Self-initiated actions result in suppressed auditory but amplified visual evoked components in healthy participants

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Abstract

Self-suppression refers to the phenomenon that sensations initiated by our own movements are typically less salient, and elicit an attenuated neural response, compared to sensations resulting from changes in the external world. Evidence for self-suppression is provided by previous ERP studies in the auditory modality, which have found that healthy participants typically exhibit a reduced auditory N1 component when auditory stimuli are self-initiated as opposed to externally initiated. However, the literature investigating self-suppression in the visual modality is sparse, with mixed findings and experimental protocols. An EEG study was conducted to expand our understanding of self-suppression across different sensory modalities. Healthy participants experienced either an auditory (tone) or visual (pattern-reversal) stimulus following a willed button press (self-initiated), a random interval (externally initiated, unpredictable onset), or a visual countdown (externally initiated, predictable onset—to match the intrinsic predictability of self-initiated stimuli), while EEG was continuously recorded. Reduced N1 amplitudes for self- versus externally initiated tones indicated that self-suppression occurred in the auditory domain. In contrast, the visual N145 component was amplified for self- versus externally initiated pattern reversals. Externally initiated conditions did not differ as a function of their predictability. These findings highlight a difference in sensory processing of self-initiated stimuli across modalities, and may have implications for clinical disorders that are ostensibly associated with abnormal self-suppression.

Descriptors: Motor control, Visual processes, ERPs, Action monitoring

Self-suppression refers to the reduced neurophysiological and phenomenological response to sensations produced by our own actions, relative to identical sensations produced by the external world—the archetypal example being the fact that it is difficult to tickle oneself (Weiskrantz, Elliott, & Darlington, 1971). Self-suppression is believed to result from an internal forward model, in which sensory feedback is predicted on the basis of a copy of the motor command, known as an efference copy (Wolpert, Ghahramani, & Jordan, 1995). In contrast to sensations caused by changes in the external world, self-initiated actions are typically associated with little to no discrepancy between actual and predicted sensory feedback. Consequently, the central nervous system tends to be less responsive to the sensory consequences of self-initiated actions than to identical sensations evoked by externally initiated events. This framework, together with its neurophysiological foundation, is well supported across the animal kingdom (Crapse & Sommer, 2008).

In humans, self-suppression has been demonstrated using various psychophysical approaches (Blakemore, Frith, & Wolpert, 1999; Cardoso-Leite, Mamassian, Schutz-Bosbach, & Waszak, 2010; Sato, 2008). For instance, participants have been shown to judge self-initiated tones as softer than externally initiated tones (Weiss, Herwig, & Schütz-Bosbach, 2011). Researchers have also increasingly turned to ERP and event-related field (ERF) paradigms, measured with EEG and magnetoencephalography (MEG) respectively, in order to index the cortical suppression of self-initiated sensations. Healthy participants have been observed to exhibit a reduced amplitude of the N1 component of the auditory evoked potential (AEP; i.e., the negative component observed approximately 100 ms after auditory stimulus onset) when the auditory stimulus is self- versus externally initiated. This finding has been observed for both willed vocalizations (Curio, Neuloh, Numminen, Jousmaki, & Hari, 2000; Heinks-Maldonado, Mathalon, Gray, & Ford, 2005) and button press-elicited stimuli (Aliu, Houde, & Nagarajan, 2009; Baess, Jacobsen, & Schröger, 2008; Martikainen, Kaneko, & Hari, 2005;

McCarthy & Donchin, 1976; Schafer & Marcus, 1973). Notably, patients with schizophrenia have been observed to exhibit subnormal levels of auditory N1 suppression to self-initiated auditory sensations (Ford et al., 2001; Whitford et al., 2011), which has been taken as evidence for the self-monitoring abnormalities proposed to underlie the most characteristic clinical features of the disorder (Feinberg, 1978; Frith, 2005).

Self-suppression research has primarily focused on the auditory domain, and comparatively little data are available with respect to self-suppression in the visual domain. To our knowledge, three previous studies have investigated specific electrophysiological responses to self-initiated visual stimuli, all of which employed button press-elicited stimuli, but in markedly different paradigms (Gentsch & Schutz-Bosbach, 2011; Hughes & Waszak, 2011; Schafer & Marcus, 1973). Additionally, Stenner, Bauer, Haggard, Heinze, and Dolan (2014) have examined prestimulus neural oscillations using a visual contrast discrimination task. Gentsch and Schutz-Bosbach (2011) measured visual evoked potentials (VEPs) to arrow stimuli produced by either the participant or the computer, but this was embedded within a visual forced-choice response task in which the arrow stimuli were subliminally primed to address a separate question regarding conscious experience of agency. Schafer and Marcus (1973) employed a less complex design, comparing the VEP of self-paced photic flashes that were either self- or machine initiated. Both of these studies observed reduction of the visual N1 component for self-initiated visual stimuli at anterior electrodes, but not at occipital sites—where visual ERP amplitudes are typically maximal (Luck, 2012; Odom et al., 2010; O'Shea, Roeber, & Bach, 2009). In contrast, Hughes and Waszak (2011), who investigated VEP responses to self-initiated visual checkerboards, reported increased visual P1 amplitude at an occipital site. The inconsistent pattern of results for electrophysiological suppression to self-initiated visual stimuli stands in contrast with the large and consistent body of evidence for N1 suppression to self-initiated auditory stimuli.

The primary aim of the present study was to clarify whether electrophysiological suppression of self-initiated stimuli occurs across both auditory and visual modalities in healthy participants. To our knowledge, the study by Schafer and Marcus (1973) is the only previous study to compare self-suppression in the auditory and visual sensory domains in the same participants—they identified unambiguous self-suppression of auditory stimuli, but, as mentioned above, only mixed support for self-suppression to visual stimuli. Given the increasing prominence of self-suppression in the literature, and its possible role in psychotic symptomology, it is sensible to determine whether it is present in sensory modalities other than the auditory domain.

Additionally, the present study aimed to quantify the contribution of temporal predictability in any observed effects of self-initiation. As discussed by Hughes, Desantis, and Waszak (2013), a key difference between self-initiated and externally initiated conditions in many self-suppression paradigms is that the first is temporally predictable (i.e., the participant chooses when to press the button, and can thus anticipate in time when the stimulus will occur), while the second is not. This raises the possibility that the self-suppression phenomenon is attributable, at least in part, to differences in the temporal predictability of the stimuli.

