Movement Planning Determines Sensory Suppression: An Event-related Potential Study

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Abstract

■ Sensory suppression refers to the phenomenon that sensory input generated by our own actions, such as moving a finger to press a button to hear a tone, elicits smaller neural responses than sensory input generated by external agents. This observation is usually explained via the internal forward model in which an efference copy of the motor command is used to compute a corollary discharge, which acts to suppress sensory input. However, because moving a finger to press a button is accompanied by neural processes involved in preparing and performing the action, it is unclear whether sensory suppression is the result of movement planning, movement execution, or both. To investigate this, in two experiments, we compared ERPs to self-generated tones that were produced by voluntary, semivoluntary, or involuntary button-presses, with externally generated tones that were produced by a computer. In Experiment 1, the semivoluntary and involuntary button-presses were initiated by the participant or experimenter, respectively, by electrically stimulating the median nerve in the participant's forearm, and in Experiment 2, by applying manual force to the participant's finger. We found that tones produced by voluntary button-presses elicited a smaller N1 component of the ERP than externally generated tones. This is known as N1-suppression. However, tones produced by semivoluntary and involuntary button-presses did not yield significant N1-suppression. We also found that the magnitude of N1-suppression linearly decreased across the voluntary, semivoluntary, and involuntary conditions. These results suggest that movement planning is a necessary condition for producing sensory suppression. We conclude that the most parsimonious account of sensory suppression is the internal forward model. ■

INTRODUCTION

Sensory input caused by our own actions is experienced differently from the same inputs when produced by an external agent. For instance, we do not perceive a shifting environment when we move our eyes, but we can tell when our environment shifts, we judge our speech as unfamiliar when we hear it replayed to us compared to when we produce it, and we are unable to tickle ourselves, even if we are ticklish. But, how does the brain determine whether sensory input is self- or externally generated? The internal forward model (Miall & Wolpert, 1996) postulates that when we perform an action, such as move our eyes, mouth, or fingers, an efference copy is issued in parallel (Von Holst & Mittelstaedt, 1950). This efference copy is used to compute a neural prediction—a corollary discharge (Sperry, 1950)—of the sensory consequences of the action. If the corollary discharge matches the sensory input, the sensory input is tagged as self-generated and neural and perceptual responses are suppressed—this phenomenon is called sensory suppression (Horváth, 2015; Schröger, Marzecová, & SanMiguel, 2015; Hughes, Desantis, & Waszak, 2013; Bendixen, SanMiguel, & Schröger, 2012; for an alternative explanation of this phenomenon, see Press, Kok, & Yon, 2020; Reznik & Mukamel, 2019; Yon, Gilbert, de Lange, & Press, 2018). Alternatively, if the corollary discharge does not match the sensory input, or if the sensory input is not accompanied by a corollary discharge, the sensory input is tagged as externally generated (Straka, Simmers, & Chagnaud, 2018; Schneider & Mooney, 2018; Crapse & Sommer, 2008; Poulet & Hedwig, 2007; Schütz-Bosbach & Prinz, 2007). For this reason, it is thought that the brain has a sense of agency over sensory inputs that are "explained away" by a corollary discharge (Haggard, 2017). The aim of this study was to investigate the role of movement planning, which is defined as the process of preparing (rather than executing) the motor command, in producing sensory suppression.

One way to investigate the phenomenon of sensory suppression is to use EEG and the self-stimulation paradigm (Horváth, 2015; Schafër & Marcus, 1973). In this paradigm, participants listen to tones that are either self-generated by moving their finger to press a button or externally

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generated by a computer. The typical finding is that self-generated tones elicit a smaller N1—an ERP signature of auditory cortex processing (Woods, 1995; Näätänen & Picton, 1987)—than externally generated tones (Neszmélyi & Horváth, 2017; Elijah, Le Pelley, & Whitford, 2016; Mifsud et al., 2016; Oestreich et al., 2016; van Elk, Salomon, Kannape, & Blanke, 2014; Knolle, Schröger, & Kotz, 2013; SanMiguel, Todd, & Schröger, 2013; Saupe, Widmann, Trujillo-Barreto, & Schröger, 2013; Timm, SanMiguel, Saupe, & Schröger, 2013; Bäß, Jacobsen, & Schröger, 2008). This is known as N1-suppression and is thought to reflect the operation of an efference copy and corollary discharge (Horváth, 2015; Schröger et al., 2015; Hughes et al., 2013; Bendixen et al., 2012). Because the amplitude of N1 decreases as tones become quieter (Mulert et al., 2005), N1-suppression is consistent with the observation that self-generated tones are perceived as being less salient than externally generated tones (Desantis, Weiss, Schütz-Bosbach, & Waszak, 2012; Weiss, Herwig, & Schütz-Bosbach, 2011a, 2011b). Some studies have also shown that self-generated tones elicit a smaller P2 than externally generated tones (Mifsud et al., 2016; Horváth, 2013; Knolle et al., 2013; SanMiguel et al., 2013). This is known as P2-suppression (Horváth, 2015). However, because the functional significance of P2 and P2-suppression is currently unknown (Horváth, 2015; Crowley & Colrain, 2004), this finding is difficult to interpret.

Despite the extensive use of the self-stimulation paradigm, relatively little is known about the role of movement planning in this paradigm (but see Voss, Ingram, Haggard, & Wolpert, 2006). Specifically, because moving a finger to press a button is accompanied by neural processes involved in preparing and performing the action, it is unclear whether sensory suppression is the result of movement planning, movement execution, or both (Horváth, 2015). Recently, Timm, SanMiguel, Keil, Schröger, and Schönwiesner (2014) investigated this issue by comparing the magnitude of sensory suppression to tones that were produced by voluntary or involuntary button-presses. In the voluntary condition of their experiment, participants intentionally moved their finger to press a button to produce a tone; thus, the button-press was planned by participants. In the involuntary condition, the experimenters forced participants to unintentionally move their finger to press a button to produce a tone by stimulating their primary motor cortex with TMS; thus, the button-press was not planned by participants. Similar to previous studies, there was also an externally generated condition in which tones were produced by a computer. Timm et al. (2014) found that tones produced by voluntary button-presses elicited a smaller N1–P2 complex—the peak-to-peak difference between N1 and P2 (Näätänen & Picton, 1987)—than externally generated tones. This is known as N1–P2 suppression (Horváth, 2015). However, tones produced by involuntary button-presses did not yield significant N1–P2 suppression. Moreover, they found that the magnitude of N1–P2 suppression was larger in the voluntary condition than in the involuntary condition. These results suggest that movement planning is a necessary condition for producing sensory suppression.

