnitude of the alterations (all $ps > 0.41$; see Results section in Supplementary File S1). To quantify this null finding we performed Bayesian analyses using JASP. We found that there was substantially more evidence for the null hypothesis, indicating that there was neither an effect of aspect, $BF_{10} = 0.09$, nor one of alteration, $BF_{10} = 0.04$, nor one of an Aspect \times Alteration interaction, $BF_{10} = 0.11$.

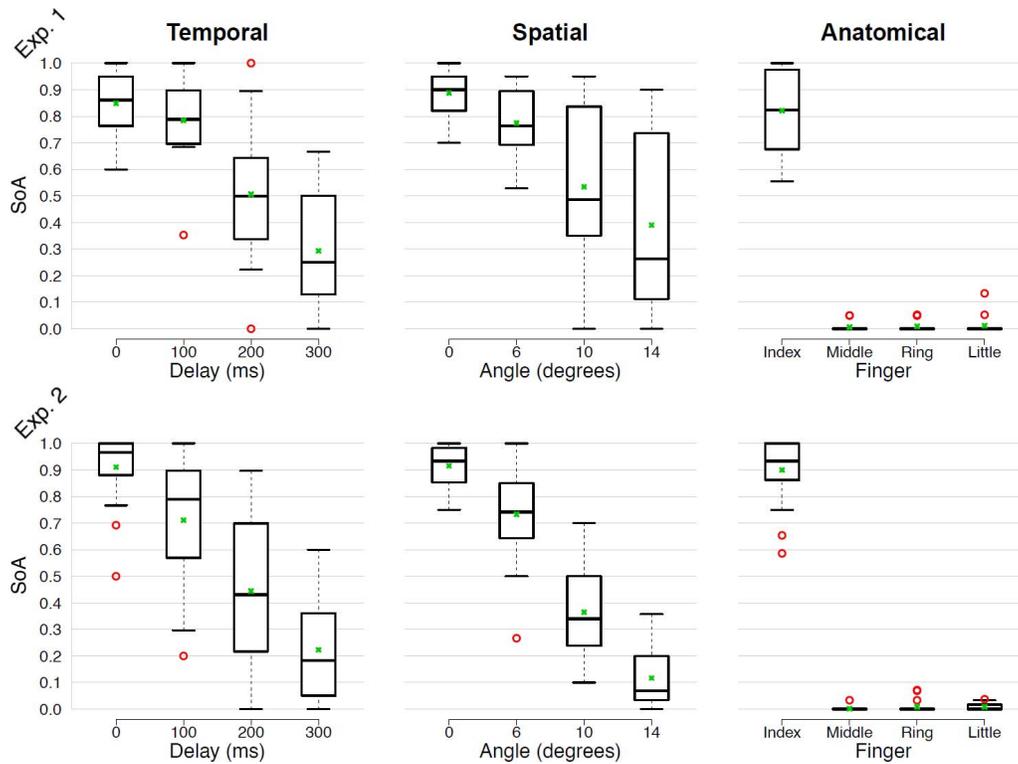


Figure 2. Sense of agency ratings across all three aspects in Experiments 1 (top) and 2 (bottom). Green X represents the group mean. The y-axis is the same for all plots and represents the proportion of trials in which participants reported the observed movement as identical to the movement they conducted.

Experiment 2

As hypothesized, preregistered analyses revealed main effects of both aspect and alteration. The main effect of aspect, $F(2, 38) = 74.41$, $p < 0.001$, $\eta^2 = 0.8$, was driven by lower SoA ratings in the anatomical aspect ($M_{\text{anatomical}} = 0.23$, $SD_{\text{anatomical}} = 0.39$) compared to the temporal and spatial aspects ($M_{\text{temporal}} = 0.57$, $SD_{\text{temporal}} = 0.34$; $M_{\text{spatial}} = 0.53$, $SD_{\text{spatial}} = 0.34$). The main effect of alteration, $F(3, 57) = 344.36$, $p < 0.001$, $\eta^2 = 0.95$, was driven by the decrease in SoA ratings as alteration magnitude increased ($M_{\text{alt0}} = 0.91$, $SD_{\text{alt0}} = 0.11$; $M_{\text{alt1}} = 0.48$, $SD_{\text{alt1}} = 0.38$; $M_{\text{alt2}} = 0.27$, $SD_{\text{alt2}} = 0.27$; $M_{\text{alt3}} = 0.12$, $SD_{\text{alt3}} = 0.16$). The analysis also revealed an Aspect \times Alteration interaction, $F(6, 114) = 62.17$, $p < 0.001$, $\eta^2 = 0.77$, driven by a large difference in the rate of SoA change by alteration between the anatomical and temporal aspects, $F(1, 19) = 88.78$, $p < 0.001$, $\eta^2 = 0.82$, and the anatomical and spatial, $F(1, 19) = 196$, $p < 0.001$, $\eta^2 = 0.91$; no significant difference was found between the temporal and spatial aspects, $F(1, 19) = 1.53$, $p \approx 0.23$, $\eta^2 = 0.08$, $BF_{10} = 0.47$ (see Figure 2).