To address these aims, the present study measured electrophysiological responses to both self-initiated auditory and visual stimuli in a single group of healthy participants, and compared them to physically identical, externally initiated stimuli, while also controlling for temporal predictability between the conditions. Auditory stimuli consisted of pure tones, such as those commonly used in studies of AEPs (e.g., Baess et al., 2008). Pattern reversals were selected for visual stimuli, as they are known to elicit robust VEPs with less intersubject and intrasubject variability than other forms of luminance-change stimulation, such as flash and pattern-onset stimuli (Luck & Kappenman, 2012; Odom et al., 2010). Stimuli were initiated by either a participant's willed button press (the active condition; i.e., self-initiated), at random intervals (the passive condition; i.e., externally initiated, unpredictable onset), or following a visual countdown (the cued condition, i.e., externally initiated, predictable onset, to match the intrinsic predictability of self-initiated stimuli). A motor condition, in which no stimuli occurred, was also included to control for neural activity associated with the act of pressing a button.

In accordance with previous studies, we predicted that participants would exhibit significantly reduced auditory N1 response to self-initiated tones relative to both predictable and unpredictable externally initiated tones. We also predicted suppression of early visual components of the VEP (namely, N75, P100, and N145) in response to self-initiated pattern reversals, based on the universal (i.e., multimodal) nature of the forward model framework on which self-suppression is based, notwithstanding inconsistent results in the small number of previous studies that have investigated self-initiated visual stimuli.

Method

Participants

Forty-five introductory psychology students at the University of New South Wales (UNSW), Sydney, were recruited through an online experiment management system (Sona Systems). Participants received course credit in exchange for their time and provided written, informed consent prior to participating. This study was approved by the UNSW Human Research Ethics Advisory Panel (Psychology). No participants reported having a psychotic mental disorder based on DSM-IV-TR criteria. Five participants were excluded from the analysis due to low signal-to-noise ratio. Of the remaining 40 participants, 28 were female, 37 were right-handed, and the mean age was 19.7 years ($SD = 3.9$).

Procedure

Participants sat in a quiet, dimly lit room, 60 cm in front of a computer monitor (BenQ XL2420T, $1{,}024 \times 768$ pixels, 144 Hz, $24''$ width). Following the completion of a demographics questionnaire, EEG was continuously recorded while participants completed a computer task programmed in MATLAB (MathWorks, Natick, MA). As described below, the task consisted of four conditions (active, motor, passive, and cued) run in two sensory modalities (auditory and visual) for a total of eight homogenous, 60-trial blocks. The order of these blocks was randomized for each participant. Each block was preceded by five practice trials to ensure participants understood instructions and to emphasize the need for self-paced rather than speeded responses in the active conditions. The entire experimental procedure (see Figure 1 for an overview) took approximately 45 min to complete.

Auditory task. The active condition measured electrophysiological responses associated with self-initiated stimuli. A fixation cross was presented on the screen, and participants were instructed to respond at will by pressing a button on a low-latency response pad
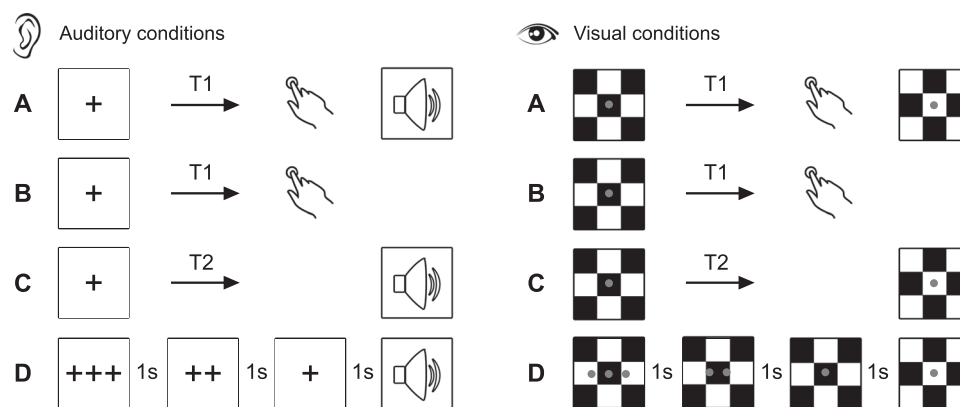
Figure 1. Experimental procedure. There were four conditions for both auditory (tone) and visual (pattern-reversal) stimuli. A. Active condition (self-initiated stimuli). Following presentation of a fixation target, participants pressed a button at will. Immediately after the duration of this response (T1), a tone was binaurally delivered or the pattern was reversed in auditory and visual conditions, respectively. B. Motor condition. This was identical to the active condition except that it resulted in no stimulus delivery. C. Passive condition (externally initiated, unpredictable onset). This was identical to the active condition, except that stimulus delivery occurred after a variable delay (T2) rather than involving participant input. D. Cued condition (externally initiated, predictable onset). In this condition, stimulus delivery occurred following a series of countdown screens separated by 1 s each.

(Cedrus Corporation, Model RB-530) with their dominant hand. Pressing the button caused a tone (100 ms duration, 500 Hz frequency, 70 dB SPL) to be delivered immediately to their headphones (Philips, Model SHL4500GY). The motor condition was identical to the active condition except that pressing the button did not cause a tone to be delivered. The ensuing EEG activity was subsequently subtracted from the active condition in order to remove the EEG activity associated with pressing the button, as is standard practice in studies of this nature (Baess et al., 2008; Ford, Gray, Faustman, Roach, & Mathalon, 2007; Martikainen et al., 2005; Whitford et al., 2011). Trials in the passive condition began with a fixation target, followed by a uniformly distributed random interval (0.5–2.5 s) before a tone was delivered without participant input, which aimed to assess participants' electrophysiological response to an externally initiated, temporally unpredictable stimulus. Lastly, trials in the cued condition delivered tones following a countdown composed of fixation targets (i.e., +++, then ++, then +), each of which were separated by a 1,000-ms interval. The cued condition aimed to assess participants' EEG response to an externally initiated, temporally predictable stimulus. All four conditions had random intervals (1–2 s) between stimulus onset (or in the motor condition, button pressing) and the start of the succeeding trial.

Visual task. Pattern-reversal stimuli were checkerboards (0.25° black and white checks, 100 cd/m^2 mean luminance, full field). In the active condition, a fixation dot was superimposed on a static checkerboard, to which participants were instructed to respond at will by pressing a button on the response pad. This response caused an abrupt pattern reversal (i.e., black squares to white and white squares to black), and the reversed pattern persisted for 1,500 ms to prevent visual offset contamination. In the motor condition, the checkerboard remained static following the button press. In the passive condition, a reversal occurred without participant input after a uniformly distributed random interval (0.5–2.5 s). Lastly, in the cued condition, the reversal occurred after a countdown composed of fixation targets (i.e., • • •, then • •, then •), each of which were separated by a 1,000-ms interval. As in the auditory blocks, all four conditions had random intertrial intervals (1–2 s).