The aims of this study are as follows. First, we attempted to replicate and extend the findings of Timm et al. (2014) with techniques other than TMS. This is important, because the precise effects of TMS on the brain are unknown (Miniussi, Harris, & Ruzzoli, 2013), and it is possible that TMS may have interfered with the neural processes responsible for producing sensory suppression. Thus, we used techniques that act on the peripheral, rather than the central, nervous system. Specifically, in Experiment 1, we forced participants to unintentionally move their finger to press a button to produce a tone by electrically stimulating the median nerve in their forearm with an electrical stimulator, and in Experiment 2, by applying manual force to the participant's finger. If movement planning is a necessary condition for producing sensory suppression, we hypothesize N1-suppression for the voluntary condition but not for the involuntary condition. Second, it is unclear whether volition should be operationalized as a binary construct—voluntary versus involuntary—or as a continuous construct. To explore this, we used a semivoluntary condition in which participants intentionally initiated involuntary button-presses themselves. Specifically, in Experiment 1, participants electrically stimulated the median nerve in their forearm with the electrical stimulator, and in Experiment 2, they applied manual force to one of their fingers. Because the semivoluntary condition requires a voluntary action to execute the involuntary action, if volition is a binary construct, we hypothesize similar N1-suppression effects for the voluntary and semivoluntary conditions. If, however, volition is a continuous construct, then we hypothesize a downward trend in the magnitude of N1-suppression across the voluntary, semivoluntary, and involuntary conditions.

EXPERIMENT 1

Method

Participants

Forty-one students from UNSW Sydney participated in our study for course credit. All participants gave written informed consent before the experiment and reported having normal hearing in both ears. Data from five participants were excluded from further analyses because of excessive artifacts in the EEG recording (> 75% of epochs meeting the rejection criteria; see below). Mean age of the remaining participants (19 female, 34 right-handed) was 20 (SD = 3) years. The experiment was approved by UNSW Sydney's Human Research Ethics Advisory Panel (Psychology) and was conducted in accordance with the ethical standards laid down in the Declaration of Helsinki (World Medical Association, 2004).

Apparatus, Stimuli, and Procedure

The experiment consisted of 18 blocks, each of which consisted of 50 trials. In two blocks, participants performed the *voluntary condition* (see Figure 1A): Participants intentionally moved a finger on their right hand to press a button on a standard computer mouse to produce a 1000-Hz tone (200 msec long including 10-msec rise and fall times; 75 dB SPL) through headphones (AKG K77). In two different blocks, participants performed the *semivoluntary condition* (see Figure 1B): Participants intentionally moved a finger on their left hand to press a button on an electrical stimulator (PowerLab 4/25T), which sent an electrical current (M = 7.5 mA, SD = 2.14 mA) to a bar electrode placed above the median nerve along their right, inner forearm, forcing them to unintentionally move a finger on their right hand to press a button to produce a tone through headphones. In both of these conditions, participants were instructed to keep a constant pace between button-presses of about 2–3 sec. In two different blocks, participants performed the *involuntary condition* (see Figure 1C): The experimenter pressed a button on the electrical stimulator, forcing participants to unintentionally move a finger on their right hand to press a button to produce a tone through headphones. The experimenter kept a constant pace between button-presses of approximately 2–3 sec. Collectively, these conditions are known as the *self-generated conditions*.

Immediately after a block of trials containing the voluntary, semivoluntary, or involuntary conditions, participants performed the *externally generated condition* (see Figure 1D–1F): Participants passively listened to the same sequence of tones that they had just generated. The approach of "playing back" the self-generated sequence ensures that the intersound interval between any two tones is identical for the self- and externally generated conditions. This is important because the amplitude of N1 increases as the intersound interval becomes larger (SanMiguel et al., 2013; Budd, Barry, Gordon, Rennie, & Michie, 1998; Davis, Mast, Yoshie, & Zerlin, 1966).

To control for motor-related activity present in the self-generated conditions but not in the externally generated condition, participants performed the *motor conditions*. The motor conditions were identical to the self-generated conditions, except that the button-press did not produce a tone. Specifically, in two blocks, participants performed the *voluntary motor condition* (see Figure 1G): Participants intentionally moved a finger on their right hand to press a button, but no tone was produced. In two different blocks, participants performed the *semivoluntary motor condition* (see Figure 1H): Participants intentionally moved a finger on their left hand to press a button on the electrical