Similar to Experiment 1, sensitivity (A') was high across all aspects and highest in the anatomical ($\overline{A'}_{\text{temporal}} = 0.83$, $\overline{A'}_{\text{spatial}} = 0.85$, $\overline{A'}_{\text{anatomical}} = 0.97$; see Supplementary Figure S1), while bias values (B'')

indicated that participants had a self-attribution bias in the temporal and spatial aspects but a tendency to categorize as non-self in the anatomical aspect ($\overline{B''}_{\text{temporal}} = -0.55$, $\overline{B''}_{\text{spatial}} = -0.54$, $\overline{B''}_{\text{anatomical}} = 0.71$). A' values between the different aspects showed high, positive, and significant correlations: temporal-spatial $r = 0.54$, $p < 0.01$; temporal-anatomical $r = 0.64$, $p < 0.01$; spatial-anatomical $r = 0.45$, $p < 0.05$. Likewise, B'' values showed significant positive correlations: temporal-spatial $r = 0.7$, $p < 0.001$; temporal-anatomical $r = 0.61$, $p < 0.01$; spatial-anatomical $r = 0.59$, $p < 0.01$.

Correlations between A' (across all aspects) and SPQ-B scores were not significant (all $ps > 0.17$, BF_{10} ranging from 0.36 to 0.69; see Supplementary Table S1), nor were correlations between A' and any of the SPQ-B subscales (all $ps > 0.09$, BF_{10} ranging from 0.16 to 1.3; see Supplementary Table S2).

Discussion

This study investigated the sensorimotor mechanisms defining the boundaries of the bodily self across the temporal, spatial, and anatomical aspects. Several findings arise from these experiments: First, sensitivity

to disparities between actions and their visual consequences varies between different sensorimotor aspects, yet is similar between experiments (see Figure 2 and Supplementary Figure S1). Second, participants' sensorimotor sensitivity was highly correlated between aspects, suggesting that a central mechanism may be involved in SoA across different types of sensorimotor mismatches. Finally, participants' bias in both experiments for attributing an action to self or other was also highly and positively correlated.

Consistent with previous reports on SoA, we found that increased disparity between one's actions and their visual outcomes reduces SoA over the action. This was true for alterations both in the temporal aspect (i.e., delays) and in the spatial aspect (i.e., angular deviations), which both showed a graded reduction of SoA as a function of alteration magnitude. Our results in both experiments are in close accord with previous data regarding the limits of SoA in the temporal and angular aspects (Farrer, Bouchereau, et al., 2008; Franck et al., 2001; Limanowski, Kirilina, & Blankenburg, 2017). Our results did not show a significant difference between the temporal and spatial aspects in SoA decrease ($BF_{10} = 0.13$). In contrast, Farrer, Bouchereau, et al. (2008) used a paradigm allowing participants to attribute actions to "self", "self with bias", or "another agent", and found a difference in attribution between temporal and spatial conditions for extreme alterations ($\geq 50^\circ$ and 1,100 ms). In the anatomical aspect, when a movement was enacted by a different finger, participants immediately became aware of the discrepancy, even when the veridical timing and spatial characteristics of the movements were retained. Such heightened sensitivity to alterations in the anatomical aspect has been shown before, in both healthy individuals and those with schizophrenia, using video technologies (Daprati et al., 1997; Franck et al., 2001). However, recent studies using anatomically incongruent visual feedback (on virtual or robotic hands) have shown that it can cause participants to misattribute their movement to the viewed finger (Salomon et al., 2016) or may have a more graded impact on SoA (Caspar et al., 2015). It is likely that these differences stem from the fact that participants in the current study were required to move only their index finger, thus enhancing the salience of incongruent anatomical feedback. However, it is important to remember that when the visual feedback is anatomically incongruent, this is inherently confounded with spatial distance (e.g., visual movement of the little finger is both anatomically and spatially incongruent). It is likely that the reduction of SoA found for the anatomical aspect of action is related to both anatomy and distance effects.