Data collection and reduction. EEG was continuously recorded with a BioSemi ActiveTwo system using sintered Ag-AgCl electrodes in an electrode cap at 64 scalp sites, positioned according to the extended 10-20 system, at a sampling rate of 2048 Hz. During off-line preprocessing, auditory blocks were rereferenced to the averaged mastoid electrodes, as is common protocol for AEPs, while visual blocks were rereferenced to the electrode Fz, as is common protocol for pattern-reversal-induced VEPs (Odom et al., 2010). Bipolar vertical electrooculogram (EOG) was derived from electrode Fp1 and an electrode below the left eye, and horizontal EOG was derived from electrodes on the left and right outer canthi. Data were band-pass filtered from 0.05 to 30 Hz using a phase-shift free Butterworth filter and separated into 600-ms epochs, consisting of 100-ms prestimulus to 500-ms poststimulus. Data were baseline corrected from −100 to 0 ms. Vertical and horizontal EOG data were used to correct for eye movement artifacts using a regression-based algorithm (Gratton, Coles, & Donchin, 1983). All individual trials with EEG or EOG activity exceeding ± 50 µV were excluded from further analysis, resulting in a mean rejection rate of 7.3% ± 5.7% (*SD*) trials per block and participant. We then averaged individual trials for each condition to produce ERPs for each participant. Lastly, for each participant, motor waveforms were subtracted from the active waveforms for both modalities to produce difference waveforms, as is typical in self-suppression studies of this nature (Baess et al., 2008; Ford et al., 2007; Martikainen et al., 2005; Whitford et al., 2011). These difference waveforms are hereafter referred to as self waveforms.

For all statistical analyses, individual ERP component amplitudes were measured as the mean of the voltage in intervals centered on the group-average peak latencies of each condition. Following visual inspection of the group averages, these intervals were determined as 20 ms for N1, 40 ms for P2, 10 ms for N75 and P100, and 40 ms for N145. For auditory blocks, we identified our components of interest at electrode Cz, due to its characteristically large N1 amplitude subsequent to bilateral auditory stimulation (Ford et al., 2007). Due to our inclusion of the cued condition, the auditory P2 component was also examined, as it may better reflect suppression associated with temporal certainty (Sowman, Kuusik, & Johnson, 2012). For visual blocks, we identified our components
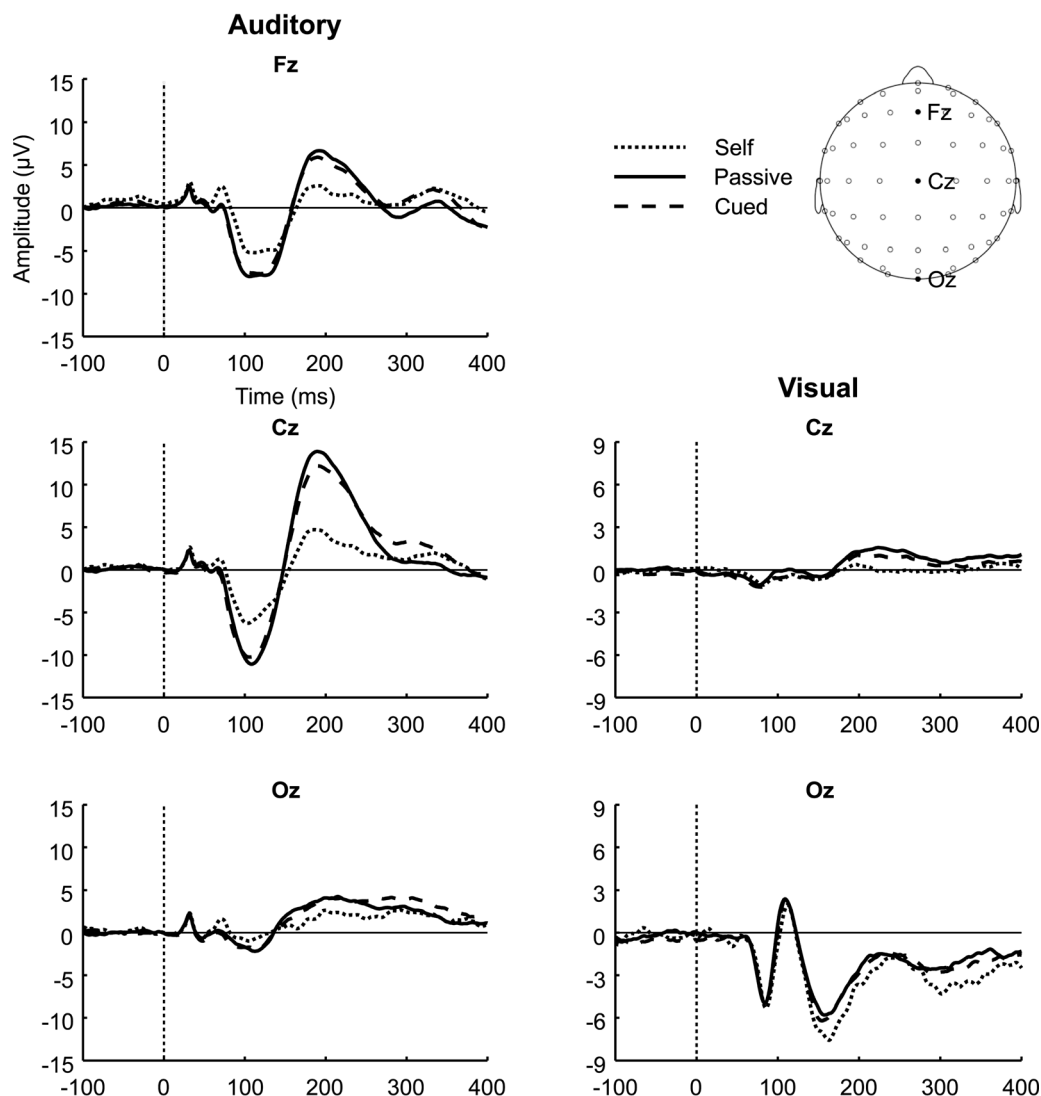
Figure 2. Left: ERPs for the auditory task recorded at electrodes Fz, Cz, and Oz (referenced to mastoids) for self, passive, and cued conditions. Right: ERPs for the visual task recorded at electrodes Cz and Oz (referenced to Fz) for self, passive, and cued conditions. ERPs for the self conditions were calculated by subtracting the appropriate motor condition from the active condition. The *x* axis represents time in milliseconds (ms) and the *y* axis amplitude in microvolts (μV).

of interest at electrode Oz to conform with standard protocol for VEPs, as that is where amplitude is typically the largest (Odom et al., 2010). For auditory and visual blocks, we conducted our analyses at electrodes Fz, Cz, and Oz.