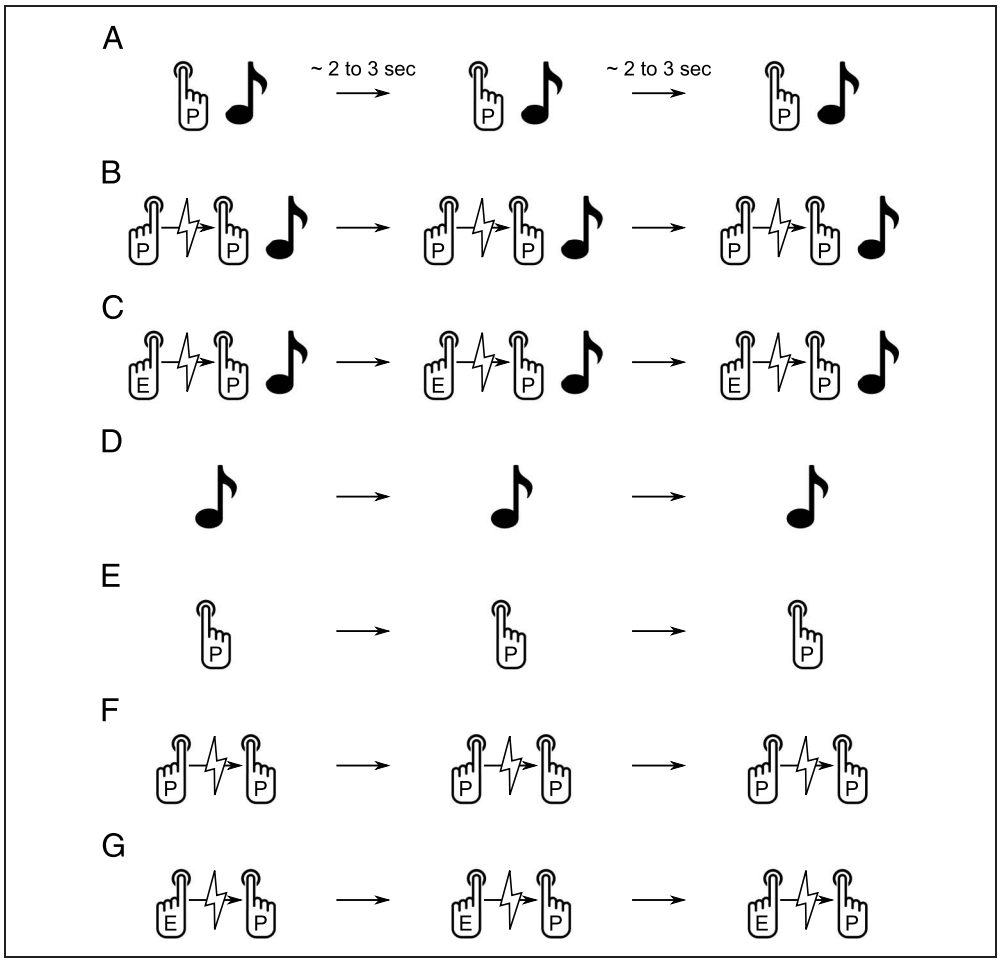

Figure 1. Procedure for Experiment 1. (A) In the voluntary condition, participants intentionally pressed a button every 2–3 sec to hear a tone through headphones. (B) In the semivoluntary condition, participants intentionally pressed a button on an electrical stimulator, forcing them to unintentionally press a button to hear a tone. (C) In the involuntary condition, the experimenter pressed a button on the electrical stimulator, forcing the participant to unintentionally press a button to hear a tone. (D) In the externally generated conditions, participants passively listened to the tones generated by them in the self-generated conditions. (E–G) The motor conditions were identical to the self-generated conditions, except that the button-presses did not produce a tone. P = participant; E = experimenter.

stimulator, forcing them to unintentionally move a finger on their right hand to press a button, but no tone was produced. Similar to the self-generated conditions, participants were instructed to keep a constant pace between button-presses of about 2–3 sec. In the remaining two blocks, participants performed the *involuntary motor condition* (see Figure 1I): The experimenter pressed a button on the electrical stimulator, forcing participants to unintentionally move a finger on their right hand to press a button, but no tone was produced. The experimenter kept a constant pace between button-presses of approximately 2–3 sec. The order of blocks containing the different conditions was counterbalanced across participants.

EEG Acquisition

The EEG was recorded with a BioSemi ActiveTwo system from 64 Ag/AgCl active electrodes placed according to the extended 10–20 system (FP1, FPz, FP2, AF7, AF3, AFz, AF4, AF8, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO7, PO3, POz, PO4, PO8, O1, Oz, O2, Iz). A vertical EOG was recorded by placing an electrode above (we used FP1) and below the left eye; a horizontal EOG was recorded by placing an electrode on the outer canthus of each eye. We also placed an electrode on each mastoid. The sampling rate of the EEG was 2048 Hz.

ERP Preprocessing

We used BrainVision Analyzer 2.1 to preprocess the EEG data. We re-referenced the data off-line to the electrodes on the mastoids, and we filtered the data using a half-amplitude 0.1- to 30-Hz phase-shift free Butterworth filter (48 dB/Oct slope), as well as a 50-Hz Notch filter. We extracted the epochs from –400 to 400 msec relative to tone onset for the self- and externally generated conditions and to the button-press in the motor conditions; we corrected the epochs for eye-blink and movement artifacts using the technique described in Gratton, Coles, and Donchin (1983) and Miller, Gratton, and Yee (1988); and we excluded all epochs with signals exceeding peak-to-peak amplitudes of 200 μV at any EEG channel. Approximately 15% of all trials were rejected. We baseline-corrected all epochs to their mean voltage from −400 to −200 msec to avoid the artifact of the electrical stimulator in the semivoluntary and involuntary conditions, and we computed an ERP for each condition. On average, ERPs were computed from 80 (SD = 30) voluntary, 81 (SD = 33) semivoluntary, 74 (SD = 31) involuntary, 80 (SD = 30) voluntary-motor, 75 (SD = 30) semivoluntary-motor, 75 (SD = 29) involuntary-motor, and 280 (SD = 14) external epochs. We subtracted the motor ERPs from their respective self-generated ERPs, as is typical in studies using the self-stimulation paradigm (Horváth, 2015). All of our analyses were conducted on the motor-corrected self-generated ERPs.

ERP Analysis

We analyzed the N1 at the vertex (Cz) in the time window of 71–91 msec, and we analyzed the P2 at the vertex in the time window of 152–172 msec. We chose this electrode site to be consistent with the literature on N1- and P2-suppression (Horváth, 2015), and we selected these time windows using the collapsed localizer technique described in Luck and Gaspelin (2017). Moreover, to facilitate a comparison between our results and those of Timm et al. (2014), we analyzed the N1–P2 complex by calculating the difference between the amplitudes of the N1 and P2 time windows.

Results

Figure 2A shows the grand-averaged ERPs, Figure 2B shows the distribution of voltages over the scalp during the N1 time window, and Figure 2C shows the magnitude of the N1-suppression effects. A repeated-measures ANOVA with four levels (voluntary, semivoluntary, involuntary, and external) on the mean amplitudes of N1 was significant, $F(3, 105) = 2.76$, $p = .046$, $\eta_p^2 = .07$. Post hoc t tests found a significant difference between the voluntary and external conditions, $t(35) = 2.98$, $p = .005$, $d = 0.50$—this difference is known as N1-suppression (Horváth, 2015; Schröger et al., 2015; Hughes et al., 2013; Bendixen et al., 2012)—however, the difference between the semivoluntary and external conditions was not significant, $t(35) = 0.89$, $p = .380$, $d = 0.15$, nor was the difference between the involuntary and external conditions, $t(35) = 1.00$, $p = .323$, $d = 0.17$. Post hoc t tests also found a significant difference between the voluntary and involuntary conditions, $t(35) = 2.22$, $p = .033$, $d = 0.37$; however, the difference between the voluntary and semivoluntary conditions was not significant, $t(35) = 1.51$, $p = .139$, $d = 0.25$, nor was the difference between the semivoluntary and involuntary conditions, $t(35) = 1.24$, $p = .222$, $d = 0.21$. In addition, a trend analysis with three levels (voluntary, semivoluntary, and involuntary) on the magnitude of the N1-suppression effects found a significant linear trend, $F(1, 35) = 4.93$, $p = .033$, $\eta_p^2 = .12$. These results suggest that movement planning is a necessary condition for producing sensory suppression, in that only voluntarily produced tones yielded N1-suppression, and that decreasing volition decreased the magnitude of sensory suppression, in that the magnitude of N1-suppression linearly decreased across the voluntary, semivoluntary, and involuntary conditions.