Our results show that participants' sensitivity was positively correlated between aspects. Across both experiments, sensorimotor sensitivity in one aspect

could explain a considerable proportion of the variance for sensitivity in another aspect (R^2 scores ranging from 0.2 to 0.4). This finding suggests that the comparison of predictive motor signals (forward models) with afferent sensory feedback across temporal, spatial, and anatomical aspects may be subserved by similar mechanisms. This is most likely due to the fact that SoA judgments across aspects all rely on comparisons between visual, motor proprioceptive, and tactile signals, such that participants with high sensorimotor abilities may show enhanced sensitivity across all aspects. However, detection of discrepancies based on these signals is quite different between aspects. For example, sensitivity to alterations in the temporal aspect must rely on comparison of onset timing relations between visual and sensorimotor signals. Brain-imaging studies have shown that this is processed in parietal and cerebellar regions (Blakemore & Sirigu, 2003; Farrer, Frey, et al., 2008; Leube et al., 2003; MacDonald & Paus, 2003; Salomon, Malach, & Lamy, 2009; van Kemenade et al., 2018). However, detecting discrepancies in the spatial or anatomical aspects may require different computations, taking into account continuous action plans and somatotopic representations associated with frontal and parietal regions as well as the extrastriate body area (David et al., 2007; Farrer et al., 2003). While there are several possible interpretations of our finding of correlations in SoA sensitivity between aspects (e.g., inter-subject variability in visuo-proprioceptive perception, cortical noise levels), we believe that the comparison of sensorimotor predictions and their consequences also relies on some aspect-general mechanisms possibly implemented in the parietal or cerebellar regions (Blakemore & Sirigu, 2003; Imamizu, Kuroda, Yoshioka, & Kawato, 2004; Wolpert & Kawato, 1998).

Beyond sensitivity, participants also showed correlated bias measures across aspects (Table 1). Bias in SoA tasks is indicative of participants' propensity to attribute an action to themselves or an external source irrespective of sensitivity. Self-attribution biases as found in the spatial and temporal aspects have been previously documented (Farrer, Bouchereau, et al., 2008; Franck et al., 2001; Moore & Fletcher, 2012; Salomon et al., 2009), but to the best of our knowledge correlations of bias between sensorimotor prediction aspects have not been reported. This finding suggests that across the different aspects, participants used similar criteria to decide whether a movement was their own or not. This provides further support for aspect-general mechanisms underlying SoA judgments.

Regarding possible links between SoA and symptoms of psychosis, our data did not produce any clear results. In Experiment 1, induction of sensorimotor conflicts did not bias participants to judge non-words as words (all $BFs < 0.33$, suggesting evidence for the

null hypothesis). Furthermore, in Experiment 2 we investigated putative links between schizotypal traits and SoA errors (Asai & Tanno, 2007, 2008). Contrary to previous studies, we found no significant correlation between SPQ-B scores and SoA sensitivity measures. We supplemented this preregistered analysis with an exploratory analysis correlating each of the SPQ-B subscales and sensitivity measures. Once again, no significant correlations were found; in fact, most Bayes factors for the SPQ-B Cognitive-Perceptual subscale (which we thought most likely to reflect perceptual aspects of aberrant SoA) ranged from 0.16 to 0.32, suggesting at least three times more evidence for the null hypothesis (see Supplementary Tables S1 and S2). It is possible that these differences stem from the fact that our paradigm tested SoA using an embodied paradigm in which actions and alterations were presented in the context of a body, whereas Asai and Tanno employed action-outcome contingences that were non-embodied, for which predictions likely reflect less robust prior associations (for a similar discussion, see Christensen & Grünbaum, 2018). Furthermore, our sample size was optimized for statistical power relating to the main SoA task but may be underpowered for correlations with subjective questionnaires such as the SPQ-B.

In summary, our results show that processing of SoA across different sensorimotor aspects is highly correlated in both sensitivity and bias measures. We believe that such correlations could stem from central, aspect-general predictive mechanisms underlying the demarcation of the self. Our findings are in accord with current theories assigning a central role to sensorimotor predictive processes in establishing a model of the self (Allen & Friston, 2018; Apps & Tsakiris, 2014; Blakemore & Frith, 2003; Clark, 2013; Salomon, 2017). In this view, the brain is viewed as a predictive machine attempting to minimize surprise by generating predictions to explain sensory states (Clark, 2013; Friston, 2010). The current work shows that such predictive models of action consequences are related both at the level of objective performance (sensitivity) and at the level of the subjective criterion (bias). Further studies including brain imaging and populations with deficits in self-models may pinpoint the neural systems responsible for defining the boundaries of the sensorimotor self.

Keywords: sense of agency, sensorimotor conflict, virtual reality, multisensory integration

Acknowledgments

This study was supported by Israeli Science Foundation Grant (1169/17) and a National Institute

for Psychobiology in Israel grant to RS. We would like to thank Michal Somekh for her help in collecting the data.

Commercial relationships: none.

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