Statistical analysis. To investigate the effect of condition on mean amplitude of the identified components, we conducted a separate one-way analysis of variance (ANOVA) for each sensory modality and for each electrode. In cases where the assumption of sphericity was violated, a Greenhouse-Geisser correction was applied, and for significant main effects, underlying simple effects were explored with post hoc contrasts. Lastly, to compare the effect of self-initiation on mean amplitudes across sensory modalities, measures for each component were calculated based on absolute differences between self- and externally initiated conditions. This represented 10 measures in total: 5 Components (N1, P2, N75, P100, N145) × 2 Contrasts (self-passive and self-cued). Participants' resultant measures were then compared using bivariate Pearson correlations and two-tailed tests of significance, and

cross-modal comparisons were reported (i.e., N1/N75, N1/P100, N1/N145, P2/N75, P2/P100, and P2/N145). A similar correlative analysis using ratio measures (i.e., self divided by passive or cued) was also conducted. All analyses were performed in SPSS version 22 (IBM Corp., Armonk, NY).

Results

Auditory Task

For the N1 component, a one-way ANOVA showed a significant main effect of condition, $F(2,80) = 25.07$, $p < .001$, $\eta_p^2 = .39$. This indicated that mean N1 amplitude at electrode Cz differed between self ($M = -5.95$), passive ($M = -10.59$), and cued ($M = -10.07$) conditions (see Figure 2 and Figure 3). Post hoc tests indicated that self significantly differed from both passive, $F(2,39) = 16.95$, $p < .001$ (see Figure 4), and cued, $F(2,39) = 12.60$, $p < .001$, but that passive and cued did not differ from each other, $F(2,39) = 0.16$, $p = .40$.
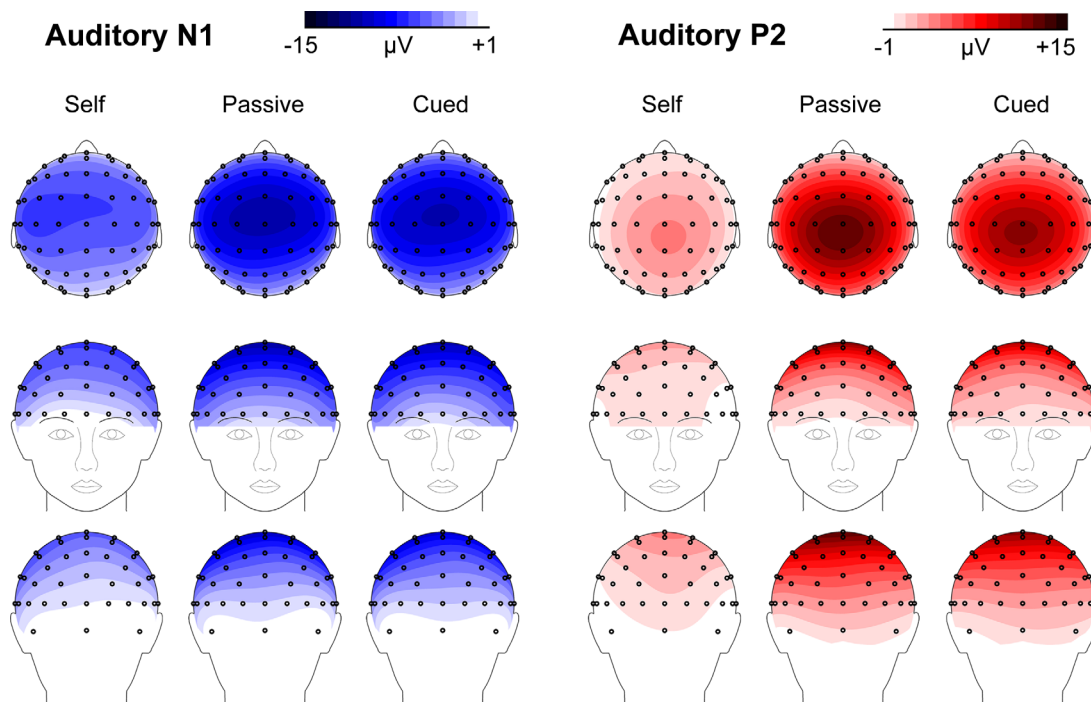
Figure 3. Topographic maps for the auditory N1 and P2 components. Scalp topographies are shown in the N1 and P2 time windows for the self, passive, and cued conditions.

There was also a significant main effect of condition for the P2 component, $F_{(2,80)} = 62.03$, $p < .001$, $\eta_p^2 = .61$. This indicated that mean P2 amplitude at electrode Cz differed between self ($M = 4.2$), passive ($M = 13.0$), and cued ($M = 11.4$) conditions (see Figures (2 and 3)). Post hoc tests indicated that self significantly differed from both passive, $F_{(2,39)} = 68.67$, $p < .001$ (see Figure 4), and cued, $F_{(2,39)} = 48.23$, $p < .001$. In addition, passive and cued significantly differed, $F_{(2,39)} = 1.68$, $p = .016$.

Visual Task

For the N75 component, a one-way ANOVA did not show a main effect of condition, $F_{(2,80)} = 0.52$, $p = .565$, $\eta_p^2 = .01$. This indicated that mean N75 amplitude at electrode Oz did not differ between self ($M = -4.26$), passive ($M = -4.78$), and cued ($M = -4.14$). Similarly, a main effect of condition was not evident for the P100 component, $F_{(2,80)} = 0.60$, $p = .552$, $\eta_p^2 = .02$. This indicated that mean P100 amplitude at electrode Oz did not differ between self ($M = 1.17$), passive ($M = 1.74$), and cued ($M = 1.66$).

However, for the N145 component, a one-way ANOVA revealed a main effect of condition, $F_{(2,82)} = 4.61$, $p = .013$, $\eta_p^2 = .11$. This indicated that mean N145 amplitude at electrode Oz differed between self ($M = -6.76$), passive ($M = -5.22$), and cued ($M = -5.43$) conditions (see Figure 2 and Figure 5). Post hoc tests indicated that self significantly differed from both passive, $F_{(2,41)} = 1.25$, $p = .006$ (see Figure 4), and cued, $F_{(2,41)} = 1.16$, $p = .050$, but that passive and cued did not differ from each other, $F_{(2,41)} = 0.02$, $p = .636$.