Figure 2D shows the magnitude of the P2-suppression effects. A repeated-measures ANOVA on the mean amplitudes of P2 was not significant, $F(3, 105) = 0.82$, $p = .485$, $\eta_p^2 = .02$. Planned t tests found a significant difference between the voluntary and external conditions, $t(35) = 2.88$, $p = .007$, $d = 0.48$—this difference is known as P2-suppression (Horváth, 2015)—however, the difference between the semivoluntary and external conditions was not significant, $t(35) = 0.76$, $p = .453$,

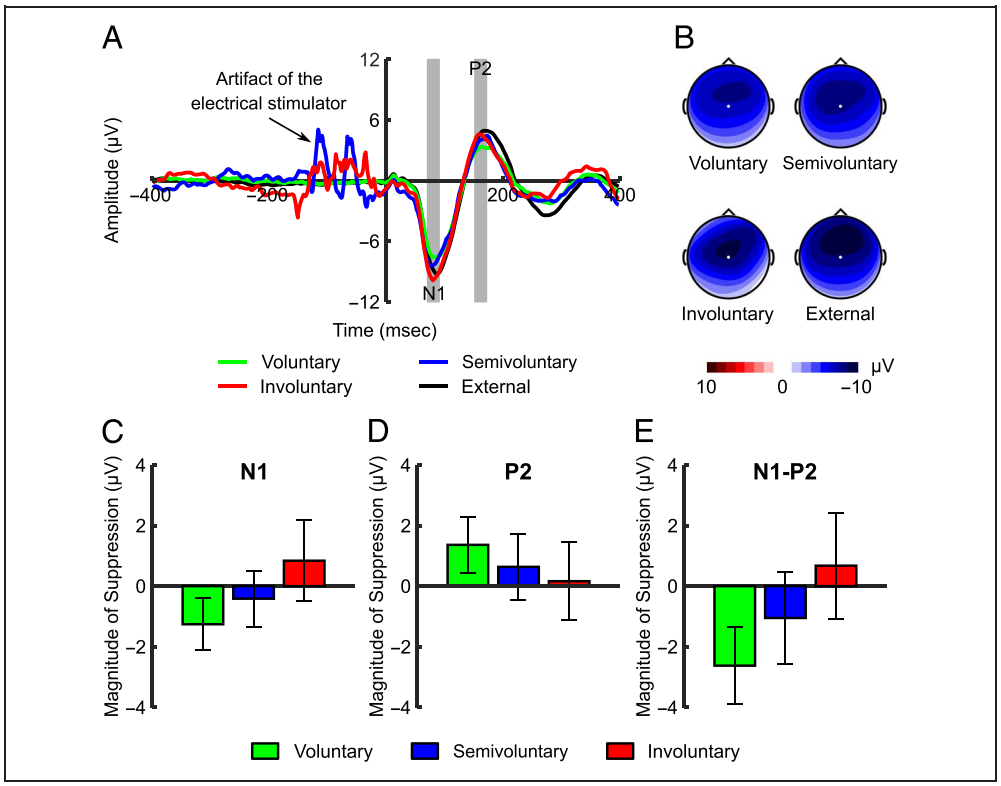

Figure 2. Results for Experiment 1. (A) The line graph shows the grand-averaged ERPs for each condition at the vertex, showing time (msec) on the *x* axis, with 0 indicating the onset of the tone, and voltage (μV) on the *y* axis, with positive voltages plotted upward. The gray bars show the N1 (71–91 msec) and P2 (152–172 msec) time windows. (B) The voltage maps show the distribution of voltages over the scalp during the N1 time window. (C) The bar graphs show the magnitude of the N1-suppression effects, (D) the P2-suppression effects, and (E) the N1–P2 suppression effects.

$d = 0.13$, nor was the difference between the involuntary and external conditions, $t(35) = 0.15$, $p = .880$, $d = 0.03$. Planned t tests also found that the difference between the voluntary and semivoluntary conditions was not significant, $t(35) = 0.81$, $p = .424$, $d = 0.14$; that the difference between the voluntary and involuntary conditions was not significant, $t(35) = 1.00$, $p = .323$, $d = 0.17$; and that the difference between the semivoluntary and involuntary conditions was not significant, $t(35) = 0.45$, $p = .657$, $d = 0.08$. In addition, a trend analysis on the magnitude of the P2-suppression effects found that the linear trend was not significant, $F(1, 35) = 1.01$, $p = .323$, $\eta_p^2 = .03$. These results show that only voluntarily produced tones yielded P2-suppression.

Figure 2E shows the magnitude of the N1–P2 suppression effects. A repeated-measures ANOVA on the mean amplitudes of the N1–P2 complex was significant, $F(3, 105) = 4.55$, $p = .005$, $\eta_p^2 = .12$. Post hoc t tests found a significant difference between the voluntary and external conditions, $t(35) = 5.33$, $p < .001$, $d = 0.89$—this difference is known as N1–P2 suppression (Horváth, 2015)—however, the difference between the semivoluntary and external conditions was not significant, $t(35) = 1.25$, $p = .221$, $d = 0.21$, nor was the difference between the involuntary and external conditions, $t(35) = 0.61$, $p = .547$, $d = 0.10$. Post hoc t tests also found a significant difference between the voluntary and involuntary conditions, $t(35) = 2.74$, $p = .010$, $d = 0.46$; however, the difference between the voluntary and semivoluntary conditions was not significant, $t(35) = 1.71$, $p = .096$, $d = 0.29$, nor was the difference between the semivoluntary and involuntary conditions, $t(35) = 1.75$, $p = .089$, $d = 0.29$. In addition, a trend analysis on the magnitude of the N1–P2 suppression effects found a significant linear trend, $F(1, 35) = 7.50$, $p = .010$, $\eta_p^2 = .18$. These results are consistent with Timm et al. (2014), in that they show that voluntarily produced tones yielded N1–P2 suppression, whereas involuntarily produced tones did not.

EXPERIMENT 2

Method

Participants

Thirty-eight students from UNSW Sydney participated in our study for course credit. All participants gave written informed consent before the experiment and reported having normal hearing in both ears. Mean age of the participants (26 female, 36 right-handed), was 22 (SD = 6) years.

Apparatus, Stimuli, and Procedure

The experiment consisted of 18 blocks, each of which consisted of 50 trials. In two blocks, participants performed the *voluntary condition* (see Figure 3A): Participants intentionally moved a finger on their right hand to press a button to produce a tone through headphones. In two different blocks, participants performed the *semivoluntary condition* (see Figure 3B): Participants intentionally used a finger on their left hand to push down on one of their fingers on their right hand, forcing them to unintentionally move the finger on their right hand to press a button to

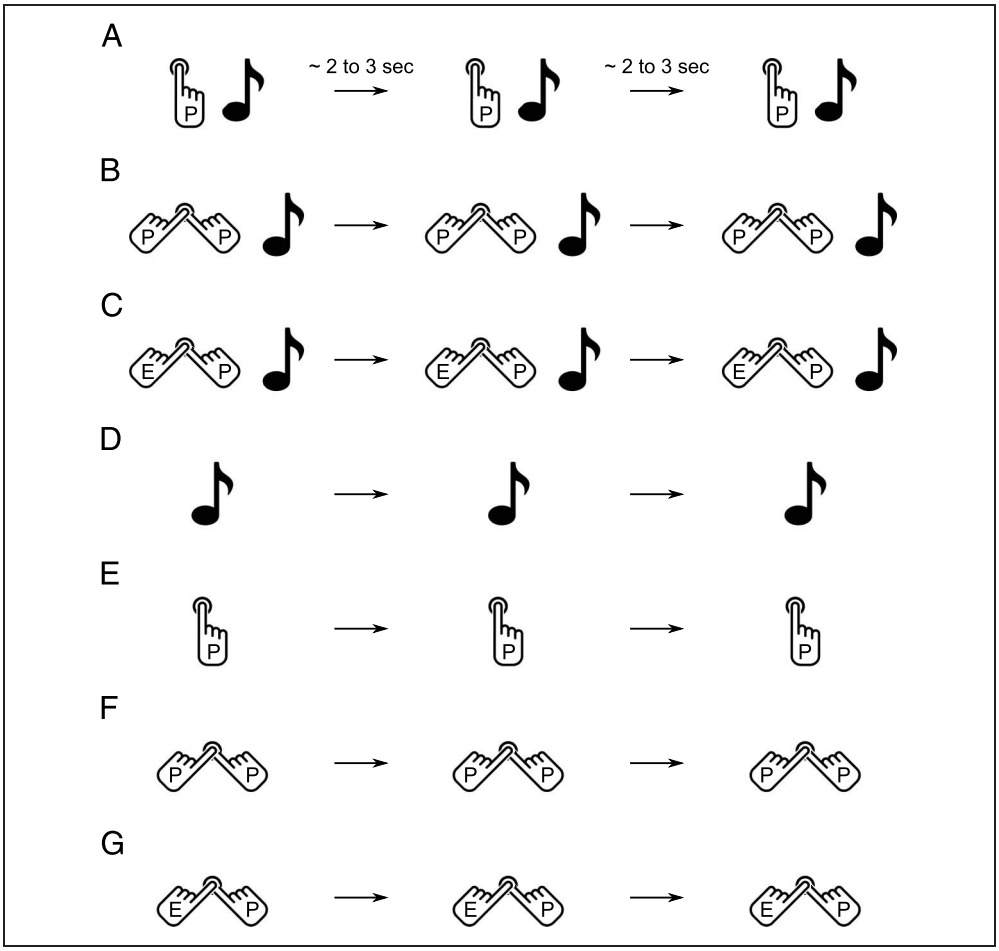

Figure 3. Procedure for Experiment 2. (A) In the voluntary condition, participants intentionally pressed a button every 2–3 sec to hear a tone through headphones. (B) In the semivoluntary condition, participants intentionally pushed down on one of their fingers, forcing them to unintentionally press a button to hear a tone. (C) In the involuntary condition, the experimenter pushed down on one of the participant's fingers, forcing them to unintentionally press a button to hear a tone. (D) In the externally generated conditions, participants passively listened to the tones generated by them in the self-generated conditions. (E–G) The motor conditions were identical to the self-generated conditions, except that the button-presses did not produce a tone. P = participant; E = experimenter.

produce a tone through headphones. In both of these conditions, participants were instructed to keep a constant pace between button-presses of about 2–3 sec. In two blocks, participants performed the *involuntary condition* (see Figure 3C): The experimenter pushed down on one of the participants' fingers on the right hand, forcing participants to unintentionally move the finger on their right hand to press a button to produce a tone through headphones. The experimenter kept a constant pace between button-presses of approximately 2–3 sec. Collectively, these conditions are known as the *self-generated conditions*.

Immediately after a block of trials containing the voluntary, semivoluntary, or involuntary conditions, participants performed the *externally generated condition* (see Figure 3D–3F): Participants passively listened to the same sequence of tones that they had just generated.

Participants also performed the *motor conditions*, which were identical to the self-generated conditions, except that the button-press did not produce a tone. Specifically, in two blocks, participants performed the *voluntary-motor condition* (see Figure 3G): Participants intentionally moved a finger on their right hand to press a button, but no tone was produced. In two different blocks, participants performed the *semivoluntary-motor condition* (see Figure 3H): Participants intentionally used a finger on their left hand to push down on one of their fingers on their right hand, forcing them to unintentionally move a finger on their right hand to press a button, but no tone was produced. Similar to the self-generated conditions, participants were instructed to keep a constant pace between button-presses of about 2–3 sec. In the remaining two blocks, participants performed the *involuntary-motor condition* (see Figure 3I): The experimenter pushed down on one of the participants' fingers on their right hand, forcing participants to unintentionally move the finger on their right hand to press a button, but no tone was produced. The experimenter kept a constant pace between button-presses of approximately 2–3 sec. The order of blocks containing the different conditions was counterbalanced across participants.

EEG Acquisition

The EEG recording was identical to Experiment 1.

ERP Preprocessing

The ERP preprocessing was identical to Experiment 1. On average, ERPs were computed from 79 (*SD* = 28) voluntary, 79 (*SD* = 28) semivoluntary, 80 (*SD* = 30) involuntary, 80 (*SD* = 32) voluntary-motor, 80 (*SD* = 30) semivoluntary-motor, 80 (*SD* = 31) involuntary-motor, and 277 (*SD* = 21) external epochs.