Correlations Between Sensory Suppression Measures

For self–passive measures, no significant correlations were observed across sensory modalities (i.e., N1/N75, N1/P100, N1/N145, P2/N75, P2/P100, P2/N145) using either absolute,

$r(2,38) < \pm .117$, $p \geq .473$, or ratio, $r(2,38) < \pm .274$, $p \geq .087$, calculations. Similarly, no significant correlations were observed across sensory modalities for self–cued measures using either absolute, $r(2,38) < \pm .224$, $p \geq .164$, or ratio, $r(2,38) < \pm .101$, $p \geq .539$, calculations. See Figure 6 for scatter plots comparing
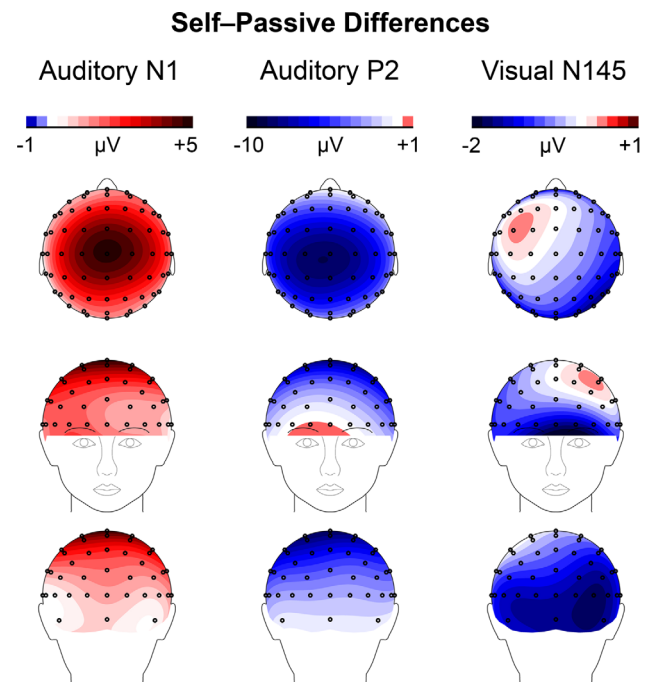
Figure 4. Topographic maps of self–passive difference waves for the auditory N1, auditory P2, and visual N145. Scalp topographies are shown in the N145 time windows for self conditions, referenced to either linked mastoids (auditory data) or site Fz (visual data).
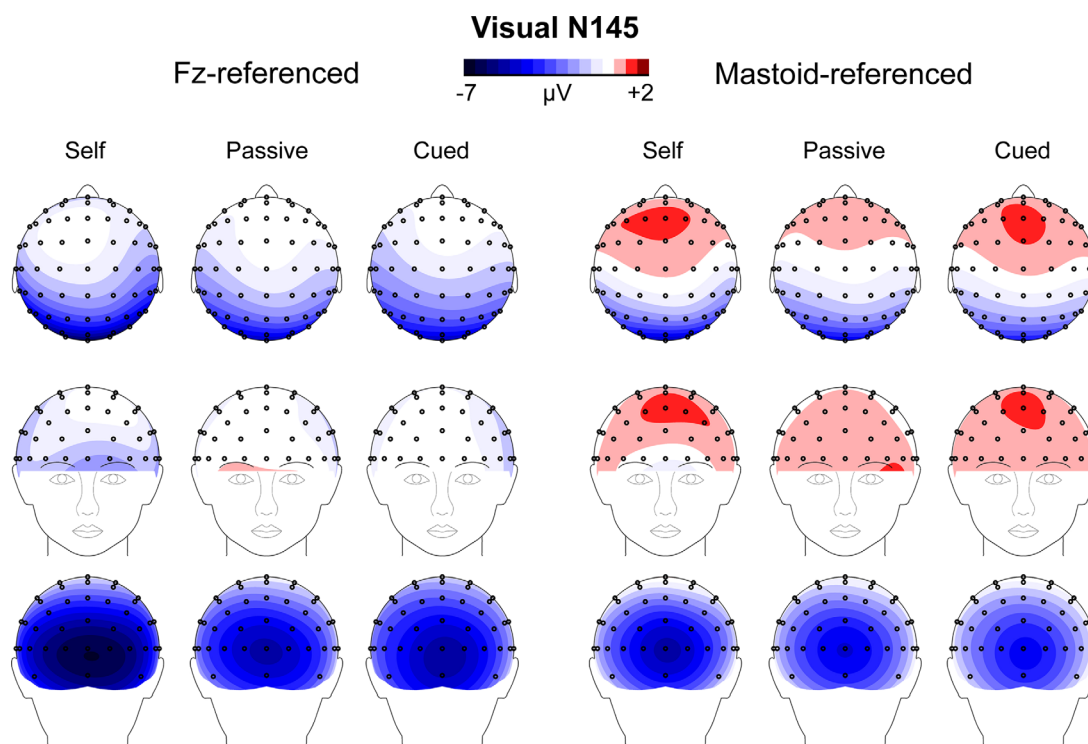
Figure 5. Topographic maps for the visual N145 component. Scalp topographies are shown in the N145 time windows for the self, passive, and cued conditions, referenced to either linked mastoids or site Fz.

self- and externally initiated conditions using the N1 and N145 absolute measures.

Reaction Times

Mean reaction times for each self-initiated condition were compared to check for possible behavioral differences between the auditory and visual tasks. Reaction times in the auditory tasks—active ($M = 811$ ms, $SD = 631$ ms); motor ($M = 830$ ms, $SD = 758$ ms)—were similar to those in the visual tasks—active ($M = 893$ ms, $SD = 486$ ms); motor ($M = 971$ ms, $SD = 531$ ms). A one-way ANOVA did not present a main effect, $F(2,80) = 0.80$, $p = .497$, $\eta_p^2 = .02$, which indicated that participants' reaction times did not

differ as a function of either condition (active or motor) or modality (auditory or visual).

Evaluating Possible Refractoriness Contributions

Mean interstimulus intervals (ISIs) differed between conditions, although the size of this intercondition difference was similar across modalities (see Appendix). Given the connection between refractoriness and N1 amplitude (Budd, Barry, Gordon, Rennie, & Michie, 1998), we conducted post hoc analyses to quantify the possible contribution this may have had to our effects.

To begin with, each participant's average ISI for each of the four conditions (active, passive, cued, motor) were entered as centered covariates in the ANOVAs described above. The outcomes
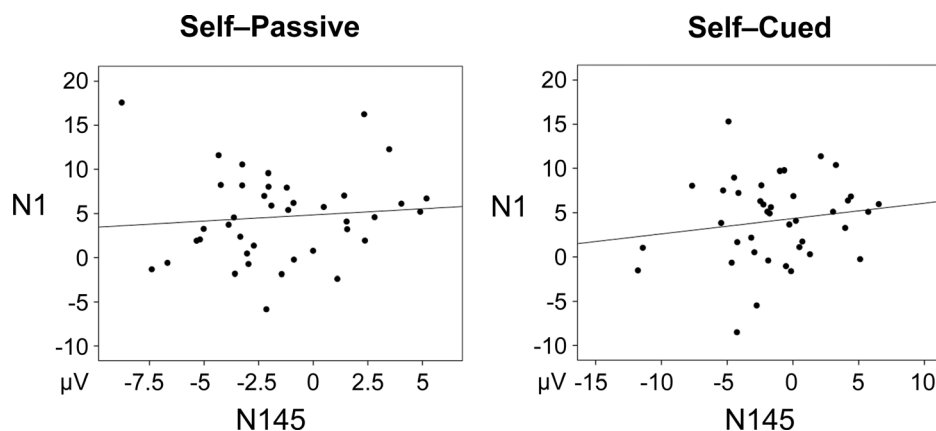
Figure 6. Scatter plots of absolute differences between self and passive conditions (left) and self and cued conditions (right). All axes represent mean amplitude in microvolts (μV) across the time windows of the respective components (auditory N1 and visual N145).

were identical; that is, the main effects for each component remained, and all self–passive contrasts remained significant (see Appendix for details). We also conducted independent samples *t* tests for each component on a median split of participants based on their ISI difference scores, calculated by subtracting ISI in the passive condition from ISIs in the active condition for each modality. There were no significant between-condition differences or trends (for all components, $t(38) < \pm 1.528$, $p \geq .135$, see Appendix), which indicated that ISIs were not having a consistent influence on component amplitude.

Additionally, we conducted a bivariate correlation analysis of participants' ISI difference scores with their self-initiation measures (i.e., self–passive, mean amplitudes) for all components. In the auditory modality, there was no significant correlation for either absolute ($r < \pm .235$, $p > .144$) or ratio ($r < \pm .124$, $p > .446$) measures. Likewise, in the visual modality, there was no significant correlation for either absolute ($r < \pm .204$, $p > .207$) or ratio ($r < \pm .305$, $p > .056$) measures. Lastly, we checked correlations between participants' ISI difference scores and N1 mean amplitude for each condition, and found no significant correlations (self: $r = -.114$, $p = .483$; passive: $r = -.263$, $p = .101$; cued: $r = -.138$, $p = .398$).

Supplementary Post Hoc Analyses at Extra Sites

For a more complete view of activity across the scalp, post hoc one-way ANOVAs were conducted for mean amplitudes at frontal (Fz) and occipital (Oz) sites for auditory components, and at a central (Cz) site for visual components. To further test the visual task, we also rereferenced visual data to linked mastoids and analyzed activity at electrodes Fz, Cz, and Oz. The details of these post hoc analyses are described below; in summary, for the auditory task, the pattern of results at both Fz and Oz was identical to results at Cz reported above, except that passive and cued did not significantly differ in mean P2 amplitude. For the visual task, no main effects occurred at any electrode site.

Auditory task. For electrode Fz, there was a significant main effect of condition for the N1 component, $F(2,80) = 12.92$, $p < .001$, $\eta_p^2 = .25$. This indicated that mean N1 amplitude differed between self ($M = -5.11$), passive ($M = -7.77$), and cued ($M = -7.53$) conditions, where self significantly differed from both passive, $F(2,39) = 4.76$, $p < .001$, and cued, $F(2,39) = 3.34$, $p < .001$, but passive and cued did not differ from each other, $F(2,39) = 0.03$, $p = .612$. Similarly, there was a significant main effect for the P2 component, $F(2,80) = 17.02$, $p < .001$, $\eta_p^2 = .30$. This indicated that mean P2 amplitude differed between self ($M = 2.15$), passive ($M = 5.94$), and cued ($M = 5.32$) conditions, where self significantly differed from both passive, $F(2,39) = 10.72$, $p < .001$, and cued, $F(2,39) = 7.75$, $p < .001$, but passive and cued did not differ from each other, $F(2,39) = 0.21$, $p = .265$.

For electrode Oz, there was a significant main effect of condition for the N1 component, $F(2,80) = 3.88$, $p = .025$, $\eta_p^2 = .09$. This indicated that mean N1 amplitude differed between self ($M = -0.81$), passive ($M = -1.86$), and cued ($M = -1.85$) conditions, where self significantly differed from both passive, $F(2,39) = 0.51$, $p = .019$, and cued, $F(2,39) = 0.50$, $p = .029$, but passive and cued did not differ from each other, $F(2,39) < 0.01$, $p = .931$. Similarly, there was a significant main effect for the P2 component, $F(2,80) = 6.22$, $p = .005$, $\eta_p^2 = .14$. This indicated that mean P2 amplitude differed between self ($M = 1.87$), passive ($M = 3.62$), and cued ($M = 3.42$) conditions, where self signifi-

cantly differed from both passive, $F(2,39) = 1.89$, $p = .007$, and cued, $F(2,39) = 1.40$, $p = .011$, but passive and cued did not differ from each other, $F(2,39) = 0.02$, $p = .633$.

Visual task. For Fz-referenced data at electrode Cz, there were no main effects of condition for any component. This indicated that for the N75 component, $F(2,80) = 2.19$, $p = .128$, $\eta_p^2 = .05$, mean amplitude at electrode Cz did not differ between self ($M = -0.88$), passive ($M = -1.60$), and cued ($M = -1.04$) conditions. Similarly, for the P100 component, $F(2,80) = 1.36$, $p = .262$, $\eta_p^2 = .03$, mean amplitude at electrode Cz did not differ between self ($M = -0.49$), passive ($M = -0.02$), and cued ($M = -0.47$) conditions. Lastly, for the N145 component, $F(2,80) = 0.45$, $p = .642$, $\eta_p^2 = .01$, mean amplitude at electrode Cz did not differ between self ($M = -0.37$), passive ($M = -0.14$), and cued ($M = -0.50$) conditions.

For mastoid-referenced data, there were no main effects. For all sites (Oz, Cz, Fz), mean amplitude did not differ between self, passive, and cued conditions for the N75 component, $F(2,80) \leq 1.65$, $p \geq .200$, $\eta_p^2 \leq .05$; P100 component, $F(2,80) \leq 0.94$, $p \geq .379$, $\eta_p^2 \leq .03$; or N145 component, $F(2,80) \leq 1.99$, $p \geq .154$, $\eta_p^2 \leq .05$.