ERP Analysis

The ERP analysis was identical to Experiment 1, except that we analyzed the N1 in the time window of 76–96 msec and the P2 in the time window of 147–167 msec. We selected these time windows using the collapsed localizer technique described in Luck and Gaspelin (2017).

Results

Figure 4A shows the grand-averaged ERPs, Figure 4B shows the distribution of voltages over the scalp during the N1 time window, and Figure 4C shows the magnitude of the N1-suppression effects. A repeated-measures ANOVA on the mean amplitudes of N1 was significant, $F(3, 111) = 3.17$, $p = .027$, $\eta_p^2 = .08$. Post hoc t tests found a significant difference between the voluntary and external conditions, $t(37) = 3.35$, $p = .002$, $d = 0.54$—this difference is known as N1-suppression (Horváth, 2015; Schröger et al., 2015; Hughes et al., 2013; Bendixen et al., 2012)—however, the difference between the semivoluntary and external conditions was not significant, $t(37) = 1.71$, $p = .097$, $d = 0.28$, nor was the difference between the involuntary and external conditions, $t(37) = 1.00$, $p = .324$, $d = 0.16$. Post hoc t tests also found a significant difference between the voluntary and involuntary conditions, $t(37) = 2.19$, $p = .035$, $d = 0.35$; however, the difference between the voluntary and semivoluntary conditions was not significant, $t(37) = 1.35$, $p = .185$, $d = 0.22$, nor was the difference between the semivoluntary and involuntary conditions, $t(37) = 0.51$, $p = .616$, $d = 0.08$. In addition, a trend analysis on the magnitude of the N1-suppression effects found a significant linear trend, $F(1, 37) = 4.77$, $p = .035$, $\eta_p^2 = .11$. These results are entirely consistent with Experiment 1.

Figure 4D shows the magnitude of the P2-suppression effects. A repeated-measures ANOVA on the mean amplitudes of P2 was significant, $F(3, 111) = 6.41$, $p < .001$, $\eta_p^2 = .15$. Post hoc t tests found a significant difference between the semivoluntary and external conditions, $t(37) = 2.30$, $p = .027$, $d = 0.37$—this difference is known as P2-suppression (Horváth, 2015)—however, the difference between the voluntary and external conditions was not significant, $t(37) = 1.63$, $p = .111$, $d = 0.27$, nor was the difference between the involuntary and external conditions, $t(37) = 1.80$, $p = .081$, $d = 0.29$. Post hoc t tests also found a significant difference between the voluntary and involuntary conditions, $t(37) = 3.09$, $p = .004$, $d = 0.50$, and between the semivoluntary and involuntary conditions, $t(37) = 3.51$, $p = .001$, $d = 0.57$; however, the difference between the voluntary and semivoluntary conditions was not significant, $t(37) = 1.15$, $p = .257$, $d = 0.19$. In addition, a trend analysis on the magnitude of the N1-suppression effects found a significant linear trend, $F(1, 37) = 9.57$, $p = .004$, $\eta_p^2 = .21$. These results show that only voluntarily and semivoluntarily produced tones yielded P2-suppression.

Figure 4E shows the magnitude of the N1–P2 suppression effects. A repeated-measures ANOVA on the mean amplitudes of the N1–P2 complex was significant, $F(3, 111) = 16.93$, $p < .001$, $\eta_p^2 = .31$. Post hoc t tests found a significant difference between the voluntary and external conditions, $t(37) = 4.77$, $p < .001$, $d = 0.77$, and between

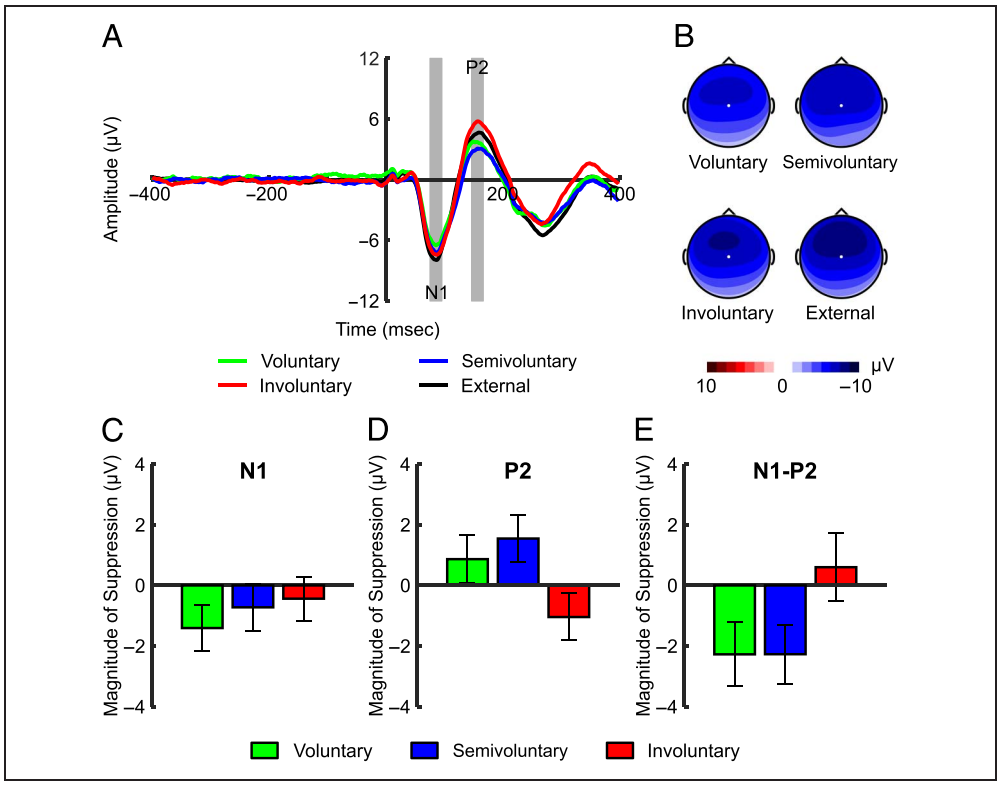

Figure 4. Results for Experiment 2. (A) The line graph shows the grand-averaged ERPs for each condition at the vertex, showing time (msec) on the x axis, with 0 indicating the onset of the tone, and voltage (μV) on the y axis, with positive voltages plotted upward. The gray bars show the N1 (76–96 msec) and P2 (147–167 msec) time windows. (B) The voltage maps show the distribution of voltages over the scalp during the N1 time window. (C) The bar graphs show the magnitude of the N1-suppression effects, (D) the P2-suppression effects, and (E) the N1–P2 suppression effects.

the semivoluntary and external conditions, $t(37) = 3.76$, $p < .001$, $d = 0.61$—these differences are known as N1–P2 suppression (Horváth, 2015)—however, the difference between the involuntary and external conditions was not significant, $t(37) = 1.34$, $p = .189$, $d = 0.22$. Post hoc t tests also found a significant difference between the voluntary and involuntary conditions, $t(37) = 5.25$, $p < .001$, $d = 0.85$, and between the semivoluntary and involuntary conditions, $t(37) = 5.32$, $p < .001$, $d = 0.86$; however, the difference between the voluntary and semivoluntary conditions was not significant, $t(37) < 0.01$, $p = .993$, $d < 0.01$. In addition, a trend analysis on the magnitude of the N1–P2 suppression effects found a significant linear trend, $F(1, 37) = 27.53$, $p < .001$, $\eta_p^2 = .43$. These results are consistent with Timm et al. (2014), in that they show that voluntarily produced tones yielded N1–P2 suppression, whereas involuntarily produced tones did not.

DISCUSSION

As hypothesized, the results of this study show that tones produced by voluntary button-presses yielded N1-suppression, in that they elicited a smaller N1 than externally generated tones. In contrast, tones produced by involuntary button-presses did not yield significant N1-suppression. These results are consistent with studies showing that voluntary movements yield sensory suppression effects in the auditory (Neszmélyi & Horváth, 2017; Elijah et al., 2016; Mifsud et al., 2016; Oestreich et al., 2016; van Elk et al., 2014; Knolle et al., 2013; SanMiguel et al., 2013; Saupe et al., 2013; Timm et al., 2013; Bäß et al., 2008) and tactile (Christensen et al., 2007; Bays, Flanagan, & Wolpert, 2006; Bays, Wolpert, & Flanagan, 2005, Blakemore, Wolpert, & Frith, 1998) domains and that involuntary movements do not yield sensory suppression effects in the auditory (Timm et al., 2014) or tactile (Haggard & Whitford, 2004; Chronicle & Glover, 2003) domains. Moreover, these results are consistent with animal studies (Schneider & Mooney, 2018; Crapse & Sommer, 2008) in that they suggest that corollary discharges are generated by the brain during movement planning, which was present in the voluntary condition and absent in the involuntary condition, rather than during movement execution, which was present in both conditions. Furthermore, if corollary discharges are generated during movement planning, then it is likely that they originate in premotor cortex or supplementary motor area, both of which are thought to be responsible for movement planning (Cisek & Kalaska, 2005; Romo, Hernández, & Zainos, 2004). Indeed, all of this is entirely consistent with recent theoretical accounts of the neural implementation of the internal forward model (Schneider & Mooney, 2018; Straka et al., 2018; Crapse & Sommer, 2008; Poulet & Hedwig, 2007; Schütz-Bosbach & Prinz, 2007).

As mentioned above, the results of this study are consistent with Timm et al. (2014), in that both studies found that the voluntary condition yielded sensory suppression whereas the involuntary condition did not. However, there are at least four important methodological differences between their study and ours. First, they used TMS to force participants to unintentionally move their finger to press a button to produce a tone. Notably, TMS produces a loud clicking noise, which may have affected the N1 and P2 elicited by the tone (Bender et al., 2005; Nikouline, Ruohonen, & Ilmoniemi, 1999; Tiitinen et al., 1999). In contrast, we electrically stimulated the median nerve in the participant's forearm or applied manual force to the participant's finger, neither of which produces an audible sound. Second, to minimize the effects of TMS on the ERPs, they inserted a 100-msec delay between the button-press and the tone. However, one complication with this is that delays are known to reduce the magnitude of sensory suppression effects (Behroozmand, Sangtian, Korzyukov, & Larson, 2016; Elijah et al., 2016; Oestreich et al., 2016; Chen, Chen, Liu, Huang, & Liu, 2012; Whitford et al., 2011; Behroozmand, Liu, & Larson, 2010; Blakemore et al., 1998). In contrast, our procedure did not require us to insert a delay between the button-press and the tone. Third, they focused on the N1–P2 complex. Given that previous studies have differentiated N1- and P2-suppression effects (Timm, Schönwiesner, Schröger, & SanMiguel, 2016; Knolle, Schröger, Baess, & Kotz, 2012; Sowman, Kuusik, & Johnson, 2012), this makes it impossible to determine whether movement planning affected N1-suppression, P2-suppression, or both. In contrast, we isolated N1 and P2 separately, and we observed a clear effect of movement planning on the magnitude of N1-suppression. Despite these methodological differences, the fact that the results of Timm et al. (2014) and this study are essentially identical provides converging evidence for the importance of movement planning in producing sensory suppression.

Fourth, we extended upon the work of Timm et al. (2014) by using the semivoluntary condition. In this condition, participants electrically stimulated the median nerve in their forearm with the electrical stimulator or applied manual force to one of their fingers. That is, participants' voluntary use of the electrical stimulator or manual force meant that they involuntarily moved their finger to press a button to produce a tone. Importantly, this condition allowed us to distinguish between rival hypotheses about volition and whether it should be operationalized as a binary or continuous construct. Specifically, if volition is a binary construct, then one would expect similar N1-suppression effects for the voluntary and semivoluntary conditions, because both conditions require participants to intentionally move their finger to press a button to produce a tone. Alternatively, if volition is a continuous construct, then one would expect a downward trend in the magnitude of N1-suppression across the voluntary, semivoluntary, and involuntary conditions. The results of this study support the latter possibility: We found that the magnitude of N1-suppression was largest in the voluntary

condition, intermediate (though not statistically significant) in the semivoluntary condition, and absent in the involuntary condition, and that the magnitude of N1-suppression linearly decreased across the voluntary, semivoluntary, and involuntary conditions. This pattern of results is hypothesized by the internal forward model (Miall & Wolpert, 1996), in that the magnitude of sensory suppression should reflect the extent to which the corollary discharge matches the sensory consequences of the action. However, because the delay between the intentional action and the tone may have been longer in the semivoluntary condition than in the voluntary condition, and because the appearance of the button on the electrical stimulator and the participant's finger did not perfectly resemble the appearance of the button on the computer mouse, it is possible that these factors may have affected the processes involved in movement planning, which may have influenced our results.