Discussion

The primary aim of the present study was to investigate the effect of self-initiation on sensory processing in both auditory and visual domains in healthy participants. As predicted, we observed electrophysiological suppression of the N1 component of the AEP to self-initiated auditory stimuli (button press-elicited tones). However, in contrast, we observed an increase in the amplitude of the N145 component of the VEP to self-initiated visual stimuli (button press-elicited pattern reversals). Furthermore, there was no correlation between participants' level of electrophysiological sensory suppression in the auditory and visual tasks. Taken together, these results suggest that electrophysiological suppression of self-initiated sensations may not occur across all sensory modalities, but may instead be specific to certain modalities such as audition. Indeed, the results of the present study suggest that self-initiated, button press-elicited visual stimuli may in fact cause an amplification—rather than suppression—of the visual N145 component.

An additional aim was to quantify the contribution of temporal predictability to any observed differences in response between self- and externally initiated stimuli. There was a difference in P2, but not N1 response between passive and cued conditions in the auditory tasks, but no difference at any component in the visual tasks. This suggests that temporal predictability was involved to a minor degree in basic sensory processing of the tones used in this study, but not the pattern-reversal stimuli.

In the auditory domain, self-initiated tones evoked significantly attenuated auditory N1 amplitude compared to both externally initiated conditions (i.e., passive and cued). This result corroborates the substantial body of literature showing sensory suppression of auditory stimuli (e.g., Baess et al., 2008; Ford et al., 2001; Heinks-Maldonado et al., 2005). In terms of temporal predictability, auditory N1 response did not differ between the passive and cued conditions, but there was a difference in P2 response. This contrasts somewhat with earlier studies that have found attenuation of AEP responses to temporally predictable stimuli for both externally initiated conditions (Ford et al., 2007; Lange, 2009; Oestreich et al., 2015; Schafer, Amochaev, & Russell, 1981) and, by controlling sound onset delay, self-initiated conditions (Baess et al., 2008). Substantial methodological diversity exists: Lange (2009) relied on the temporal rhythm of the stimuli (i.e., the tones themselves

became temporal cues) while the present study used a visual countdown similar to Ford et al. (2007). These different methods of temporal orienting may have varying contributions to attention and prediction—see Lange (2013) for a review. Notably, the countdown method contains an element of temporal uncertainty, as it requires an estimation of the time elapsed between the final cue and the tone. This could be avoided by use of a spectrogram-style cue as employed in Oestreich et al. (2015). In short, we speculate that residual uncertainty explains the lack of an expected cued effect at N1, which consequently suggests that P2 is more sensitive to this form of manipulation. This also supports the emerging notion that differences at P2 may be instructive in the comparison of self- versus externally initiated auditory stimuli (SanMiguel, Todd, & Schröger, 2013).

With regard to our auditory task design, a strength of the current design was that the order of the conditions was fully randomized; that is, self did not have to precede passive, as is the case in traditional yoked designs. However, a limitation of the current design is that it required us to estimate ISIs in the passive and cued conditions. Our estimation was slightly (but significantly) too generous in that ISIs in self-initiated blocks ended up longer than in externally initiated blocks by approximately 600 ms on average. This raises the possibility that refractoriness moderated N1 amplitude, though this is more pronounced with ISIs shorter than in the present study (Budd et al., 1998). Several follow-up analyses we conducted suggest that refractoriness was not responsible for our effects, as described in Results, with additional details presented in Appendix. In particular, there was no correlation between ISI and N1 amplitude, and the results did not change when participants' centered ISIs for the four conditions were included as nuisance covariates.

In the visual domain, self-initiated pattern reversals evoked significantly augmented visual N145 amplitude at electrode Oz compared to both externally initiated conditions (i.e., passive and cued), while no difference was observed between self- or externally initiated conditions in terms of visual N75 or P100 response. This lack of modulation in early response contrasts with previous self-initiation studies involving visual stimuli, which have shown attenuation at vertex (but not occipital) electrode sites (Gentsch & Schutz-Bosbach, 2011; Schafer & Marcus, 1973) or posterior enhancement (Hughes & Waszak, 2011). However, the present finding of increased response at N145 to self-initiated pattern-reversal stimuli is novel. Importantly, this was not an artificial effect produced by referencing, as suppression was not evident at anterior sites around the Fz reference, as can be seen in the mastoid-referenced data (Figure 5), and lack of main effects for post hoc analyses conducted at Cz and Fz with such data. This seems to differ from Schafer and Marcus (1973), who reported self-initiated suppression of visual components at the vertex, but did not report frontal or topographical data. Thus, the pattern of effects in the current study is that self-initiation leads to reduced AEPs but increased visual evoked potentials. Interestingly, ongoing electrophysiological investigation of mice has also demonstrated heightened responsiveness to visual stimuli (Niell & Stryker, 2010)—but suppression to auditory stimuli (Zhou et al., 2014)—as the animals freely move (see also Schneider, Nelson, & Mooney, 2014). This relationship could represent an important prioritization of visual over auditory stimuli in our sensory-guided interaction with the environment. Alternatively, it may reflect processing based on the natural contingencies between actions and resultant sensations. Simple motor acts, such as finger movements, often lead to auditory sensations (e.g., tapping one's finger on the table), but less often lead to abrupt, dramatic visual sensations (e.g., full-

field visual stimulation as in the present study). Less frequently reinforced contingencies (i.e., motor–visual) are proportionally more likely to contain important information than stronger contingencies (i.e., motor–auditory), which may explain processing enhancement and attenuation of these respective tasks. This possibility further underlines the call by Horváth (2015) for systematic investigation into action–effect contingency.

The amplified N145 response to self-initiated stimuli in the present study may also be compared to the visual enhancement reported by Hughes and Waszak (2011) mentioned earlier, although they analyzed the P1 component of electrophysiological response evoked by pattern-onset stimuli. Shawkat and Kriss (2000) have directly compared VEPs evoked by pattern onset/offset and pattern-reversal stimuli—manipulating contrast of the checkerboards in a stepwise fashion to morph between the two types of stimulation—and indicated that the reversal N145 component may be analogous not to the P1, but to the N1 component elicited by pattern onset. Given that attention has been shown to enhance both N1 and P1 response to pattern-onset stimuli (Clark & Hillyard, 1996), it is possible that observed amplification of the N145 in the current study could be caused by an increase in attention to self-initiated pattern reversals. Indeed, nonstimulus-related modulation unique to the N145 component of the pattern-reversal VEP is not surprising, given the likelihood that the N145 is generated over a wider cortical area than the N75 and P100 components (Shigeto, Tobimatsu, Yamamoto, Kobayashi, & Kato, 1998). When comparing pattern-onset and pattern-reversal stimuli, it is also worth mentioning that both are simple and involve low-level representations. Contrary to the visual enhancement found in response to these stimuli, Hughes and Waszak (2014) report sensory attenuation for high-level stimuli (faces and houses). A parametrical investigation of the influence of visual stimulus complexity on neurophysiological sensory attenuation would be a worthwhile continuation of these findings.