In general, the results of Experiments 1 and 2 are in agreement at the N1 and P2. Specifically, we found that the voluntary condition yielded N1-suppression, whereas the semivoluntary and involuntary conditions did not, and that the magnitude of N1-suppression linearly decreased across the voluntary, semivoluntary, and involuntary conditions. We also found that the voluntary condition yielded P2-suppression, whereas the involuntary condition did not. However, there are two notable discrepancies between Experiments 1 and 2: The semivoluntary condition yielded P2-suppression in Experiment 2 but not in Experiment 1, and the magnitude of P2-suppression linearly decreased across the voluntary, semivoluntary, and involuntary conditions in Experiment 1 but not in Experiment 2. These discrepancies are likely related. One possible explanation for them is that the distance between participants' left hand, which used the electrical stimulator in Experiment 1 or applied manual force to one of the fingers on their right hand in Experiment 2, and right hand, which pressed the button to produce the tone in both experiments, decreased from Experiment 1 to Experiment 2, which may have affected the P2. This is consistent with studies showing that self-generated touch yields larger sensory suppression effects when the hands are close together compared to when they are apart (Kilteni & Ehrsson, 2017a, 2017b; Bays & Wolpert, 2008), presumably because the internal forward model (Miall & Wolpert, 1996) does not predict the sensory consequences of self-generated touch when the hands are too far apart to reach each other. Of course, because the functional significance of P2 and P2-suppression is currently unknown (Horváth, 2015; Crowley & Colrain, 2004), we concede that this is speculation. Future studies should consider elucidating the neural mechanisms that give rise to the P2, as well as exploring its sensitivity to experimental manipulations.

So far, we have interpreted the results of this study in terms of the internal forward model (Miall & Wolpert, 1996) in which an efference copy of the motor command is used to compute a corollary discharge, which acts to suppress neural and perceptual responses to the sensory input. However, there are at least three alternative interpretations. First, because self-generated tones are attended and temporally predictable whereas externally generated tones are not, it is possible that these differences could explain sensory suppression (Horváth, 2015). Nevertheless, this seems unlikely because studies continue to show N1-suppression effects when controlling for attention (Saupe et al., 2013; Timm et al., 2013) and temporal prediction (Oestreich et al., 2015; Lange, 2011; Bäß et al., 2008; Ford, Gray, Faustman, Roach, & Mathalon, 2007; Schafër, Amochaev, & Russell, 1981). Furthermore, if differences in attention and/or temporal prediction are the cause of sensory suppression, then one would expect the semivoluntary condition to yield N1-suppression, because it is attended and temporally predictable. The results of this study do not support this. Second, it is possible that the only requirement for sensory suppression is temporal proximity between the action and its sensory consequence (Horváth, Maess, Baess, & Tóth, 2012). However, if this were true, then one would expect the semivoluntary and involuntary conditions to yield N1-suppression effects, because both involve button-presses that are immediately followed by a tone. Again, the results of this study do not support this. Third, it has recently been suggested that sensory suppression is not the result of an internal forward model; instead, it is the result of predictive signals that enhance responses from neurons tuned for the sensory consequences of our actions and suppress responses from neurons that are tuned away (Press et al., 2020; Reznik & Mukamel, 2019; Yon et al., 2018). However, distinguishing between these theories is beyond the scope of this study. As such, we conclude that the most parsimonious account of sensory suppression is the internal forward model.

An important feature of the internal forward model (Miall & Wolpert, 1996) is that it allows the brain to distinguish between self- and externally generated sensory input. However, this distinction appears to be blurred in schizophrenia, because patients hear voices they attribute to others (auditory–verbal hallucinations) and they have abnormal beliefs that their actions and thoughts are controlled by others (delusions of control; Fletcher & Frith, 2009; Schneider, 1957). In both of these cases, the common denominator is that self-generated information is perceived as being produced by an external agent. These observations prompted Feinberg (1978) and Frith (1987) to suggest that these symptoms might be caused by an impaired internal forward model. Evidence consistent with this comes from studies showing that patients yield smaller N1-suppression effects than healthy controls (Whitford, 2019; Ford et al., 2014; Ford et al., 2007, Whitford et al., 2011; Heinks-Maldonado et al., 2007; Ford, Mathalon, Heinks, et al., 2001; Ford, Mathalon, Kalba, et al., 2001). The results of this study contribute to our understanding of schizophrenia, in that they show that N1-suppression is the result of planned motor acts, rather than motor acts per se. This suggests that the smaller N1-suppression effects in patients compared to

healthy controls reflects deficits in the sensorimotor processes involved in planning actions. This is also consistent with the finding that patients elicit a smaller readiness potential, an ERP associated with movement planning (Kornhuber & Deecke, 1965), than healthy controls (Ford et al., 2014). Given that it is possible to modify cognitive deficits in schizophrenia with training (Dale et al., 2016; Penadés et al., 2013; Subramaniam et al., 2012; Vinogradov, Fisher, & de Villers-Sidani, 2012), and given that it is possible to modify N1-suppression effects with training (Elijah et al., 2016; Elijah, Le Pelley, & Whitford, 2018), it is possible that internal forward model deficits in schizophrenia might also be modifiable. This is a job for future research.

In conclusion, the aim of this study was to determine whether sensory suppression is the result of movement planning, movement execution, or both. To accomplish this, in two experiments, we compared ERPs to self-generated tones that were produced by voluntary, semivoluntary, or involuntary button-presses, with externally generated tones that were produced by a computer. In Experiment 1, the semivoluntary and involuntary button-presses were initiated by the participant or experimenter, respectively, by stimulating the median nerve in the participant's forearm, and in Experiment 2, by pushing down on the participant's finger. We found that tones produced by voluntary button-presses yielded N1-suppression, in that they elicited a smaller N1 than externally generated tones. However, tones produced by semivoluntary and involuntary button-presses did not yield significant N1-suppression. We also found that the magnitude of N1-suppression linearly decreased across the voluntary, semivoluntary, and involuntary conditions. These results replicate and extend the findings of Timm et al. (2014), who found N1–P2 suppression in the voluntary condition but not in the involuntary condition. Furthermore, these results suggest that movement planning is a necessary condition for producing sensory suppression and that volition should be operationalized as a continuous construct. We conclude that these results shed new, important light on the function and dysfunction of the internal forward model (Miall & Wolpert, 1996).

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Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were M(an)/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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