Regarding temporal prediction in the visual tasks, the lack of difference between passive and cued conditions suggests that there was no effect of temporal prediction on visual processing in the current study. This is consistent with the finding that temporal attention to visual stimuli seems to increase early neural response only when the task is perceptually demanding (Correa, Lupianez, Madrid, & Tudela, 2006), as opposed to the perceptually simple task used in the present study. In view of the finding that self-initiation amplified N145 response, the lack of difference between externally initiated conditions indicates that if the amplification is, in fact, due to increased attention, this attention would need to be directed toward nontemporal features of the stimulus.

The final result of interest was the lack of any significant correlation between participants' electrophysiological response modulation in the auditory and visual tasks; in particular, auditory N1 attenuation was not quantitatively related to visual N145 amplification. This suggests that the effects of self-initiation may be sensory specific, but more work is required on the underlying neurophysiological mechanisms that may be producing this differential processing. It is possible that a higher-level, nonsensory-specific process may also have contributed to the reported effects of self-generation. Accordingly, designs that attempt to isolate sensory and nonsensory subcomponents of the N1 component are highly relevant (SanMiguel et al., 2013), as are emerging lines of enquiry beyond stimulus-evoked responses, such as alpha oscillations (Stenner et al., 2014). The possibility of sensory specificity is interesting because of potential implications with regard to the prevalence of psychotic symptoms in disorders such as schizophrenia.

Following the theoretical link between abnormal sensory suppression and psychotic symptoms (Feinberg, 1978; Frith, 2005), the apparent sensory specificity of electrophysiological response to self-initiated stimuli may lend insight to the prevalence and pathology underlying auditory and visual hallucinations. It may also shed light on why auditory hallucinations are so much more common than visual hallucinations in patients with schizophrenia. In this study of healthy participants, there was no apparent relationship between auditory and visual effects, and it would be worthwhile to examine if this were also true in a population with schizophrenia.

In sum, the present study undertook an investigation of self-initiated sensations in both auditory and visual domains using the same participants, the first since Schafer and Marcus (1973) and the first to report within-subject comparisons. The results indicated that electrophysiological sensory attenuation occurs in response to self-initiated auditory, but not visual, sensations in healthy participants. These findings highlight the importance of several continuing areas of investigation, including the impact on sensory processing across sensory modalities of factors such as contingency, temporal predictability, and stimulus complexity.

Appendix

Interstimulus Intervals

Additional analyses were conducted to investigate the possible contributions of refractoriness, given that mean stimulus onset-to-onset delays were found to differ in the auditory (active: 3,422 ms; motor: 3,396 ms; passive: 4,102 ms; cued: 5,583 ms) and visual tasks (active: 5,996 ms; motor: 6,086 ms; passive: 6,588 ms; cued: 7,566 ms). ANOVAs presented here are identical to the analyses in the Results section, but with participants' centered ISIs for the four conditions as nuisance covariates. We also present independent samples t tests based on participants' ISI difference scores.

Auditory task (ISI covariates). For the N1 component, a one-way ANOVA showed a significant main effect of condition, $F(2,80) = 26.49$, $p < .001$, $\eta_p^2 = .43$. This indicated that mean N1 amplitude at electrode Cz differed between self, passive, and cued conditions, where self significantly differed from both passive, $F(2,39) = 16.24$, $p < .001$, and cued, $F(2,39) = 12.67$, $p < .001$, but passive and cued did not differ from each other, $F(2,39) = 0.15$, $p = .381$.

There was also a significant main effect for the P2 component, $F(2,80) = 61.46$, $p < .001$, $\eta_p^2 = .64$. This indicated that mean P2 amplitude at electrode Cz differed between self, passive, and cued conditions, where self significantly differed from both

passive, $F(2,39) = 64.90$, $p < .001$, and cued, $F(2,39) = 49.20$, $p < .001$, and passive and cued also significantly differed, $F(2,39) = 1.71$, $p = .018$.

Visual task (ISI covariates). For the N75 component, a one-way ANOVA did not show a main effect of condition, $F(2,80) = 0.51$, $p = .603$, $\eta_p^2 = .01$. This indicated that mean N75 amplitude at electrode Oz did not differ between self, passive, and cued conditions. Similarly, a main effect of condition was not evident for the P100 component, $F(2,80) = 0.51$, $p = .575$, $\eta_p^2 = .01$. This indicated that mean P100 amplitude at electrode Oz did not differ between self, passive, and cued conditions.

However, for the N145 component, a one-way ANOVA revealed a main effect of condition, $F(2,80) = 4.50$, $p = .014$, $\eta_p^2 = .11$. This indicated that mean N145 amplitude at electrode Oz differed between self, passive, and cued conditions, where self significantly differed from passive, $F(2,39) = 1.25$, $p = .006$, but not cued, $F(2,39) = 1.20$, $p = .060$, and passive and cued did not differ from each other, $F(2,39) = 0.02$, $p = .632$.

Independent samples t tests. Difference scores were calculated for each participant by subtracting their ISI for passive from their ISI for self for each modality (for example, using the mean ISIs described above results in -680 ms for auditory and -592 ms for visual). Then, for each modality, participants were divided into small ISI difference and large ISI difference groups based on a median split of their difference scores, and independent samples t tests were conducted comparing these groups on their mean amplitudes.

For the auditory N1 at site Cz (referenced to mastoids), there were no significant between-group differences for self, $t(38) = 1.009$, $p = .319$; passive, $t(38) = 1.528$, $p = .135$; or cued, $t(38) = 0.051$, $p = .960$. Similarly, for the P2, there were no significant between-group differences for self, $t(38) = 0.780$, $p = .440$; passive, $t(38) = -0.243$, $p = .809$; or cued, $t(38) = 1.083$, $p = .286$.

For the visual N75 at site Oz (referenced to Fz), there were no significant between-group differences for self, $t(38) = -0.351$, $p = .728$; passive, $t(38) = 0.551$, $p = .585$; or cued, $t(38) = 0.968$, $p = .339$. Similarly, for the P100, there were no significant between-group differences for self, $t(38) = -0.309$, $p = .759$; passive, $t(38) = -0.046$, $p = .964$; or cued, $t(38) = -0.009$, $p = .993$. Lastly, for the N145, there were no significant between-group differences for self, $t(38) = -1.054$, $p = .298$; passive, $t(38) = -0.117$, $p = .907$; or cued, $t(38) = -1.041$, $p = .304$.

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